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Czynniki regulujące wzrost korzeni dębu szypułkowego (*Quercus robur* L.) w warunkach naturalnych i kontenerach szkółkarskich

Factors regulating root growth of pedunculate oak (*Quercus robur* L.) in natural conditions and in nursery containers

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STRESZCZENIE

W naturalnym odnowieniu dęby rozwijają długie korzenie palowe, umożliwiające pozyskiwanie wody z głęboko położonych warstw gleby. Konsekwencją dostępu do zasobów wody mniej narażonych na jej okresowe niedobory podczas suszy jest lepsza kondycja drzewostanów dębowych. Choć bezpośredni siew żołędzi do gleby, umożliwiający głębokie zakorzenienie drzew, jest zatem korzystny dla uprawy dębu, utrzymanie ciągłości zalesień zapewnia produkcja dębów w szkółkach tak otwartych, jak i kontenerowych. Stosowane zabiegi agrotechniczne są przyczyną niekorzystnych zmian w obrębie systemu korzeniowego, prowadząc do uszkodzenia korzenia palowego, który u dębów nie ulega odnowieniu. Uszkodzenie korzenia palowego w obrębie sadzonek wyprodukowanych w szkółkach kontenerowych, promuje rozwój korzeni bocznych. Korzenie boczne nie cechują się jednak potencjałem wzrostu pozwalającym dotrzeć do głębokich warstw gleby. W konsekwencji, płytko ukorzenione sadzonki kontenerowe są bardziej narażone na obumieranie w wyniku długotrwałych susz. Dotychczas prowadzone badania nad jakością sadzonek wyprodukowanych w szkółkach kontenerowych skupiały się głównie na ocenie fenotypowej, pomijając aspekty molekularne - aspekty regulujące każdy etap wzrostu roślin, w tym rozwój systemu korzeniowego. Pomimo poznania mechanizmów leżących u podstaw wzrostu korzeni pierwotnych u roślin modelowych, zdefiniowanie czynników molekularnych kontrolujący wydłużanie korzeni palowych jest kluczowe dla zrozumienia procesów regulujących wzrost systemu korzeniowego w tym korzenia palowego w warunkach naturalnych. Zrozumienie regulacji przez czynniki endogenne procesu zarówno wydłużania, jak i hamowania wzrostu korzeni palowych w obrębie sadzonek uzyskanych w wyniku produkcji kontenerowej, pozostaje niekompletne, choć ma istotne znaczenie dla długoterminowych konsekwencji produkcji szkółkarskiej.

Celem niniejszej rozprawy doktorskiej było poznanie czynników molekularnych zaangażowanych we wzrost korzeni dębu szypułkowego (*Quercus robur* L.) oraz określenie różnic w poziomie tych czynników podczas uprawy sadzonek w kontenerach, jak i po ich przesadzeniu. Materiał do badań stanowiły korzenie palowe oraz boczne dębu szypułkowego rosnącego w systemie ryzotronowym i kontenerowym. W celu określenia konsekwencji produkcji kontenerowej dla dalszego wzrostu systemu korzeniowego analizie poddano sadzonki początkowo wzrastające w kontenerach, które następnie zostały przesadzone do systemu ryzotronowego. W trakcie analiz wykorzystano zróżnicowane morfologicznie

korzenie a także korzenie palowe na różnych etapach ich wydłużania po skiełkowaniu z żołędzia. W obrębie uzyskanego materiału wykonano analizę transkryptomu oraz określono poziom hormonów roślinnych w korzeniach dębu.

Przeprowadzone badania wykazały zróżnicowanie na poziomie transkryptomu, jak i hormonalnym w obrębie korzeni palowych i bocznych sadzonek pochodzących z różnych systemów upraw. Określono czynniki hamujące wzrost korzeni palowych podczas wzrostu sadzonek dębu szypułkowego w kontenerach w porównaniu z sadzonkami dębu szypułkowego uprawianymi w ryzotronach. Badania zdefiniowały również aktywację szeregu reakcji molekularnych zaangażowanych w ponowienie wzrostu korzeni palowych w obrębie sadzonek przesadzonych z kontenerów. Zrozumienie tych mechanizmów molekularnych może przyczynić się do modyfikacji praktyk szkółkarskich, promując wzrost korzeni palowych po wysadzeniu sadzonek na uprawie.

SUMMARY

In the context of natural regeneration, oak trees develop lengthy taproots, allowing them to draw water from deep soil layers. This access to water resources that are less prone to intermittent shortages during droughts significantly enhances the overall condition of oak stands. Consequently, the direct sowing of acorns into the soil, which facilitates deep rooting, proves to be advantageous for successful oak cultivation. However, the continuity of afforestation hinges on oak production in both open fields and container nurseries. Applied agrotechnical techniques have been found to bring about adverse changes in the root systems, resulting in taproot damage - a critical issue, particularly for oak trees since taproots do not regenerate once damaged. The harm caused to the taproot in container nurseries triggers the proliferation of lateral roots. Nonetheless, these lateral roots lack the growth potential necessary to reach the deeper soil layers. As a result, container seedlings with shallow root systems face a higher risk of perishing due to prolonged droughts. To date, the research concerning the quality of seedlings produced in container nurseries has primarily centered on phenotypic assessment, neglecting the molecular aspects governing various stages of plant growth, including the development of root systems. While the mechanisms underlying primary root growth in model plants are well understood, delineating the molecular factors that oversee taproot growth remains indispensable for comprehending the broader processes that regulate overall root system growth, including the taproot, within natural conditions. Conversely, a comprehensive grasp of the regulation by endogenous factors, pertaining to both the elongation and growth inhibition of taproots within seedlings obtained through container production, remains elusive. Nevertheless, this understanding assumes paramount significance for the long-term implications of nursery production.

This dissertation's primary objective was to unravel the molecular factors underpinning the growth of roots in pedunculate oak (*Quercus robur* L.) and to discern the distinctions in these factors' levels between container-grown seedlings and post-transplantation stages. The study material encompassed both taproots and lateral roots of pedunculate oak, cultivated in both rhizotron and container systems. To evaluate the repercussions of container production on subsequent root system growth, the research evaluated seedlings initially raised in containers and later transplanted into the rhizotron system. Diverse morphological root structures, including taproots at various stages of elongation following acorn germination, underwent transcriptome analysis, alongside the quantification of plant hormones in oak roots.

The study unveiled variations, both at the transcriptome and hormonal levels, within the taproots and lateral roots of seedlings originating from different cultivation systems. Factors impeding taproot growth during the container cultivation of oak seedlings, in contrast to those cultivated in rhizotrons, were conclusively identified. Furthermore, the study shed light on the activation of several molecular responses integral to the process of taproot regrowth in seedlings transplanted from containers. A profound understanding of these molecular mechanisms holds the potential to reshape nursery practices in a way that promotes taproot growth following seedling transplantation into field conditions.

WYKAZ PRAC WCHODZĄCYCH W SKŁAD ROZPRAWY DOKTORSKIEJ

W skład rozprawy doktorskiej wchodzą cztery artykuły naukowe:

Artykuł 1 - **Kościelniak P.**, Glazińska P., Kęsy J., Zadworny M. (2021) Formation and development of taproots in deciduous tree species. *Frontiers in Plant Science* 12:772567. doi:10.3389/fpls.2021.772567
IF (2021) 6,627; 100 pkt MNiSW

Artykuł 2 - **Kościelniak P.**, Glazińska P., Zadworny M. (2022) OakRootRNADB - a consolidated RNA-seq database for coding and noncoding RNA in roots of pedunculate oak (*Quercus robur*). Database: *The Journal of Biological Databases and Curation* baac097. doi:10.1093/database/baac097
IF (2022) 5,8; 100 pkt MNiSW

Artykuł 3 - **Kościelniak P.**, Glazińska P., Zadworny M. (2023) Early stages in the formation of *Quercus robur* root system: variation in gene expression is linked to the functional type of roots. Manuskrypt.

Artykuł 4 - **Kościelniak P.**, Glazińska P., Kęsy J., Mucha J., Zadworny M. (2023) Identification of genetics and hormonal factors involved in *Quercus robur* root growth regulation in different cultivation system. Manuskrypt.

WPROWADZENIE

W naturalnym odnowieniu, dęby są zdolne do wykształcenia długich korzeni palowych, umożliwiających pozyskiwanie wody z głębszych warstw gleby. Głębokie umiejscowienie systemu korzeniowego umożliwia eksplorację poziomów glebowych bardziej zasobnych w wodę i związki mineralne oraz mniej narażonych na okresowe przesuszenie. Wynikające z odnowienia naturalnego lub siewu, osiągnięcie przez korzeń palowy warstw gleby zasobnej w wodę, zwiększa zdolność dębów do przetrwania zarówno incydentalnych, jak i cyklicznych niedoborów wody (Barbeta i Peñuelas 2017; Zadworny i in. 2014). Niestety, bezpośredni siew żołędzi do gruntu niesie za sobą ryzyko dużych strat wynikających z aktywności zwierząt, dla których nasiona są istotnym źródłem pokarmu. Zabiegi prowadzące do ograniczenia szkód wynikających z żerowania zwierzyny znacznie zwiększają koszty zakładania upraw, a niektóre z nich mogą mieć szkodliwy wpływ na sadzonki, poprzez ograniczenie kiełkowania nasion, prowadząc tym samym do niejednolitego rozwoju drzewostanu (Leverkus i in. 2017; Leverkus i in. 2013; Leverkus i in. 2015). Stosowanie siewu bezpośredniego do gruntu ma zatem uzasadnienie w latach obfitości nasion lub na stanowiskach mniej narażonych na żerowanie zwierzyny. Chociaż naturalna regeneracja lub siew bezpośredni do gruntu wydają się być bardziej korzystne dla uprawy dębu z biologicznego i ekologicznego punktu widzenia, to sadzonki produkowane w szkółkach stanowią materiał zapewniający utrzymanie ciągłości zalesień, a w konsekwencji efektywne wykorzystanie zasobów nasion. Produkcja sadzonek w szkółkach otwartych, jak i kontenerowych ma również sprzyjać wykształceniu się skupionego systemu korzeniowego, o dużej liczbie korzeni bocznych, a jej efektem powinno być korzystne ukształtowanie stosunku masy korzeni do masy części nadziemnej. Zastosowanie sadzonek wyprodukowanych w szkółkach, szczególnie kontenerowych, będące powszechną praktyką odnowienia drzewostanów dębowych w Polsce, mimo potencjalnie negatywnych aspektów biologicznych (jak redukcja zmienności genetycznej czy eliminowanie lokalnych genotypów) i ekonomicznych (wynikających z wysokich kosztów produkcji) zapewnia jednak, do tej pory, ciągłość odtwarzania lasów. Niestety, produkcja dębów w szkółkach kontenerowych, jak i otwartych niesie za sobą ryzyko wystąpienia zmian w obrębie architektury systemu korzeniowego dębów. W przypadku dębu szypułkowego, korzeń palowy odcięty podczas podcinania sadzonek w trakcie ich produkcji nie ulega regeneracji (Mucha i in. 2018; Zadworny i in. 2019). Zarówno system prowadzenia produkcji sadzonek w kontenerach, jak i produkcja sadzonek w gruncie, zaburzając naturalny wzrost korzenia palowego, jest jedną

z przyczyn osłabienia dębów i zmniejszenia przeżywalności ich drzewostanów podczas długotrwałych epizodów suszy (Tsakaldimi i in. 2009). Straty ekonomiczne spowodowane wysoką śmiertelnością dębów, wynikającą z coraz częstszych i coraz intensywniejszych fal upałów, jak i będących ich konsekwencją długotrwałych susz, stanowią nasilający się problem, a zwiększająca się liczba publikacji dotycząca zamierania drzewostanów dębowych jest potwierdzeniem chęci rozwiązania zaistniałego problemu przez środowisko naukowe (Bréda i in. 2006; Rodríguez-Calcerrada i in. 2017).

W przypadku sadzonek uzyskanych w szkółkach kontenerowych, system prowadzenia ich produkcji związany jest z zaburzeniem architektury systemu korzeniowego, nie tylko poprzez zawijanie się korzeni w obrębie bryłki przy wykorzystaniu niewłaściwej kasety szkółkarskiej bądź intensywności nawożenia, ale przede wszystkim wynikającym z utraty korzenia palowego w wyniku działania tzw. noża powietrznego (ang. *air pruning*). Stosowanie otworów, umożliwiających odprowadzanie wody w dnie kaset kontenerowych, powodując uszkodzenia i obumieranie korzeni palowych wyrastających z dna kasety, prowadzi jednocześnie do zwiększenia formowania płytko umiejscowionych korzeni bocznych, zwiększając ryzyko ich zawijania (Grossnickle i El-Kassaby 2016). Zmiana wzrostu sadzonek w kontenerach, poprzez zaburzenia rozwoju korzenia palowego, może skutkować większą podatnością sadzonek na uszkodzenie, a w konsekwencji ich obumieraniem, szczególnie w warunkach niedoboru wody (Grossnickle i Ivetić 2022). Chociaż, w przypadku sadzonek wyprodukowanych w szkółkach kontenerowych wszystkie wierzchołki korzeni palowych powinny teoretycznie obumierać, to jednak w pracy Zadwornego i in. (2021) wykazano znaczący udział sadzonek cechujących się występowaniem korzenia palowego po wysadzeniu ich z kaset kontenerowych do 120 litrowych pojemników. Zatem, poznanie czynników regulujących wydłużanie korzeni palowych dębu szypułkowego, jego ustanie przed osiągnięciem dna kasety i ponowienie wzrostu po wysadzeniu sadzonek na uprawie, poprawiłoby architekturę systemu korzeniowego w obrębie materiału produkowanego w szkółkach kontenerowych. Drogą do ulepszenia stosowanych praktyk szkółkarskich są analizy biologicznych procesów zachodzących tak w trakcie wzrostu sadzonek w kontenerach, jak i po wysadzeniu ich na uprawie.

Dotychczas prowadzone badania nad jakością sadzonek w szkółkach kontenerowych, koncentrowały się głównie na ocenie ich jakości bazując na poziomie fenotypowym lub analizie procesów fizjologicznych, zaniedbując aspekt molekularny, determinujący wzrost i rozwój korzeni. Konieczność uwzględnienia specyfiki roślin drzewiastych jest o tyle ważna, że procesy

regulujące tworzenie korzeni mogą być uniwersalne lub niezwykle specyficzne, a sam rozwój korzeni może być powiązany z długością życia rośliny (jednoroczna lub wieloletnia). U jednorocznej rośliny modelowej, jaką jest *Arabidopsis*, dość dokładnie poznano molekularne mechanizmy regulujące tworzenie i modyfikację wzrostu korzeni pierwotnych/zarodkowych. W przypadku długożyjących dębów, regulacja wzrostu korzenia palowego musi obejmować nie tylko kontrolę jego wydłużania w pierwszym roku życia, ale również zapewniać potencjał do ponowienia jego wzrostu w latach kolejnych, a może i specyficznie w okresach suszy, czy podczas działania innych stresów biotycznych i abiotycznych. Prawdopodobnie proces ten podlega bardziej złożonej kontroli, a sieć regulacyjna zawiera więcej czynników odpowiadających za potencjał elongacyjny korzeni palowych drzew, na poziomie strukturalnym i molekularnym. Większa zdolność korzeni palowych do penetracji zwartych warstw gleby w porównaniu z korzeniami bocznymi, wynika zapewne z samego rozmiaru wierzchołka korzenia oraz mechanicznej i fizjologicznej specyfiki ich komórek merystematycznych (Clowes 2000; Pages 1995; Perilli i in. 2012). Wierzchołek wzrostu korzenia pierwotnego, zawierający komórki merystemu wierzchołkowego (RAM – ang. *root apical meristem*), jest swoistym centrum zarządzania nazwanym „mózgiem rośliny" już przez Darwina (Darwin i Darwin 1880), którego usunięcie skutkuje np. formowaniem silnie rozgałęzionego, płytkiego systemu korzeniowego (Drisch i Stahl 2015; Dubrovsky i Gómez-Lomelí 2003; Shishkova i in. 2013). Aktualna literatura potwierdza te zasadniczą rolę korzeni pierwotnych w 1) regulacji architektury całego systemu korzeniowego (Chapman i in. 2002; Sabatini i in. 2003) oraz 2) determinacji intensywnego wzrostu wertykalnego (Gupta i in. 2020; Robbins i Dinneny 2018).

Dokładne poznanie mechanizmów związanych z rozwojem korzeni u roślin drzewiastych wymaga zatem zintegrowanych analiz pozwalających ocenić czynniki determinujące wydłużanie korzeni pierwotnych w profilu glebowym (Jin i in. 2013). Rozpoznanie szlaków sygnałowych regulujących wzrost i architekturę korzeni u roślin modelowych może nie odzwierciedlać procesów zachodzących u roślin o odrębnych programach ontogenetycznych, na przykład długowiecznych dębów. Wiedza o regulacji i organizacji wzrostu korzeni na poziomie genetycznym u różnych grup organizmów będzie zatem odgrywała fundamentalną rolę (Malamy 2005). Istniejące przesłanki przemawiają za odmienną regulacją lub istnieniem zróżnicowanych szlaków sygnałowych w obrębie roślin zielnych i drzewiastych, a zróżnicowany już na poziomie embrionalnym potencjał przerastania gleby, może być ich potwierdzeniem (Augstein i Carlsbecker 2018). Chociaż w przypadku

roślin jednorocznych wykazano istnienie relacji na poziomie czynników determinujących wielkość wspomnianego już merystemu wierzchołkowego korzenia (obejmującą różne sieci regulacji genów, które z kolei są kontrolowane przez czynniki transkrypcyjne, mikroRNA czy też hormony roślinne), interakcje między różnymi czynnikami kontrolującymi szybkie wydłużanie korzeni u roślin innych niż jednoroczne pozostają nieznane (Benková i Hejatko 2009; Scheres i in. 2004; Svolacchia i in. 2020; Wendrich i in. 2017). Niektóre miRNA zidentyfikowane w korzeniach drzew, które nie zostały zidentyfikowane u roślin modelowych, takich jak *Arabidopsis*, mogą bowiem pełnić unikalną funkcję w ich rozwoju (Osakabe i in. 2014). Co więcej, sekwencyjne etapy pierwotnego wzrostu korzenia regulowane są przez czynniki transkrypcyjne (TF – ang. *transcription factor*) (Drisch i Stahl 2015; Mitsis i in. 2020; Sarkar i in. 2007), promujące transport auksyn i regulujące geny odpowiedzi na auksyny, kontrolując tym samym wzrost korzeni (Weijers i in. 2006). Dla przykładu, TF WOX (WOX 5/7 i WOX11), są nie tylko odpowiedzialne za indukcję i podtrzymanie wzrostu korzeni pierwotnych, ale także regulują rozwój korzeni bocznych wyrastających z korzeni pierwotnych (Baesso i in. 2018; Hu i Xu 2016). Identyfikacja, ale przede wszystkim zrozumienie funkcji genów promujących rozwój i elongację korzeni u drzew, aktywujących oraz dezaktywujących różne grupy genów podczas swojego długiego życia, a także wielokrotnie przekazujących sygnały między różnymi komponentami systemu korzeniowego, może dostarczyć cennych informacji o czynnikach inicjujących oraz kaskadach sygnałowych regulujących sam wzrost korzeni (Casson i Lindsey 2003; Chaiwanon i in. 2016; Slovak i in. 2016). Innym istotnym czynnikiem regulacyjnym są hormony roślinne. Dynamiczny wzrost korzeni jest wynikiem wielopłaszczyznowych interakcji między produkcją hormonów, wpływem na inicjację zarówno produkcji jak i odpowiedzi innych hormonów, ale także ich transportu, percepcji, inaktywacji, udziału w szlakach sygnałowych czy też regulacji rozwoju i funkcjonowania RAM (Casson i Lindsey 2003). Wzajemne oddziaływania, zarówno synergistyczne, jak i antagonistyczne, a także proporcja koncentracji różnych hormonów mogą wpływać na rozwój korzenia. Dla przykładu, wysokie stężenie auksyny może hamować wydłużanie korzenia, chociaż sama auksyna zaangażowana jest w inicjację tworzenia korzeni (Overvoorde i in. 2010; Zolman i in. 2000). Cytokininy, hamując z kolei nadmierny wzrost korzeni bocznych, kształtują architekturę systemu korzeniowego poprzez promowanie wzrostu korzenia głównego (Aloni i in. 2006). Etylen z kolei jest odpowiedzialny za hamowanie wydłużania korzeni, ale jego produkcja jest symulowana przez wysokie stężenia auksyn, które w niższych stężeniach nie promują jego biosyntezy (Qin i in. 2019). Etylen w zwrotnej odpowiedzi hamując transport auksyn, jednocześnie przyczynia się do hamowania wydłużania korzenia (Růžička i in. 2007).

A zatem interakcje i wzajemne oddziaływania między hormonami regulują wzrost korzeni i zapewne determinują utrzymanie dominacji wierzchołkowej korzenia pierwotnego. Podsumowując, mimo poznania mechanizmów leżących u podstaw wzrostu korzeni pierwotnych, nasze zrozumienie w jaki sposób czynniki endogenne promują lub hamują inicjację i dalszy wzrost korzeni palowych u drzew, szczególnie w obrębie sadzonek uzyskanych w trakcie produkcji kontenerowej, pozostaje niekompletne.

CELE BADAWCZE

Głównym celem niniejszej rozprawy doktorskiej jest poszerzenie stanu wiedzy o czynnikach regulujących wzrost korzeni palowych dębu szypułkowego (*Quercus robur* L.), zwłaszcza podczas produkcji sadzonek w kasetach kontenerowych. Zbadanie jakie ścieżki molekularne integrują wzrost korzeni palowych w warunkach odnowienia naturalnego i podczas produkcji w kasetach szkółkarskich, przyczyni się do pogłębienia wiedzy o zależnościach pomiędzy produkcją sadzonek w szkółkach a strukturą systemu korzeniowego dębów. Określenie biologicznych uwarunkowań wzrostu korzeni palowych, dostarczy leśnikom podstawowej wiedzy o potencjalnych zależnościach pomiędzy wykonywanymi procedurami szkółkarskimi, wpływającymi na strukturę systemu korzeniowego kontenerowych sadzonek dębów, a późniejszą odpornością drzewostanów dębowych na czynniki stresowe.

Głównym celem prac badawczych była analiza biologii rozwoju systemu korzeniowego sadzonek *Q. robur* uzyskanych poprzez siew bezpośredni do ryzotronów - układ eksperymentalny mający odzwierciedlać siew bezpośredni do gruntu, bądź pochodzących z uprawy kontenerowej poprzez: 1) identyfikację genów zaangażowanych w regulację wzrostu korzeni palowych kontenerowych sadzonek dębów oraz sadzonek uzyskanych z siewu bezpośredniego do gruntu, 2) analizę hormonalnej regulacji wzrostu korzeni palowych kontenerowych sadzonek dębów oraz pochodzących z bezpośredniego siewu nasion do gruntu.

Osiągnięcie przyjętych założeń zrealizowano poprzez wykonanie następujących zadań badawczych:

1) Studium poszczególnych etapów rozwoju korzeni pierwotnych u roślin, w kontekście wzrostu korzeni drzew na podstawie doniesień literaturowych,
2) Wykonanie sekwencjonowania (RNA-seq) transkryptomów korzeni palowych dębów uprawianych w różnych systemach i integracja danych uzyskanych podczas sekwencjonowania,
3) Analiza transkryptomu korzenia palowego i korzeni bocznych dębu w różnych systemach upraw,
4) Określenie wewnętrznych i zewnętrznych czynników regulujących rozwój korzeni u dębu szypułkowego,
5) Określenie roli hormonów roślinnych w rozwoju korzeni palowych i bocznych.

OMÓWIENIE WYNIKÓW

Uzyskane wyniki zostały zaprezentowane w postaci zestawu czterech powiązanych tematycznie artykułów, częściowo już opublikowanych. Wszystkie prace badawcze były prowadzone w oparciu o materiał roślinny, uprawiany na potrzeby realizacji niniejszej rozprawy doktorskiej w tunelu foliowym, w systemie ryzotronów i kontenerowym. Materiał do badań stanowiły korzenie palowe lub boczne sadzonek dębu szypułkowego (*Q.robur*) pobrane po ośmiu tygodniach od wysiania żołędzi do ryzotronów (ang. *rhizotron*) lub kontenerów (ang. *container*), oraz korzenie rocznych sadzonek kontenerowych pobrane po ośmiu tygodniach od przesadzenia sadzonek do ryzotronów - zwane dalej uprawą w systemie przesadzonym (ang. *transplanted*). Przesadzenie sadzonek kontenerowych wiosną następnego roku po ich uprzednim wysianiu do kaset miało na celu analizę procesów zachodzących w obrębie systemu korzeniowego sadzonek kontenerowych po ich wysadzania w terenie. Do systemu przesadzonego zostały użyte sadzonki, które podczas wzrostu w kontenerach zahamowały wydłużanie korzenia palowego - korzeń palowy nie wyrósł poza dno kontenera, a następnie ponowił wzrost po przesadzeniu sadzonek do systemu ryzotronowego. Korzenie palowe podczas zbioru materiału zostały klasyfikowane na podstawie ich długości na korzenie krótkie (5-9cm), średnie (9.5-15cm) i długie (>15.5cm). Do analiz transkryptomicznych oraz określenia poziomu wybranych hormonów roślinnych wykorzystano strefę merystematyczną i osobno strefę elongacyjną wierzchołków korzenia palowego, pobrane z co najmniej dziesięciu indywidualnych korzeni na każde powtórzenie biologiczne (Rycina 1).

Artykuł 1

Pierwszym etapem badań było **podsumowanie aktualnej wiedzy na temat zarówno indywidualnych, jak i złożonych czynników wewnętrznych regulujących rozwój i wzrost korzeni pierwotnych oraz wpływu bodźców środowiskowych na te czynniki**. W związku z tym został przygotowany artykuł przeglądowy Kościelniak i in. (2021) podsumowujący aktualną wiedzę w tym obszarze (*Artykuł 1*). Artykuł obejmował przegląd ogólnych informacji na temat morfogenezy i funkcji korzeni pierwotnych, zwłaszcza w odniesieniu do roli pełnionej przez korzenie palowe u drzew podczas suszy. Omówione zostały także czynniki endogenne, tj. geny, czynniki transkrypcyjne, miRNA i hormony roślinne mające wpływ na powstawanie i wzrost korzeni u roślin.

Artykuł 2

Drugi etap badań obejmował sekwencjonowanie transkryptomów (RNA-seq) korzeni palowych i bocznych dębów. W tym celu została wykonana analiza porównawcza transkryptomów z wykorzystaniem sekwencjonowania nowej generacji (NGS). Analizę tę przeprowadzono w oparciu o technologię sekwencjonowania przez syntezę (SBS – ang. *sequencing by synthesis*), opracowaną przez firmę Illumina. RNA-seq stanowi doskonałe narzędzie do profilowania transkryptomu i dostarcza wielu informacji na temat ekspresji genów, nawet u gatunków roślin posiadających większy genom niż rośliny modelowe. Sekwencjonowanie RNA-seq pozwoliło na wygenerowanie znacznej ilości danych, które zostały zintegrowane w postaci ogólnodostępnej bazy danych OakRootRNADB (https://oakrootrnadb.idpan.poznan.pl/) opisanej w artykule Kościelniak i in. (2022) (*Artykuł 2*), a surowe dane zostały zdeponowane w bazie danych NCBI Gene Expression Omnibus (GEO) i są dostępne pod numerem dostępu GEO GSE181860 (https://www.ncbi.nlm.nih.gov/geo/query/acc.cgi?acc=GSE181860).

Zazwyczaj, surowe dane badawcze, zdeponowane w ogólnodostępnych bazach danych, wymagają specjalistycznego oprogramowania, umożliwiającego ich przetwarzanie oraz komputerów o dużej mocy obliczeniowej. Może zatem zajść znaczne ograniczenie ich rozpowszechnienia i dostępności. Ograniczenia te podkreślają potrzebę tworzenia baz, prezentujących dane w prostej, bezpośredniej i przystępnej do zrozumienia dla końcowego użytkownika formie. Postawione zadania te wypełnia przygotowana baza, bowiem celem jej wykonania była **integracja wyników RNA-seq w postaci sekwencji transkryptów kodujących białka a także lncRNA (ang. *long non-coding RNA*) oraz miRNA (na podstawie prekursorów miRNA)**. Ponadto baza zawiera informację zarówno o znanych, jak i po raz pierwszy zidentyfikowanych miRNA oraz lncRNA. Zdeponowane sekwencje zostały adnotowane do powszechnie znanych baz danych jak Pfam, GO, KEGG itp. Dodatkowo, baza wskazuje, czy dana sekwencja koduje białko będące prawdopodobnie czynnikiem transkrypcyjnym, regulatorem transkrypcji czy regulatorem chromatyny. Na podstawie przypuszczalnych sekwencji białkowych kodowanych przez zidentyfikowane transkrypty, ustalono także ich przewidywaną lokalizację komórkową. OakRootRNADB może być wykorzystana jako punkt wyjścia do różnorodnych badań (analiz ekspresji genów i ncRNA (ang. *non-coding RNA*), filogenetycznych) u dębu szypułkowego, a także innych gatunków roślin wieloletnich, zwłaszcza drzew. Poza identyfikacją czynników genetycznych zaangażowanych we wzrost korzeni palowych, baza zawiera również informacje na temat transkryptomu korzeni bocznych oraz korzeni palowych charakteryzujących się różną

morfologią (o większej średnicy, tzw. grubych, zamierających oraz jednocześnie grubych i zamierających), a także zawiera informacje o transkryptomie korzeni w zależności od terminu wysiewu czy też strefy wzrostu korzenia. Dane transkryptomiczne uzyskane w ramach przeprowadzonych prac pozwalają zidentyfikować podobieństwa i różnice w globalnych profilach ekspresji genów w komórkach korzeni różnych gatunków roślin. **OakRootRNADB daje zatem możliwość poszerzenia naszej wiedzy na temat aktywności transkrypcyjnej genomu w systemie korzeniowym drzew oraz oceny potencjalnej roli genów w mechanizmach pośredniczących nie tylko we wzroście, ale i wielu innych procesach podczas rozwoju korzeni.**

Artykuł 3

Udzielenie odpowiedzi na pytanie o czynniki odgrywające szczególną rolę w kontroli wzrostu korzenia palowego w różnych typach upraw, wymaga najpierw poszerzenia wiedzy o wzory wzrostu korzeni palowych sadzonek dębu szypułkowego w warunkach naturalnych. Należy przede wszystkim określić na ile ścieżki regulujące wzrost korzenia palowego dębu szypułkowego są tożsame z występującymi u roślin modelowych. Dotychczasowe badania wykazały, że inicjacja wzrostu i tempo wertykalnego przerastania gleby przez korzenie, zależne jest od grupy systematycznej, do której dany gatunek należy (Clowes 2000). Wzrost korzenia jest jednak przede wszystkim kształtowany poprzez geny oraz interakcję z czynnikami je regulującymi: czynnikami transkrypcyjnymi, miRNA czy hormonami roślinnymi (Carlsbecker i in. 2010; Casson i Lindsey 2003; Chen i in. 2022; Xuan i in. 2016). Wyzwaniem jest ocena, w jaki sposób czynniki te umożliwiają korzeniom palowym szybki wzrost i zapewniają potencjał osiągnięcia głębokich warstw gleby. Równie istotne dla kształtowania architektury i funkcjonowania systemu korzeniowego są różnice bądź podobieństwa występujące pomiędzy molekularnymi mechanizmami regulującymi wzrost korzenia palowego a wzorami ekspresji uruchamianymi podczas wzrostu korzeni bocznych, wyrastających z korzenia palowego. Pozycje literaturowe wskazują również na brak jednoznaczności w kwestii samego wzoru transkryptomicznego pomiędzy oboma typami korzeni roślin wieloletnich. Istotne dla zdefiniowania potencjału wzrostu w ciągu długiego życia roślin drzewiastych jest również określenie poziomu aktywności genetycznej w ujęciu dynamicznym, zarówno tuż po skiełkowaniu, na początkowych etapach wzrostu kilkucentymetrowego korzenia, jak i na dalszych etapach wydłużania, kiedy korzeń osiąga długość kilkunastu centymetrów i więcej. Większość spośród dotychczas przeprowadzonych badań, koncentrowała się na analizach genomu roślin w jednym punkcie czasowym (Marks i in. 2021).

Warte wyjaśnienia są również kwestie dotyczące relacji pomiędzy morfologią merystemu, czy też szerzej szerokością korzenia, a procesami zachodzącymi podczas początkowych etapów wzrostu korzenia palowego. Trzecia z prac podejmuje tę problematykę. Głównym celem *Artykułu 3,* była ocena **1) zmian we wzorach ekspresji genów podczas wydłużania korzenia palowego, 2) zmian w transkryptomie korzenia palowego w zależności od jego morfologii, 3) specyfiki profilu ekspresji pomiędzy korzeniami palowymi a bocznymi**. W artykule zostały przeanalizowane wierzchołki wzrostu korzenia palowego oraz korzeni bocznych, zawierające strefę merystematyczna. Korzenie palowe sklasyfikowano ponadto w zależności od ich morfologii (korzeń palowy o pogrubionej średnicy, zamierający korzeń palowy oraz zamierający i pogrubiony jednocześnie). Sadzonki dębu szypułkowego rosły w systemie ryzotronowym przez osiem tygodni. Zastosowanie systemu ryzotronowego pozwoliło na obserwację korzeni palowych z uwzględnieniem ich morfologii w warunkach zbliżonych do naturalnych. Dane o poziomie ekspresji transkryptów użyte w *Artykule 3* zostały zawarte w bazie danych OakRootRNADB i przypisane do zbioru danych 1 (*Dataset 1*). Duża ilość wygenerowanych danych stworzyła konieczność zastosowania narzędzi bioinformatycznych do ich wizualizacji tj. analizę DEGs (ang. *Differentially Expressed Genes),* pozwalającą na przedstawienie zróżnicowanych wzorców ekspresji genów między różnymi wariantami badawczymi, ze szczególnym uwzględnieniem genów kodujących czynniki transkrypcyjne oraz genów zaangażowanych w metabolizm hormonów roślinnych. Wykorzystana została także klasyfikacja funkcjonalna oparta o kategorie GO (ang. *Gene Ontology*), umożliwiająca klasyfikację według funkcji produktu genu (MF, ang. *Molecular Function*), procesu biologicznego w jakim może on brać udział (BP, ang. *Biological Process*) czy też lokalizacji komórkowej produktu genu (CC – ang. *Cellular Component*). Wykonana została również analiza funkcjonalna w oparciu o bazę danych KEGG (ang. *Kyoto Encyclopedia of Genes and Genomes*).

Analiza transkryptomiczna wykazała występowanie znaczących różnic w ekspresji genów w zależności od długości korzeni. Największe różnice stwierdzono pomiędzy wierzchołkami wzrostu krótkich i średnich korzeni palowych (5403 genów ulegających zróżnicowanej ekspresji). Z kolei większa liczba genów o podwyższonym profilu ekspresji (2043 genów), porównując średnie i długie korzenie palowe, może wskazywać na zmiany ekspresji wynikające nie tylko z wydłużania korzenia palowego, ale przede wszystkim z wyrastania korzeni bocznych, co przedstawia również duża liczba genów o podwyższonym profilu ekspresji w korzeniach bocznych (*Artykuł 3, Rycina 2*). Spadek liczby genów

o podwyższonej ekspresji w korzeniach palowych może zatem odzwierciedlać istnienie dominacji wierzchołkowej korzenia palowego, przejawiającej się zależnością pomiędzy powstawaniem korzeni bocznych a zmniejszeniem poziomu ekspresji genów w wierzchołku wzrostu korzenia palowego. Zależny od długości korzeni palowych, moment formowania korzeni bocznych, jednoznacznie sugeruje, że ekspresja genów w korzeniach palowych może wpływać na wzorzec ekspresji w korzeniach bocznych i regulować ich wzrost. Niezależnie od pochodzenia korzeni bocznych (wyrastających z korzeni palowych średnich lub długich) odnotowano niski stopień pokrywających się genów ulegających zwiększonej ekspresji. Zwiększony poziom aktywności transkrypcyjnej genu *MYB93*, zaobserwowany w korzeniach bocznych formowanych w obrębie średnich lub długich korzeni palowych (*Artykuł 3, Tabela uzupełniająca 1*) zachodzi wraz ze zwiększeniem liczby wzbogaconych ścieżek metabolicznych (KEGG) związanych z kwasami tłuszczowymi (*Artykuł 3, Rycina 5*) odpowiedzialnymi za indukcję i późniejszy wzrost korzeni bocznych. Badania z wykorzystaniem mutantów *Arabidopsis*, cechujących się niedoborem długołańcuchowych kwasów tłuszczowych, wykazały bowiem kluczowe znaczenie MYB93 w regulacji wzrostu korzeni bocznych, poprzez jego aktywację w odpowiedzi na wysoki poziom długołańcuchowych kwasów tłuszczowych. Brak tych ostatnich hamował formowanie i wzrost korzeni bocznych (Uemura i in. 2022). Ponadto, wykazano zaangażowanie auksyn w regulację wzrostu korzeni bocznych poprzez biosyntezę długołańcuchowych kwasów tłuszczowych za pośrednictwem MAPK (Mitogen-activated protein kinase), który jest regulowany przez ERF13 (Ethylene-responsive transcription factor 13) (Lv i in. 2021). Wykazana w niniejszym artykule, wzbogacona ścieżka szlaku sygnałowego MAPK (*Artykuł 3, Rycina 5*) zsynchronizowanego ze zwiększoną ekspresją genu kodującego ERF13 w korzeniu palowym (Ethylene-responsive transcription factor 13) (*Artykuł 3, Tabela uzupełniająca 2*), sugeruje inicjację rozwoju korzeni bocznych u dębu szypułkowego poprzez sprzężenie auksyny z MAPK. Zależności te jak dotychczas były tylko zdawkowo poruszane w literaturze przedmiotu, a u roślin drzewiastych po raz pierwszy wykazano występowanie tego procesu. Również analiza DEG, wykazała podwyższony poziom ekspresji genu *LRP1* zarówno w średnich, jak i długich korzeniach palowych o standardowej morfologii oraz obniżony poziom ekspresji w krótkich korzeniach palowych. Wynik ten pozostaje w sprzeczności z doniesieniem Singh i in. (2020), którzy wykazali ekspresję *LRP1* na wszystkich etapach rozwoju korzeni bocznych, ale nie w obrębie korzeni pierwotnych. Wytłumaczeniem rozbieżności wyników jest bardzo krótki czas trwania badań z udziałem *Arabidopsis*, której siewki rosły tylko przez 7 dni. W niniejszym artykule (*Artykuł 3*) możemy mieć zatem do czynienia albo ze specyficznym mechanizmem

występującym tylko u dębu szypułkowego, albo z wykazaniem uniwersalnych relacji, uwidocznionych dzięki odpowiedniej długości doświadczenia, obejmującej różne procesy zachodzące podczas wydłużania korzenia palowego. Wykazane już we wcześniejszych doniesieniach literaturowych, zależności pomiędzy wydłużeniem korzenia palowego a pojawieniem się korzeni bocznych (Pages 1995), w niniejszym artykule zostały zobrazowane na poziomie molekularnym i mogą wynikać z aktywności genów kodujących czynniki transkrypcyjne: bHLH12, TCP15 i WRKY75. Te czynniki transkrypcyjne, wraz ze zwiększoną ekspresją *LRP*, zwłaszcza w średnim korzeniu palowym, regulują alokację zasobów zawartych w żołędziu i intensyfikują wzrost elongacyjny korzenia palowego kosztem wzrostu korzeni bocznych, zwłaszcza w początkowej fazie wzrostu tego pierwszego (Ding i in. 2009; Li 2015; Zhang i in. 2021). Wykazana w szlaku KEGG zwiększona równocześnie biosynteza diterpenoidów w korzeniu palowym, mogąca być wyrazem biosyntezy brassinosteroidów (grupy tetracyklicznych diterpenoidów) - promujących rozwój korzeni bocznych, kontrastuje zarazem ze zwiększoną ekspresją genów związanych z biosyntezą cytokininy (zeatyny) (*Artykuł 1, Rycina 13*). Cytokinina poprzez antagonizm względem auksyn (Fukaki i Tasaka 2009; Peres i in. 2019) negatywnie reguluje rozwój korzeni bocznych (*Artykuł 3, Rycina 12*). Hamowanie wzrostu korzeni bocznych może sprzyjać wzrostowi korzeni palowych, co z kolei intensyfikuje ich wydłużanie i zapewnia dominację wierzchołkową (Bao i in. 2004). Wyniki te potwierdzają przyjęte założenie o kluczowej roli procesów zachodzących na poziomie molekularnym w wierzchołku wzrostu korzenia palowego w kształtowaniu wzrostu systemów korzeniowych dębu szypułkowego.

Wzór ekspresji genów w wydłużającym się korzeniu palowym był również zależny od samej morfologii korzenia, rozumianej jako jego grubość, bądź zmian wynikających z zamierania. Porównanie transkryptomów korzeni o różnej morfologii może odgrywać szczególną rolę w określeniu czynników i procesów regulujących ustanie wzrostu korzeni palowych. W niniejszym artykule wykazano, że ustanie wzrostu korzenia palowego jest związane z aktywacją szlaków sygnałowych promujących ich pogrubianie, a także ze zwiększaniem ekspresji genów kodujących czynniki transkrypcyjne AIL5, MYB59 i bHLH154 (*Artykuł 3, Tabela uzupełniająca 3*), odpowiedzialnych za regulację podziałów w komórkach macierzystych korzeni (Mu i in. 2009). Zwiększona ekspresja genów kodujących wymienione TF, regulując cykl komórkowy, hamuje wydłużanie korzenia pierwotnego powodując jego jednoczesne zgrubienie. Większa średnica korzeni palowych, a zatem i ich merystemów, w korzeniach w których wzrost ustał, może charakteryzować sadzonki kontenerowe o dużym

potencjale ponowienia wzrostu po ich przesadzeniu (Zadworny i in. 2021). Badania przeprowadzone przy użyciu systemu ryzotronowego, który umożliwia wzrost sadzonek dębu w warunkach zbliżonych do naturalnych, nie tylko pozwalają na lepsze zrozumienie procesów molekularnych regulujących rozwój systemu korzeniowego długożyjących drzew, ale mogą również wpłynąć na praktyki stosowane podczas produkcji materiału sadzeniowego w szkółkach kontenerowych.

W niniejszej pracy doktorskiej podjęto się również analizy zagadnienia związanego z określeniem procesów molekularnych, na poziomie ekspresji genów, zachodzących podczas zamierania korzeni. Zamierające korzenie charakteryzowały się występowaniem obniżonej ekspresji genów kodujących TF, w porównaniu z prawidłowo funkcjonującymi wierzchołkami korzeni palowych o standardowej morfologii. Korzenie zamierające wykazywały zwiększoną ekspresję genów z rodziny *ERF*, spośród których ERF115 kontroluje podziały komórkowe w korzeniu, a jego aktywność jest regulowana przez dwa antagonistyczne mechanizmy: proteolizę sterowaną przez ligazę ubikwityny i kompleks APC/C(CCS52A2). Czynniki te ograniczają zależną od brassinosteroidów ekspresję ERF115. Ograniczenie aktywności ERF115 odpowiada za regulację cyklu komórkowego oraz utrzymuje pulę komórek macierzystych, kiedy komórki otaczające komórki macierzyste są uszkodzone (Heyman i in. 2013). Zwiększenie ekspresji *ERF115* poprawia z kolei zdolność komórek macierzystych do regeneracji, w którym to procesie pośredniczy akumulacja auksyn (Heyman i in. 2013). Wyniki te naświetlają rolę ERF115 jako pozytywnego regulatora regeneracji komórek macierzystych, wskazując procesy zaangażowane podczas ponowienia wzrostu korzenia palowego. Chociaż badania na *Arabidopsis* wykazały taki sam mechanizm, jednakże ze względu na krótki cykl trwania eksperymentu, nie powiązano wówczas roli ERF115 z ponowieniem wzrostu korzenia pierwotnego (Canher i in. 2022). Dodatkowo, wykazano, że zwiększona aktywność ERF115, zwiększając wrażliwość na auksyny, promuje dojrzewanie ksylemu i tworzenie korzeni bocznych. Generowanie tkanek przewodzących wodę w nowo powstałym korzeniu palowym oraz nowych korzeniach bocznych formowanych w obrębie korzenia palowego, wskazuje na szczególną rolę ERF115 w zdefiniowaniu potencjału ponowienia wzrostu korzeni palowych (Canher i in. 2022).

Analiza ekspresji genów zaangażowanych w biosyntezę hormonów oraz genów kodujących czynniki transkrypcyjne pozwoliła na zidentyfikowanie potencjalnych różnic nie tylko w profilach ich ekspresji, ale również umożliwia zdefiniowanie odmiennej aktywności genów kodujących elementy szlaków transdukcji sygnału i odpowiedzi

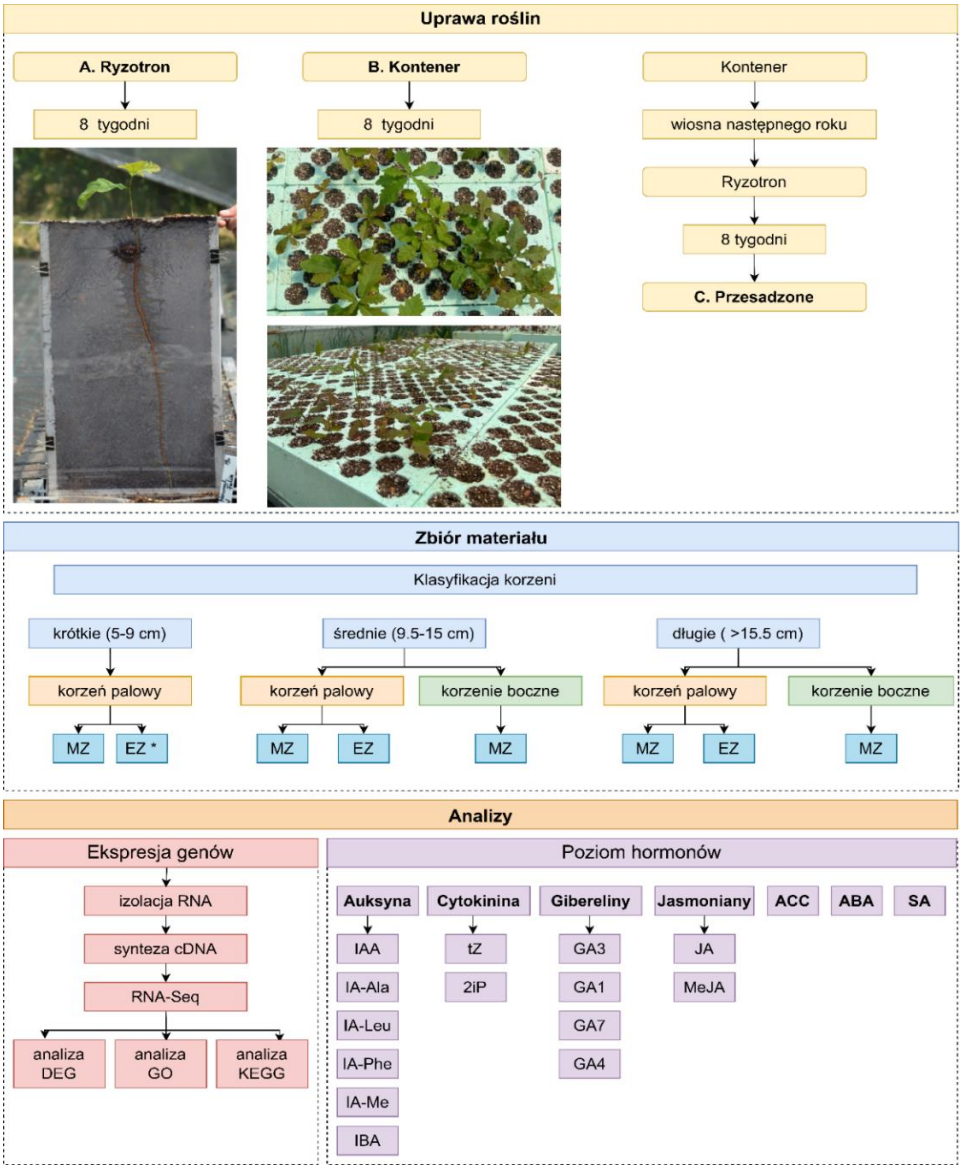
hormonalnej, bądź czynników transkrypcyjnych w zależności od wielkości i morfologii korzeni palowych i bocznych. Poznanie tak zróżnicowanych wzorców ekspresji genów poprawia nasze zrozumienie rozwoju korzeni palowych i bocznych u dębu szypułkowego na poziomie genetycznej sieci regulacyjnej, potwierdzając założenie o kluczowej roli regulacyjnej wierzchołka wzrostu korzeni palowych w kształtowaniu wzrostu korzeni dębu.

Artykuł 4

Zasadnicze dla niniejszej rozprawy było określenie czynników zaangażowanych w wydłużanie korzeni podczas wzrostu sadzonek dębu szypułkowego w systemie kontenerowym w porównaniu do wzrostu sadzonek dębów rosnących w systemie ryzotronowym. Jak do tej pory, analiza jakości sadzonek w szkółkach kontenerowych koncentrowała się głównie na badaniach ich morfologii lub badaniach fizjologicznych. Kwestie związane z aspektem molekularnym, zwłaszcza w kontekście procesów regulujących wzrost korzeni palowych sadzonek, tak w samych kontenerach, jak i po wysadzeniu na uprawie były pomijane. Najistotniejsze dla poprawienia kondycji upraw zakładanych z materiału szkółkarskiego jest głębsze ukorzenienie i dostęp do zlokalizowanych niżej pokładów wody. Lepsze zaopatrzenie w wodę może polepszyć kondycję drzewostanów dębowych w trakcie epizodów długotrwałej suszy. Jak już wcześniej wspomniano, wpływ uszkodzenia korzenia palowego podczas wzrostu sadzonek w kontenerach może skutkować ich większą podatnością na niekorzystne warunki środowiskowe (Grossnickle i Ivetić 2022). Jednakże, w obrębie sadzonek wyprodukowanych w kontenerach nie wszystkie cechują się nieodwracanie uszkodzonym korzeniem palowym, albowiem aż 55% sadzonek kontenerowych po ich przesadzeniu do 120 litrowych pojemników ponawiało jego wzrost co wykazał Zadworny i in. (2021). Określenie, w jaki sposób ekspresja genów wraz z sygnałami hormonalnymi, regulują wzrost korzeni dębu, zostało przeprowadzone poprzez wykonanie analizy transkryptomu oraz poziomu różnych hormonów roślinnych w korzeniach, i przedstawione w *Artykule 4*, którego celem było: **1) określenie zmian we wzorcach ekspresji genów podczas wydłużania korzeni w systemie kontenerowym i ryzotronowym oraz po ich przesadzeniu, 2) określenie poziomu hormonów w obrębie korzeni palowych i bocznych sadzonek dębu szypułkowego w systemie kontenerowym, ryzotronowym i przesadzonym, 3) analiza specyfiki profilu ekspresji genów między różnymi strefami korzenia palowego (strefa merystematyczna i elongacyjna) oraz korzeni bocznych (strefa merystematyczna).**

Do przeprowadzenia analiz poziomu transkryptów zawartych w *Artykule 4* zostały wykorzystane dane umieszczone w bazie danych OakRootRNADB i przypisane do zbioru

danych 2 (*Dataset 2)*. Do badań wykorzystane zostały sadzonki dębu rosnące w ryzotronach lub kontenerach osiem tygodni po wysianiu żołędzi oraz początkowo rosnące w kontenerach, a po roku przesadzone do ryzotronów, w których wzrastały przez osiem tygodni. Niezależnie od systemu uprawy, zbiór materiału nastąpił w tym samym czasie. Wyniki analiz transkryptomu zostały przedstawione za pomocą identyfikacji DEG, a następnie poddane analizie funkcjonalnej GO i KEGG. Analiza poziomu hormonów została wykonana dla siedmiu grup hormonów roślinnych. Szczegółowy schemat wykonanych analiz został przedstawiony na Rycinie 1.



Rycina 1. Układ eksperymentalny, zastosowany w *Artykule 4* (uprawa roślin, zbiór materiału oraz wykonane analizy). MZ – strefa merystematyczna; EZ – strefa elongacyjna; IAA – kwas indolilo-3-octowy; IBA – kwas indolilo-3-masłowy; IA-Ala – kwas indolilo-3-octowy-L-alanina; IA-Leu – kwas indolilo-3-octowy-L-leucyna; IA-Phe – kwas indolilo-3-

octowy-L-fenyloalanina; IA-ME – kwas indolilo-3-octowy-L-metionina; tZ – trans-zeatyna; 2iP – 2-izopentyloadenina; GA3, GA1, GA7, GA4 – giberelina 3,1,7,4; JA – kwas jasmonowy; MeJA – jasmonian metylu; ACC - kwas 1-aminocyklopropano-1-karboksylowy; ABA – kwas abscysynowy; SA – kwas salicylowy. Gwiazdka (*) oznacza wariant badawczy, dla którego nie wykonano sekwencjonowania. Na podstawie *Artykułu 4*.

Analiza transkryptomu wykazała liczne zmiany w poziomie ekspresji genów pomiędzy korzeniami rosnącymi w różnych systemach uprawy. Porównując sadzonki rosnące w ryzotronach i kontenerach, liczba genów o zróżnicowanej ekspresji wzrastała wraz z wydłużaniem się korzenia palowego u tych pierwszych, zarówno w strefie merystematycznej jak i elongacyjnej. Jednakże, liczba genów o obniżonym profilu ekspresji była zdecydowanie większa (4811 genów o obniżonej ekspresji vs 1736 genów o podwyższonej ekspresji) w sadzonkach ryzotronowych w strefie merystematycznej niż w sadzonkach kontenerowych (*Artykuł 4, Rycina 2*). Takie zwiększenie ekspresji genów w obrębie sadzonek kontenerowych może być przejawem odpowiedzi korzenia palowego na dorastanie do dna kasety kontenerowej i prawdopodobnie odzwierciedla molekularne mechanizmy zaangażowane w regulację wydłużania korzeni. Klasyfikacja funkcjonalna wykazała również zwiększenie ekspresji genów biorących udział w procesach biologicznych związanych z "odpowiedzią komórkową na bodziec aminokwasowy" w sadzonkach ryzotronowych (*Artykuł 4, Rycina 3*), wskazując na zaangażowanie czynników transkrypcyjnych regulujących zmiany stanu lub aktywności komórki w potencjał elongacyjny korzenia palowego w ryzotronie. W korzeniach palowych sadzonek dębów rosnących w ryzotronie miał miejsce wzrost ekspresji genów związanych z gospodarką jonów: transport jonów wapnia, sygnalizacja za pośrednictwem wapnia, aktywność kanału wapniowego, aktywność receptora glutaminianu, sygnalizacja wapniową odpowiedzialna za utrzymanie ciągłości wydłużania korzeni (Qiu i in. 2020). Wyniki ponownie sugerują wysoki potencjał wzrostu korzenia palowego, oraz stwarzają potencjalną możliwość agrotechnicznych manipulacji w wyniku oddziaływania na ekspresję genów i produkcję hormonów. Stłumiona ekspresja genów, związanych z gospodarką wapniem i jego rolą w przekazywaniu sygnałów na poziomie komórkowym w sadzonkach kontenerowych, potwierdza założenie o wapniu jako kluczowym czynniku zaangażowanym we wzrost i wydłużanie korzeni palowych. Modulacja gospodarką wapnia może zatem odgrywać zasadniczą rolę podczas produkcji szkółkarskiej. Przed powszechnym wprowadzeniem tej modyfikacji w szkółkach kontenerowych wymagane są jednak szersze badania opisanego zjawiska.

Kwestią wymagającą szczególnego wyjaśnienia było określenie procesów zachodzących w obrębie systemu korzeniowego sadzonek kontenerowych po ich przesadzeniu do ryzotronów (przesadzone) w porównaniu do sadzonek ryzotronowych, których warunki przypominały wzrost korzeni bezpośrednio w glebie. Wzrost sadzonek w systemie ryzotronowym wpłynął na obniżenie liczby genów o zróżnicowanej ekspresji (DEGów) (*Artykuł 4, Rycina 5*) w obrębie strefy merystematycznej i elongacyjnej wydłużającego się korzenia palowego w ryzotronie w porównaniu do korzeni przesadzonych. Odnotowano większą liczę genów o obniżonej ekspresji w korzeniach ryzotronowych i jednocześnie wyższą ekspresję genów w korzeniach sadzonek przesadzonych. Uzyskany wynik sugeruje istnienie potencjału regeneracyjnego, umożliwiającego nie tylko ponowienie wzrostu, ale i jego utrzymanie po przesadzeniu sadzonek z kontenera do ryzotronu. Zwiększona ekspresja dużej liczby genów w przesadzonych sadzonkach kontenerowych może być zatem przejawem zdolności do ponowienia elongacji korzenia palowego.

Porównując wzrost korzeni sadzonek kontenerowych i przesadzonych, zaobserwowano znaczną liczbę genów o zróżnicowanej ekspresji (DEGów), zwłaszcza w korzeniach krótkich, zarówno u sadzonek kontenerowych i przesadzonych. Zaobserwowano jednocześnie wyższą częstotliwość genów o zwiększonej ekspresji w porównaniu z liczbą genów o obniżającej się ekspresji (8076 vs 3998), w ponawiających wzrost korzeniach palowych u sadzonek przesadzonych niż u korzeni palowych sadzonek ryzotronowych tej samej kategorii długości (*Artykuł 4, Rycina 5*). Może to sugerować istnienie zależności pomiędzy wysoką aktywnością genów a zdolnością korzeni palowych drzew do ponowienia wzrostu. Wzór zwiększonej ekspresji genów w sadzonkach kontenerowych po ich przesadzeniu do ryzotronów nie był jednak stały. Obserwowany, wraz z wydłużaniem korzenia, spadek częstotliwości występowania genów o zwiększonej ekspresji wynika z wysokiego tempa wzrostu tuż po skiełkowaniu i zachodzącej wówczas dużej proliferacji komórek (Svolacchia i in. 2020). Zbliżony do profilu ekspresji genów sadzonek rosnących bezpośrednio w ryzotronach, profil ekspresji w obrębie korzeni palowych sadzonek przesadzonych sugeruje duży potencjał regeneracyjny tych ostatnich. Zwiększona aktywność genów związanych ze specjalizacją tkanek, czy procesami wzmacniającymi korzeń palowy, jak lignifikacja czy suberynizacja w obrębie korzeni palowych sadzonek przesadzonych, sugeruje że korzenie sadzonek przesadzonych z kontenerów do ryzotronów podczas ponowienia wzrostu korzeni palowych, uruchamiają mechanizmy molekularne zbliżone do zachodzących w sadzonkach uzyskanych drogą bezpośredniego siewu nasion do ryzotronów.

Weryfikacją profilu ekspresji genów zaangażowanych w syntezę hormonów roślinnych było określenie profilu ich poziomu w różnych systemach uprawy sadzonek dębu szypułkowego. Sadzonki przesadzone wykazywały bardziej odmienny profil hormonalny, w porównaniu do sadzonek rosnących w ryzotronach i kontenerach. Wyższe poziomy auksyn w przypadku korzeni palowych sadzonek przesadzonych z kontenerów do ryzotronów wynika z aktywowania genów zaangażowanych w biosyntezę auksyny i znajduje swoje potwierdzenie w wynikach analizy DEG, zarówno w korzeniach palowych, jak i bocznych (*Artykuł 4, Tabela uzupełniająca 2*). Ponadto zaobserwowane zostały wyższe poziomy cytokinin w strefie merystematycznej i elongacyjnej korzeni palowych sadzonek ryzotronowych, podczas gdy w obrębie ich korzeni bocznych, pobranych z długich korzeni palowych, został zaobserwowany odwrotny trend. Niższy stosunek auksyn do cytokinin może tłumaczyć intensyfikację wzrostu korzeni palowych, z kolei wyższy stosunek auksyn do cytokinin może promować rozwój korzeni bocznych, zwłaszcza w obrębie korzeni sadzonek kontenerowych, potwierdzając doniesienia Aloni i in. (2006) uzyskane dla roślin modelowych. Oprócz równowagi auksyna-cytokinina, indukowanie elongacji korzenia palowego w obrębie sadzonek ryzotronowych i przesadzonych znajduje potwierdzenie w poziomie giberelin (GA1, GA3), które są odpowiedzialne za elongację korzenia pierwotnego (Ubeda-Tomás i in. 2009). Natomiast niższe stężenie IAA niż CK i wyższe stężenie prekursora ET niż IAA wskazuje na regulacyjną rolę tych hormonów w hamowaniu wzrostu korzenia palowego w sadzonkach kontenerowych. Ponadto, wzrost stężenia ABA w sadzonkach kontenerowych, wskazuje raczej na zaangażowanie tego hormonu w utrwaleniu, zaindukowanego przez etylen, zahamowania elongacji korzeni palowych sadzonek kontenerowych (*Artykuł 4, Rycina 13*). Oprócz etylenu, hamowanie wzrostu korzeni palowych sadzonek kontenerowych może być również związane ze zwiększonym stężeniem JA i MeJA (*Artykuł 2, Rycina 15*), które promując wzrost korzeni bocznych, poprzez współwystępowanie z wzrastającym poziomem ABA, mogą wywierać hamujący wpływ na wzrost korzeni pierwotnych (Sun i in. 2018).

Podsumowując, wykonane w ramach realizowanej pracy doktorskiej badania potwierdziły aktywację szeregu reakcji molekularnych promujących wzrost korzeni palowych po przesadzaniu sadzonek z kontenerów. Badania zawarte w niniejszej dysertacji są kluczowe dla zrozumienia procesów umożliwiających prawidłowy wzrost drzewostanów dębowych zakładanych ze szkółek kontenerowych i mogą przyczynić się do opracowania lepszych strategii zarządzania procedurami agrotechnicznymi w warunkach globalnego ocieplenia.

PODSUMOWANIE

Do najważniejszych wyników uzyskanych podczas realizacji pracy doktorskiej należą:

1) Zsekwencjonowanie transkryptomu dębu szypułkowego (*Quercus robur* L.) z uwzględnieniem korzeni palowych oraz korzeni bocznych w różnych typach uprawy.
2) Integracja wyników uzyskanych po RNA-seq w postaci sekwencji transkryptów kodujących białka, a także lncRNA w ogólnodostępnej bazie danych.
3) Określenie zależności pomiędzy powstawaniem korzeni bocznych a zmniejszeniem poziomu ekspresji genów w wierzchołku wzrostu korzenia palowego.
4) Opisanie szlaku sygnałowego MAPK jako ścieżki odpowiedzialnej za inicjację tworzenia korzeni bocznych u korzeni dębu.
5) Wykazanie aktywności LRP1 w korzeniu palowym dębu szypułkowego jako potencjalnego czynnika promującego wydłużanie korzeni.
6) Ustalenie potencjalnego mechanizmu ustania wzrostu korzenia palowego w kasetach kontenerowych, związanego z aktywacją szlaków sygnałowych promujących ich pogrubianie i obejmującego zwiększanie ekspresji genów kodujących czynniki transkrypcyjne AIL5, MYB59 i bHLH154.
7) Określenie genu *ERF115* kodującego czynnik transkrypcyjny jako potencjalnie odpowiedzialnego za ponowienie wzrostu korzenia palowego po wysadzeniu sadzonek kontenerowych na uprawie.
8) Wskazanie wapnia jako potencjalnie kluczowego czynnika zaangażowanego we wzrost i wydłużanie korzeni palowych.
9) Wykazanie, że procesy zachodzące w obrębie sadzonek przesadzonych z kontenerów do ryzotronów, promujące wzrost korzeni palowych, są zbliżone do występujących w sadzonkach uzyskanych drogą bezpośredniego siewu nasion do ryzotronów.
10) Przedstawienie, po raz pierwszy, roli hormonów roślinnych w regulacji wzrostu korzeni dębu w różnych typach uprawy.

LITERATURA

Aloni, R., E. Aloni, M. Langhans and C.I. Ullrich. 2006. Role of cytokinin and auxin in shaping root architecture: regulating vascular differentiation, lateral root initiation, root apical dominance and root gravitropism. Annals of Botany 97:883-93.

Augstein, F. and A. Carlsbecker. 2018. Getting to the Roots: A Developmental genetic view of root anatomy and function from *Arabidopsis* to *Lycophytes*. Frontiers in Plant Science 9:1410.

Baesso, B., D. Chiatante, M. Terzaghi, D. Zenga, K. Nieminen, A.P. Mahonen, R. Siligato, Y. Helariutta, G.S. Scippa and A. Montagnoli. 2018. Transcription factors PRE3 and WOX11 are involved in the formation of new lateral roots from secondary growth taproot in *A.thaliana*. Plant Biology 20:426-432.

Bao, F., J. Shen, S.R. Brady, G.K. Muday, T. Asami and Z. Yang. 2004. Brassinosteroids interact with auxin to promote lateral root development in *Arabidopsis*. Plant Physiology 134:1624-31.

Barbeta, A. and J. Peñuelas. 2017. Increasing carbon discrimination rates and depth of water uptake favor the growth of Mediterranean evergreen trees in the ecotone with temperate deciduous forests. Global Change Biology 23:5054-5068.

Benková, E. and J. Hejatko. 2009. Hormone interactions at the root apical meristem. Plant Molecular Biology 69:383-396.

Bréda, N., R. Huc, A. Granier and E. Dreyer. 2006. Temperate forest trees and stands under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences. Annals of Forest Science 63:625-644.

Canher, B., F. Lanssens, A. Zhang, A. Bisht, S. Mazumdar, J. Heyman, S. Wolf, C.W. Melnyk and L. De Veylder. 2022. The regeneration factors ERF114 and ERF115 regulate auxin-mediated lateral root development in response to mechanical cues. Molecular Plant 15:1543-1557.

Carlsbecker, A., J.Y. Lee, C.J. Roberts, J. Dettmer, S. Lehesranta, J. Zhou, O. Lindgren, M.A. Moreno-Risueno, A. Vatén, S. Thitamadee, A. Campilho, J. Sebastian, J.L. Bowman, Y. Helariutta and P.N. Benfey. 2010. Cell signalling by microRNA165/6 directs gene dose-dependent root cell fate. Nature 465:316-21.

Casson, S.A. and K. Lindsey. 2003. Genes and signalling in root development. New Phytologist 158:11-38.

Chaiwanon, J., W. Wang, J.Y. Zhu, E. Oh and Z.Y. Wang. 2016. Information integration and communication in plant growth regulation. Cell 164:1257-1268.

Chapman, K., E.P. Groot, S.A. Nichol and T.L. Rost. 2002. Primary root growth and the pattern of root apical meristem organization are coupled. Journal of Plant Growth Regulation 21:287-295.

Chen, Z., Z. Wu, W. Dong, S. Liu, L. Tian, J. Li and H. Du. 2022. MYB transcription factors becoming mainstream in plant roots. International Journal of Molecular Sciences 23:9262.

Clowes, F.A.L. 2000. Pattern in root meristem development in angiosperms. New Phytologist 146:83-94.

Darwin, C. and F. Darwin. 1880. The power of movement in plants. John Murray.

Ding, W., Z. Yu, Y. Tong, W. Huang, H. Chen and P. Wu. 2009. A transcription factor with a bHLH domain regulates root hair development in rice. Cell Research 19:1309-11.

Drisch, R.C. and Y. Stahl. 2015. Function and regulation of transcription factors involved in root apical meristem and stem cell maintenance. Frontiers in Plant Science 6:505.

Dubrovsky, J.G. and L.F. Gómez-Lomelí. 2003. Water deficit accelerates determinate developmental program of the primary root and does not affect lateral root initiation in a Sonoran Desert cactus (*Pachycereus pringlei*, Cactaceae). American Journal of Botany 90:823-31.

Fukaki, H. and M. Tasaka. 2009. Hormone interactions during lateral root formation. Plant Molecular Biology 69:437-449.

Grossnickle, S.C. and Y.A. El-Kassaby. 2016. Bareroot versus container stocktypes: a performance comparison. New Forests 47:1-51.

Grossnickle, S.C. and V. Ivetić. 2022. Root system development and field establishment: effect of seedling quality. New Forests 53:1021-1067.

Gupta, A., A. Rico-Medina and A.I. Caño-Delgado. 2020. The physiology of plant responses to drought. Science 368:266-269.

Heyman, J., T. Cools, F. Vandenbussche, K.S. Heyndrickx, J. Van Leene, I. Vercauteren, S. Vanderauwera, K. Vandepoele, G. De Jaeger, D. Van Der Straeten and L. De Veylder. 2013. ERF115 controls root quiescent center cell division and stem cell replenishment. Science 342:860-3.

Hu, X. and L. Xu. 2016. Transcription factors WOX11/12 directly activate *WOX5/7* to promote root primordia initiation and organogenesis. Plant Physiology 172:2363-2373.

Jin, K., J. Shen, R.W. Ashton, I.C. Dodd, M.A.J. Parry and W.R. Whalley. 2013. How do roots elongate in a structured soil? Journal of Experimental Botany 64:4761-4777.

Kościelniak, P., P. Glazińska, J. Kęsy and M. Zadworny. 2021. Formation and development of taproots in deciduous tree species. Frontiers in Plant Science 12:772567

Kościelniak, P., P. Glazińska and M. Zadworny. 2022. OakRootRNADB—a consolidated RNA-seq database for coding and noncoding RNA in roots of pedunculate oak (*Quercus robur*). Database: The Journal of Biological Databases and Curation baac097.

Leverkus, A.B., M. Carrión, M. Molina-Morales and J. Castro. 2017. Effectiveness of diesel as a mammal repellent for direct seeding of acorns. Forests 8:276.

Leverkus, A.B., J. Castro, C. Puerta-Piñero and J.R. Benayas. 2013. Suitability of the management of habitat complexity, acorn burial depth, and a chemical repellent for post-fire reforestation of oaks. Ecological Engineering 53:15-22.

Leverkus, A.B., M. Rojo and J. Castro. 2015. Habitat complexity and individual acorn protectors enhance the post-fire restoration of oak forests via seed sowing. Ecological Engineering 83:276-280.

Li, S. 2015. The *Arabidopsis thaliana* TCP transcription factors: A broadening horizon beyond development. Plant Signaling & Behavior 10:e1044192.

Lv, B., K. Wei, K. Hu, T. Tian, F. Zhang, Z. Yu, D. Zhang, Y. Su, Y. Sang, X. Zhang and Z. Ding. 2021. MPK14-mediated auxin signaling controls lateral root development via ERF13-regulated very-long-chain fatty acid biosynthesis. Molecular Plant 14:285-297.

Malamy, J.E. 2005. Intrinsic and environmental response pathways that regulate root system architecture. Plant, Cell & Environment 28:67-77.

Marks, R.A., S. Hotaling, P.B. Frandsen and R. VanBuren. 2021. Representation and participation across 20 years of plant genome sequencing. Nature Plants 7:1571-1578.

Mitsis, T., A. Efthimiadou, F. Bacopoulou, D. Vlachakis, G.P. Chrousos and E. Eliopoulos. 2020. Transcription factors and evolution: An integral part of gene expression (Review). World Academy of Sciences Journal 2:3-8.

Mu, R.-L., Y.-R. Cao, Y.-F. Liu, G. Lei, H.-F. Zou, Y. Liao, H.-W. Wang, W.-K. Zhang, B. Ma, J.-Z. Du, M. Yuan, J.-S. Zhang and S.-Y. Chen. 2009. An R2R3-type transcription factor gene *AtMYB59* regulates root growth and cell cycle progression in *Arabidopsis*. Cell Research 19:1291-1304.

Mucha, J., A.M. Jagodziński, B. Bułaj, P. Łakomy, A.M. Talaśka, J. Oleksyn and M. Zadworny. 2018. Functional response of *Quercus robur* L. to taproot pruning: a 5-year case study. Annals of Forest Science 75:22.

Osakabe, Y., K. Osakabe, K. Shinozaki and L.S. Tran. 2014. Response of plants to water stress. Frontiers in Plant Science 5:86.

Overvoorde, P., H. Fukaki and T. Beeckman. 2010. Auxin control of root development. Cold Spring Harbor Perspectives in Biology 2:a001537.

Pages, L. 1995. Growth patterns of the lateral roots of young oak (*Quercus robur*) tree seedlings Relationship with apical diameter. New Phytologist 130:503-509.

Peres, A., J.S. Soares, R.G. Tavares, G. Righetto, M.A.T. Zullo, N.B. Mandava and M. Menossi. 2019. Brassinosteroids, the sixth class of phytohormones: A molecular view from the discovery to hormonal interactions in plant development and stress adaptation. International Journal of Molecular Sciences 20:331

Perilli, S., R. Di Mambro and S. Sabatini. 2012. Growth and development of the root apical meristem. Current Opinion in Plant Biology 15:17-23.

Qin, H., L. He and R. Huang. 2019. The coordination of ethylene and other hormones in primary root development. Frontiers in Plant Science 10:874.

Qiu, X.-M., Y.-Y. Sun, X.-Y. Ye and Z.-G. Li. 2020. Signaling role of glutamate in plants. Frontiers in Plant Science 10:1743

Robbins, N.E. and J.R. Dinneny. 2018. Growth is required for perception of water availability to pattern root branches in plants. Proceedings of the National Academy of Sciences of the United States of America 115:E822-E831.

Rodríguez-Calcerrada, J., D. Sancho-Knapik, N.K. Martin-StPaul, J.-M. Limousin, N.G. McDowell and E. Gil-Pelegrín. 2017. Drought-induced oak decline—factors involved, physiological dysfunctions, and potential attenuation by forestry practices. Oaks physiological ecology. Exploring the functional diversity of genus *Quercus* L. 419-451.

Růžička, K., K. Ljung, S. Vanneste, R. Podhorská, T. Beeckman, J. Friml and E. Benková. 2007. Ethylene regulates root growth through effects on auxin biosynthesis and transport-dependent auxin distribution. Plant Cell 19:2197-2212.

Sabatini, S., R. Heidstra, M. Wildwater and B. Scheres. 2003. SCARECROW is involved in positioning the stem cell niche in the *Arabidopsis* root meristem. Genes & Development 17:354-358.

Sarkar, A.K., M. Luijten, S. Miyashima, M. Lenhard, T. Hashimoto, K. Nakajima, B. Scheres, R. Heidstra and T. Laux. 2007. Conserved factors regulate signalling in *Arabidopsis thaliana* shoot and root stem cell organizers. Nature 446:811-814.

Scheres, B., H. van den Toorn and R. Heidstra. 2004. Root genomics: towards digital *in situ* hybridization. Genome Biology 5:227.

Shishkova, S., M.L. Las Peñas, S. Napsucialy-Mendivil, M. Matvienko, A. Kozik, J. Montiel, A. Patiño and J.G. Dubrovsky. 2013. Determinate primary root growth as an adaptation to aridity in Cactaceae: towards an understanding of the evolution and genetic control of the trait. Annals of Botany 112:239-252.

Singh, S., S. Yadav, A. Singh, M. Mahima, A. Singh, V. Gautam and A.K. Sarkar. 2020. Auxin signaling modulates *LATERAL ROOT PRIMORDIUM1* (*LRP1*) expression during lateral root development in *Arabidopsis*. The Plant Journal 101:87-100.

Slovak, R., T. Ogura, S.B. Satbhai, D. Ristova and W. Busch. 2016. Genetic control of root growth: from genes to networks. Annals of Botany 117:9-24.

Sun, L.R., Y.B. Wang, S.B. He and F.S. Hao. 2018. Mechanisms for abscisic acid inhibition of primary root growth. Plant Signaling & Behavior 13:e1500069.

Svolacchia, N., E. Salvi and S. Sabatini. 2020. Arabidopsis primary root growth: let it grow, can't hold it back anymore! Current Opinion in Plant Biology 57:133-141.

Tsakaldimi, M., T. Tsitsoni, P. Ganatsas and T. Zagas. 2009. A comparison of root architecture and shoot morphology between naturally regenerated and container-grown seedlings of *Quercus ilex*. Plant and soil 324:103-113.

Ubeda-Tomás, S., F. Federici, I. Casimiro, G.T.S. Beemster, R. Bhalerao, R. Swarup, P. Doerner, J. Haseloff and M.J. Bennett. 2009. Gibberellin signaling in the endodermis controls *Arabidopsis* root meristem size. Current Biology 19:1194-1199.

Uemura, Y., S. Kimura, T. Ohta, T. Suzuki, K. Mase, H. Kato, S. Sakaoka, Y. Komine, K. Hotta, M. Shimizu, A. Morikami and H. Tsukagoshi. 2022. A very long chain fatty acid responsive transcription factor, MYB93, regulates lateral root development in *Arabidopsis*. bioRxiv:2022.05.24.493307.

Weijers, D., A. Schlereth, J.S. Ehrismann, G. Schwank, M. Kientz and G. Jürgens. 2006. Auxin triggers transient local signaling for cell specification in *Arabidopsis* embryogenesis. Developmental Cell 10:265-270.

Wendrich, J.R., B.K. Möller, S. Li, S. Saiga, R. Sozzani, P.N. Benfey, B. De Rybel and D. Weijers. 2017. Framework for gradual progression of cell ontogeny in the *Arabidopsis* root meristem. Proceedings of the National Academy of Sciences 114:E8922-E8929.

Xuan, W., L.R. Band, R.P. Kumpf, D. Van Damme, B. Parizot, G. De Rop, D. Opdenacker, B.K. Moller, N. Skorzinski, M.F. Njo, B. De Rybel, D. Audenaert, M.K. Nowack, S. Vanneste and T. Beeckman. 2016. Cyclic programmed cell death stimulates hormone signaling and root development in *Arabidopsis*. Science 351:384-387.

Zadworny, M., A.M. Jagodziński, P. Łakomy, J. Mucha, J. Oleksyn, J. Rodríguez-Calcerrada and K. Ufnalski. 2019. Regeneration origin affects radial growth patterns preceding oak decline and death - insights from tree-ring δC-13 and δO-18. Agricultural and Forest Meteorology 278:12.

Zadworny, M., A.M. Jagodziński, P. Łakomy, K. Ufnalski and J. Oleksyn. 2014. The silent shareholder in deterioration of oak growth: common planting practices affect the long-term response of oaks to periodic drought. Forest Ecology and Management 318:133-141.

Zadworny, M., J. Mucha, A.M. Jagodziński, P. Kościelniak, P. Łakomy, M. Modrzejewski, K. Ufnalski, R. Żytkowiak, L.H. Comas and J. Rodríguez-Calcerrada. 2021. Seedling regeneration techniques affect root systems and the response of *Quercus robur* seedlings to water shortages. Forest Ecology and Management 479:11.

Zhang, Y., N. Mitsuda, T. Yoshizumi, Y. Horii, Y. Oshima, M. Ohme-Takagi, M. Matsui and T. Kakimoto. 2021. Two types of bHLH transcription factor determine the competence of the pericycle for lateral root initiation. Nature Plants 7:633-643.

Zolman, B.K., A. Yoder and B. Bartel. 2000. Genetic analysis of indole-3-butyric acid responses in *Arabidopsis thaliana* reveals four mutant classes. Genetics 156:1323-37.

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Formation and Development of Taproots in Deciduous Tree Species

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Trees are generally long-lived and are therefore exposed to numerous episodes of external stimuli and adverse environmental conditions. In certain trees e.g., oaks, taproots evolved to increase the tree's ability to acquire water from deeper soil layers. Despite the significant role of taproots, little is known about the growth regulation through internal factors (genes, phytohormones, and micro-RNAs), regulating taproot formation and growth, or the effect of external factors, e.g., drought. The interaction of internal and external stimuli, involving complex signaling pathways, regulates taproot growth during tip formation and the regulation of cell division in the root apical meristem (RAM). Assuming that the RAM is the primary regulatory center responsible for taproot growth, factors affecting the RAM function provide fundamental information on the mechanisms affecting taproot development.

Keywords: root architecture, trees, genes, transcription factors, hormones, miRNA, drought

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INTRODUCTION

Roots, functionally and structurally diverse, form an integrated system allowing for water and nutrient acquisition (Freschet et al., 2021a). Many aspects of root foraging are determined by differences in root types. The exploitation of soil water is primarily carried out by the smallest and most ephemeral roots, i.e., absorptive roots (McCormack et al., 2015, 2017). The development of taproots, allows for the production of absorptive roots in deep soil layers (Bleby et al., 2010; Mackay et al., 2020). Given the essential role of a plant's root system, understanding the relationship between the root structure and function, should include an assessment of the relationship between taproot development and absorptive root formation. Together they play an important role in regulating water potential in plants and may also have significant consequences for the hormonal interactions and signaling described in the review hereafter.

Despite the important functions of taproots in many woody plants, significant questions remain on how internal and external factors control the growth and development of taproots. Genes, hormones, and microRNAs regulate every stage of root development (Petricka et al., 2012). However, it is unclear, if these regulating components interact with each other to control individual cell division, growth, and differentiation, and taproot development as a whole. Taproot development is determined at the embryonic stage, through the directed regulation of cell division and expansion, which is also influenced by external changes, e.g., soil moisture. Knowledge about signaling of internal and external factors is fundamental in understanding mechanisms responsible for taproot growth (Lynch et al., 2012). While the identification of key regulators of root growth is essential, it is also crucial to understand how these regulators interact. Major factors often achieve their function through an integrated effect on other, categorized as "composite factors" (Mitsis et al., 2020). On one hand, composite factors comprise different genes responsible for different

individual, lower-level components (like the transcriptional, post-transcriptional, translational, and post-translational components), while on the other hand integrated growth involves "underlying factors" that vary in a coordinated manner as determined by pleiotropic or highly linked genes and/or tight hormonal control (Mitsis et al., 2020).

Our present objective is to determine individual and composite factors that affect and regulate taproot development and growth, and the influence of environmental stimuli on these factors. Such knowledge could contribute to the development of seedlings cultivation strategies, which further enabling taproot restoration in container-grown trees, e.g., oaks, in which taproots are typically rendered non-functional by air pruning. For example, long-term taproot pruning reduces the access of planted oaks to water during drought periods (Zadworny et al., 2014, 2019, 2021). First, we review, general information on taproot morphogenesis and function, especially with respect to tree response to drought, second we revisit changes in hormone-regulated root development, third we investigate genetic factors influencing root formation in deciduous plants.

CHARACTERIZATION OF THE TAPROOT SYSTEM

Commonly, the classification of roots is based on the position of emergence, and the recognition that most of the functional traits of root systems as a whole are directly related to this location (Zobel and Waisel, 2010; Zobel, 2011; Freschet et al., 2021b). Primary roots in tree seedlings, known also as a taproots, develop from the central embryonic root – the radicle, forming the central axis of a root system (Zobel and Waisel, 2010; Wang et al., 2014; Freschet et al., 2021b). The initial formation of taproots are important, allowing the root system to reach rapidly water at deeper soil depths, a factor that can be extremely important for trees exposed to periods of drought (Barbeta and Peñuelas, 2017; Zadworny et al., 2019; Mackay et al., 2020). However, taproots undergo dynamic process governing root system development and architecture, including the formation of lateral and absorptive roots (Clowes, 2000). The requirements for water and nutrients in plants change over time and therefore root systems must dynamically adapt to those changing needs when the rest of the plant grows bigger (Di Iorio et al., 2005). Thus, it is important to determine where, and how, changes of the environment are sensed and transduced into root development.

Taproot Morphogenesis

A comprehensive understanding of the root growth potential arises from the apical configuration of a primary root – a synonym of taproot root (Baluška et al., 2010; Freschet et al., 2021b). The ability of taproots to penetrate compact soil layers is due to the larger size of the root apex and the rapid elongation behind the root cap (Clowes, 2000), as taproot meristematic cells have a physiological and mechanical advantage over meristematic cells, compared to other root types, e.g., lateral roots (Perilli et al., 2012). Indeed, the pattern of postembryonic root development can be projected through an analysis of the initial cells located in the root apical meristem (RAM) cells (**Figure 1**; Perilli et al., 2012; Sozzani and Iyer-Pascuzzi, 2014). Ablation of the RAM in water-limited conditions results the formation of a highly branched, shallow root system (Dubrovsky and Gómez-Lomelí, 2003; Shishkova et al., 2013; Drisch and Stahl, 2015), indicating the essential role of a taproot in root system architecture (Dolan et al., 1993; Chapman et al., 2002; Sabatini et al., 2003) for water acquisition from deeper soil layers (Robbins and Dinneny, 2018; Gupta et al., 2020).

There are three unanswered questions remaining in the regard to the taproot root meristems: (1) how does organization and cellular signaling enable a taproot to grow and penetrate deep soil layers, (2) what internal factors enable taproots to grow rapidly and penetrate deep soil layers, and (3) how does soil water limitation induce the vertical growth of taproots. Aside from the unanswered questions above, how much does the genetic control the cell division explain the continued maintenance of root growth and apical dominance of taproot meristems (Perilli et al., 2012; Sozzani and Iyer-Pascuzzi, 2014). Current findings indicate that differences in inter-tissue signaling and the relationship between tissue-types are mostly responsible for matching meristem growth and root topology patterning (Peters and Tomos, 1996). Meristem enlargement, through increased cell division, and the transition of the cells into the expansion zone, occurs not only in response to internal stimuli during plant ontogenic development, but also in direct response to water supply (Benková and Hejatko, 2009; Mira et al., 2017). It seems likely, however, that cell division predominates cell differentiation in taproot meristems over the long-term to prevent the cessation of root growth until roots reach deep soil layers (Shishkova et al., 2008).

Taproot Function in Deciduous Trees

Insufficient water availability and associated reduced water uptake by absorptive roots are the main factors contributing to global forest decline (Allen et al., 2015; Choat et al., 2018; Zadworny et al., 2021). Countering drought stress can be achieved by enhancing water acquisition and/or reducing water consumption, while increased root proliferation and taproot elongation increases water uptake from deeper soil layers (Arend et al., 2011; Tuberosa, 2012; Brunner et al., 2015). Mackay et al. (2020) reported that water acquisition in shallow soil layers declines as drought severity increases. Therefore, long taproots can improve water uptake, and help to compensate for increased water usage (Mucha et al., 2018; Skiadaresis et al., 2019), e.g., in oaks that produce a dominant taproot (Osonubi and Davies, 1981; Löf and Welander, 2004; Bréda et al., 2006; Mucha et al., 2018). Deep-rooted plants access water from deep soil layers and transport it to shallow, drier roots, increasing a plants' ability to survive due to hydraulic redistribution process (Domec et al., 2004; Smart et al., 2005; David et al., 2013). Nevertheless, such watering is rather uncommon as shallow, fine roots are abandoned and die during the dry season in some drought-adapted tree species and grow back when water is available (Montagnoli et al., 2019). This raises the question, whether water limitation contrarily accelerates taproots growth into deeper soils in response to drought.

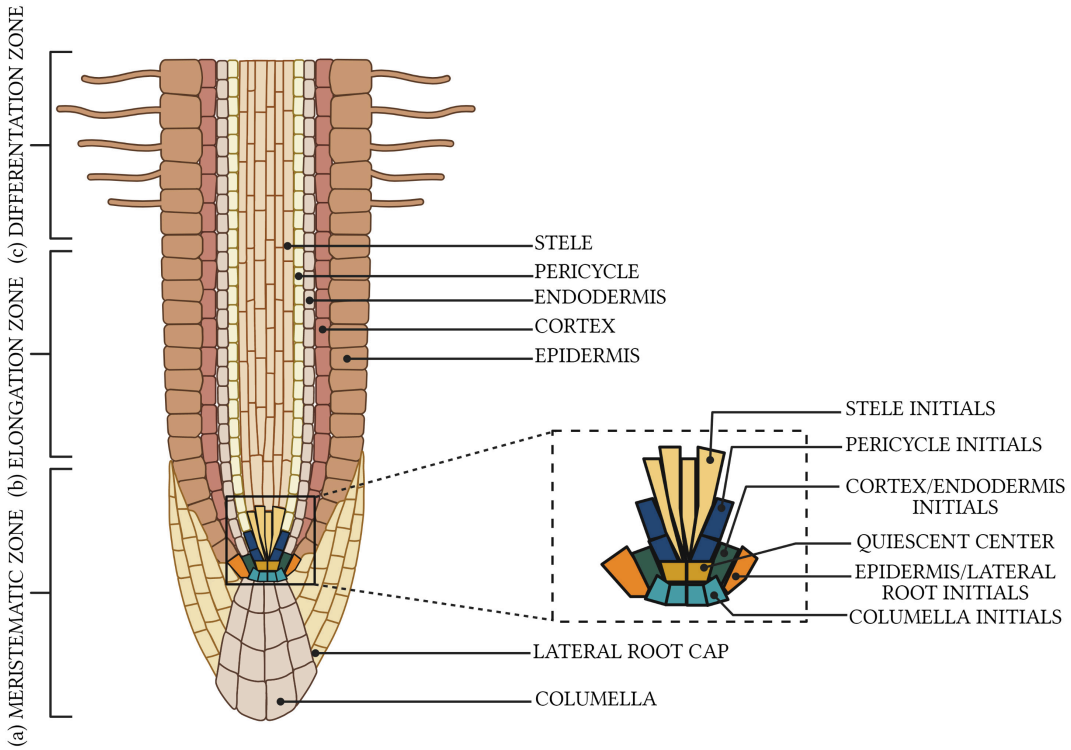

FIGURE 1 | Organization of plant root meristem. There are three distinct developmental zones: **(a)** meristematic with visible the quiescent center and initial cells in a stem cell niche, **(b)** elongation, and **(c)** differentiation. Created with BioRender.com.

Hormonal induced accumulation of osmoprotectant metabolites enabling root elongation during drought, confirms that this may be the case (Fàbregas et al., 2018). Therefore, a rigorous quantification of the components and molecular mechanisms regulating taproot growth in trees is required, especially among deciduous angiosperms, such as oak and chestnut, as deep taproots may determine resilience to drought. The first step in developing a mechanistic understanding of taproot growth would be to determine the regulatory effect of different phytohormones on cell division in the taproots RAM.

EFFECT OF PHYTOHORMONES ON ROOT GROWTH

Root growth is also regulated *via* signal transduction pathways, including complex, environmental-sensing networks. The signaling pathways regulate plant root elongation, radial growth, branching, and overall architecture (e.g., root growth and development), and concomitantly water and nutrient uptake (Jung and McCouch, 2013; Ristova et al., 2018). Importantly, individual phytohormones do not regulate root growth and development independently, but rather function in an interactive manner (**Figure 2**; Xuan et al., 2016). Increased knowledge about these interactions may help to clarify the underlying mechanism regulating the pattern of taproot growth (Zhang et al., 2017). Hormones incidence and composition can contribute to improvements of taproot growth, and could contribute to its regeneration, when damaged as a consequence of root pruning during nursery cultivation. Thus, it is important to improve our understanding of specific hormones and their influence on the development and growth of taproots.

Auxin

Auxin contributes to the positioning and formation of meristematic cells during organogenesis (Jiang and Feldman, 2010), as well as the retainment of mitotic activity in meristems (Beemster and Baskin, 2000; Galinha et al., 2007; Stepanova et al., 2008), as well as the fast elongation and differentiation of cells (Rahman et al., 2007; Benková and Hejatko, 2009; Ishida et al., 2010). Auxin accumulation in developing RAM cells has revealed that proteins, belonging to the PINFORMED family (PINs; PIN1, 2, 3, 4, 7), are necessary for the formation of an auxin gradient, and regulating the auxin distribution and acropetal transport to the root apex (Blilou et al., 2005). Auxin gradients that induce the expansion of cells and inhibit cell division in the extension zone (Blilou et al., 2005) by the expression of PLETHORA transcription factors (TFs) (Aida et al., 2004), may also regulate taproot elongation. The maintenance of root tip size and growth rate in transgenic Arabidopsis mutants in which PIN genes were silenced, provided evidence that the formation of an internal auxin gradient is indeed correlated with root development (Blilou et al., 2005; Vieten et al., 2005; Dello Ioio et al., 2007), affecting the formation, maintenance,

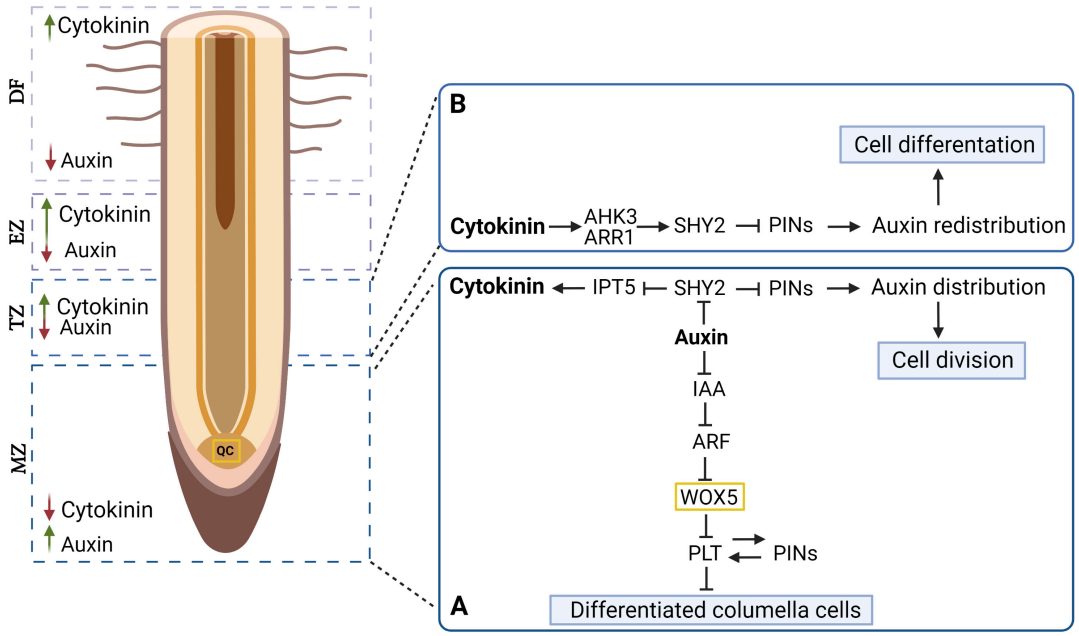

FIGURE 2 | Mechanism of auxin and cytokinin interaction in root meristem development. The distribution of auxin and cytokinin in different lots of the longitudinal section of the tree root is shown (green arrow – higher level, red arrow – lower level). **(A)** Auxin mediating WOX5 (expressed in the quiescent center cells (QC) and PLT (expressed in the stem cells surrounding the QC) expression plays a key role in the differentiation of columella cells. Also, in the apical root meristem, auxin by degrading SHY2 proteins promotes the expression of PINs, which control the auxin gradient and subsequently affect cell division. **(B)** In contrast to the auxin, cytokinin inhibits PIN expression by promoting SHY2 expression, leading to auxin redistribution and cell differentiation. PLT, PLETHORA; PINs, PINFORMED; WOX, WUSCHEL RELATED HOMEOBOX 5; ARF, AUXIN RESPONSE FACTOR; IAA, INDOLE-3-ACETIC ACID; SHY2, SHORT HYPOCOTYL 2; IPT5, ISOPENTENYL-TRANSFERASE 5; AHK3, ARABIDOPSIS HIS KINASE 3; ARR1, ARR TRANSCRIPTION FACTORS; MZ, meristematic zone; TZ, transition zone; EZ, elongation zone; DF, differentiation zone, QC, quiescent centre [based on Su et al. (2011)]. Created with BioRender.com.

and activity of RAM cells in deciduous trees (Palovaara and Hakman, 2009; Palovaara et al., 2010; Liu et al., 2014; Qi et al., 2020). PINs can significantly impact the rate of root growth and the size of the root tip (Vieten et al., 2005), possibly determining the pattern of taproot elongation in trees. Studies investigating the role of PINs in poplar (*Populus*), spruce (*Picea abies*), and pear *(Pyrus*), have reported a broader and more unique role for these proteins in auxin-controlled root development in trees (Palovaara et al., 2010; Liu et al., 2014; Qi et al., 2020). Some auxin-regulated developmental processes that are unique to woody plants (Liu et al., 2014), may directly affect the root apex expansion (also in taproots) toward wetter areas of the soil (van den Berg et al., 2016). Exploring the auxin regulatory network underlying root development will provide valuable information on the hormonal regulation of the formation and functioning of RAMs and the factors governing meristem size in plants with prominent taproots.

Cytokinins

Cytokinins, as well as auxin, are required for the establishment and maintenance of RAM, through the enhanced of mitotic activity of quiescent center cells (QC; Zhang et al., 2013). In contrast to auxin, however, cytokinins control cell differentiation and inhibit root elongation. Studies on cytokinin biosynthesis mutants have shown that cytokinins can regulate the size of RAM. Application of exogenous cytokinins caused a decrease in meristem size, by affecting the rate of meristematic cell differentiation (Dello Ioio et al., 2007). In fact, a reduction in endogenous cytokinin levels in mutants (with a cytokinin level deficiency) results in faster growth of the primary root (Werner et al., 2001). Therefore, repression of cytokinin activity may enhance drought resistance in trees, enabling deeper soil exploitation by taproot elongation (Werner et al., 2001; Calvo-Polanco et al., 2019). Nevertheless, it is essential to determine if cytokinins function alone or interactively with other hormones do contribute to drought tolerance in plants.

Ethylene

Ethylene, generating uneven transverse cell divisions in the QC of a RAM, plays a major role in inhibiting cell proliferation and root growth (Woeste et al., 1999; Schaller and Kieber, 2002; Růžička et al., 2007; Qin et al., 2019). An ethylene dependent pathway involved in inhibiting root elongation was identified in *ETHYLENE OVERPRODUCER* (*eto1*) mutants that exhibit enhanced ethylene biosynthesis, relative to wild-type plants, which produce long primary roots (Woeste et al., 1999). Higher root elongation in ethylene resistant *ETHYLENE RESISTANT 1* (*etr1*), *ETHYLENE INSENSITIVE2* (*ein2*), and *ETHYLENE INSENSITIVE3* (*ein3*) mutants also provided evidence that ethylene inhibits root growth (Růžička et al., 2007). The central function of ethylene in relation to root growth allows roots to restrict elongation when needed and extend their growth into

deeper soil layers when conditions initiate growth restoration (Negi et al., 2010; Pandey et al., 2021). A lack of alterations in the size of root meristems in these ethylene mutants is consistent with the potential ability of certain taproots to first hold back and then restart growth under specific environmental conditions (Street et al., 2016). The ability to regulate cell elongation through ethylene, cytokinin, and auxin cross-talk may represent an efficient mechanism for directing the position of roots and may also be involved in plant response to drought conditions.

Other Hormones

Gibberellins (GA), abscisic acid (ABA), and brassinosteroids (BR) are classes of hormones that can affect root development. Gibberellins act mainly on endodermal cells in root tissues, inducing an expansion of endodermal cells in the root elongation zone, which consequently limits the elongation rate of other root tissues (Ubeda-Tomás et al., 2008). The effect of ABA on root development has been shown to be concentration-dependent: low concentrations of ABA stimulate root elongation while higher concentration deters root formation (Harris, 2015; Rowe et al., 2016; Sun et al., 2020). Low concentrations of ABA enhance the activity of meristematic cells (stem cells) and alter auxin transport and signaling, while the suppressive effect of high concentrations of ABA on root growth are related to its inhibition of cell division in RAMs, as well as cells in the elongation zone (Sun et al., 2020).

Although auxin and ABA affect different aspects of root growth, high levels of ABA reduce auxin levels, which results in root growth inhibition due to the induction of PLT TFs (Yang et al., 2014; Promchuea et al., 2017). Indeed, when the level of drought is too severe, elevated levels of ABA inhibit root growth, which is why ABA is referred to as the stress hormone (Nakashima and Yamaguchi-Shinozaki, 2013). Interestingly, transgenic poplar lines with ectopic expression of *abi1* (*abscisic acid insensitive1*) exhibit an ABA insensitive phenotype, allowing plants exposed to a short-term water shortage an induction of primary root elongation (Sharp et al., 2004). The signaling pathway involving ABA interactions with ethylene, inhibits further primary root growth by increasing ethylene biosynthesis (Sharp et al., 2000; Qin et al., 2019). This suggests that the sensing of low ABA concentrations during episodes of water limitation could promote taproot growth. BR also promote root growth especially during drought periods. The BR biosynthesis maxima in the elongation zone is accomplished by the accumulation of osmoprotectant metabolites, resulting in the elongation of lateral roots and enhancing water uptake (Bao et al., 2004; Fàbregas et al., 2018; Vukašinović et al., 2021). Although examining of a specific hormone has made it possible to understand the mechanism of single hormone biosynthesis, perception, and signaling, the regulation of root development is largely dependent on the interaction of different hormone pathways.

Hormonal Cross-Talk

Dynamic root growth is a result of the interaction between hormones affecting biosynthesis, transport, inactivation, perception, signaling pathways and regulating development, maintenance, and RAM function. An increase in auxin levels contributes to lower cytokinins levels. In addition, an increase in the level of cytokinin inhibits the synthesis of auxin (Eklof et al., 1997; Nordstrom et al., 2004; Di Mambro et al., 2017). Cytokinins may also affect, polar auxin transport and the formation of a local auxin gradient during lateral root formation as well as the expression of genes involved in auxin transport (Laplaze et al., 2007; Kuderova et al., 2008). Similarly, root growth is inhibited by the balance between auxin and ethylene. In response to ethylene, auxin accumulates in RAM cells and inhibits cell elongation and cell differentiation, consequently regulating how different components of the root system develop (Casson and Lindsey, 2003). The regulatory role of this balance was demonstrated through the use of mutants in which the biosynthesis, transport, and perception of auxin was affected (Růžička et al., 2007; Stepanova et al., 2007). The inhibition of *PLETHORA (PLT)* expression by *AUXIN RESPONSE FACTOR (ARF),* which negatively regulates *WUSCHEL RELATED HOMEOBOX 5 (WOX5)* transcripts – the driver of stem cell formation – leads to distal stem cell differentiation in RAM (**Figure 2**; Su et al., 2011). Thus, the molecular interaction between auxin, cytokinins and other hormones controlling meristem development may be applied to the explanation of taproot growth. The question is which combinations regulate root elongation in a similar manner, or if the result varies in taproot vs. lateral root growth. Therefore, to understand the control of taproot growth, there is a need to explore the molecular and genetic mechanisms that regulates root development, through expression and functional analyses.

GENETIC FACTORS INVOLVED IN ROOT DEVELOPMENT

Root development, as well as the hormonal regulation, are controlled by specific genes or groups of genes categorized as composite factors (Sarkar et al., 2007; Mitsis et al., 2020). Composite factor are induced when roots begin to grow, penetrating the soil, and determine both the growth of individual roots, as well as the overall architecture of the entire root system (Wachsman et al., 2015). Therefore, targeting the activation or suppression of gene expression is a key aspect of the genetic regulation of roots (Atkinson and Halfon, 2014). The genes encoding key TFs, hormone precursors and regulatory proteins collectively affect the functioning of the taproot. Moreover, they may act differently depending on the species. Elucidating the molecular mechanisms by which specific genes control the development of taproot's RAM throughout a perennial lifetime, will provide valuable knowledge on every stage of root growth and aspect of root function (Slovak et al., 2016).

Transcription Factors Involved in Root Development

The establishment of RAM is determined by many factors, including hormone levels, intercellular signaling, and receptors that interact with specific TFs activated in response to internal and external signals (Drisch and Stahl, 2015). Indeed, TFs in plants regulate the transcription of specific genes (**Table 1**), as

TABLE 1 | The key genetic factors involved in root development.

Name	Abbr.	Family	Encodes	Functions	References
MONOPTEROS	MP	ARF	Transcription factor	root meristem establishment, pattern formation	Berleth and Jurgens, 1993
BODENLOS	BDL	AUX/IAA	Aux/IAA protein (IAA12)	root meristem establishment	Hamann et al., 2002
TARGET OF MONOPTEROS	TMO	bHLH	AP2 type transcription factor	root meristem establishment	Schlereth et al., 2010
WUSCHEL-RELATED HOMEOBOX5	WOX5	ATHB	Transcription factor	the columella stem cell identity	Sarkar et al., 2007
WUSCHEL-RELATED HOMEOBOX11	WOX11	ATHB	Transcription factor	meristem initiation, meristem maintenance and lateral root initiation	Hu and Xu, 2016
SCARECROW	SCR	GRAS	Transcription factor	maintaining the QC identity	Scheres et al., 1995
SHORTROOT	SHR	GRAS	Transcription factor	maintaining the QC identity	DiLaurenzio et al., 1996
PLETHORA	PLT	AP2/ERF	Transcription factor	maintaining the QC identity	Aida et al., 2004
ALTERED PHLOEM DEVELOPMENT	APL	MYB	MYB coiled-coil-type transcription factor	phloem identity	Bonke et al., 2003
III HOMEODOMAIN-LEUCINE ZIPPER	HD-ZIP III	HOMEODOMAIN-LEUCINE ZIPPER	Transcription factor	xylem tissues development	Carlsbecker et al., 2010

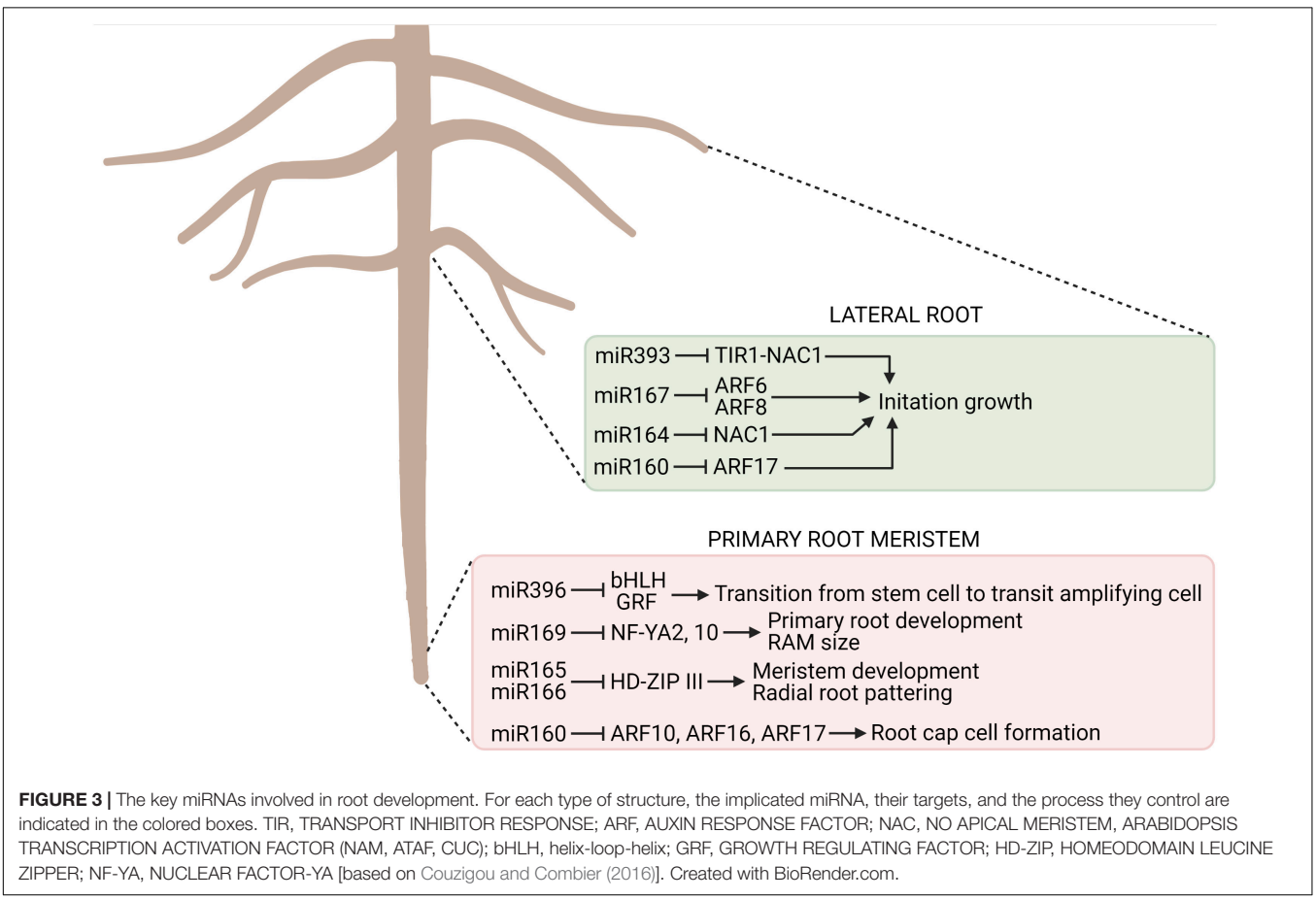

FIGURE 3 | The key miRNAs involved in root development. For each type of structure, the implicated miRNA, their targets, and the process they control are indicated in the colored boxes. TIR, TRANSPORT INHIBITOR RESPONSE; ARF, AUXIN RESPONSE FACTOR; NAC, NO APICAL MERISTEM, ARABIDOPSIS TRANSCRIPTION ACTIVATION FACTOR (NAM, ATAF, CUC); bHLH, helix-loop-helix; GRF, GROWTH REGULATING FACTOR; HD-ZIP, HOMEODOMAIN LEUCINE ZIPPER; NF-YA, NUCLEAR FACTOR-YA [based on Couzigou and Combier (2016)]. Created with BioRender.com.

well as the responses to external and internal stimuli (Mitsis et al., 2020). For example, MP-dependent TFs regulate auxin transport into cells and play a role in the generation of RAMs, and may control other auxin response genes (Weijers et al., 2006). TFs also play an important role in establishing the QC in embryonic roots and maintaining the QC in mature roots

(Forzani et al., 2014). Establishing the QC is accomplished by determining the cell organization required for columella cell identity, and maintaining the undifferentiated status of the QC, which allows the QC to activate root growth to explore new soil spaces, increase root biomass, and enhance water absorption (Motte et al., 2019). Maintaining an area of undifferentiated stem cells in the RAM provides a source of cells needed to produce new roots throughout the lifetime of plants (Sarkar et al., 2007; Drisch and Stahl, 2015).

The ability of taproots to grow deeper may be associated with the maintenance of the columella stem cells in the distal meristem of root tip and regulation of auxin distribution as in lateral roots (Savina et al., 2020). Engaged in the above processes, WOX TFs (WOX 5/7 and WOX11) play a key role in inducing and sustaining primary roots growth, as well as generations of lateral roots, from a primary root (Hu and Xu, 2016; Baesso et al., 2018). For example, in poplar trees, the WOX TFs, WOX 4/5/11 and 12, regulate the development of new lateral roots originating from taproot (Baesso et al., 2020). Tree root systems can extend to considerable widths and depths, thus WOX increasing the ability of a tree to adapt to adverse abiotic and biotic conditions, such as drought or mechanical damage, to which they are exposed continuously. Indeed specific TFs associations have profound effects on plant resistance to drought e.g., the formation of root non-hair cells (Schiefelbein et al., 2014), the differentiation of root epidermal trichoblasts into root hair cells (Clowes, 2000; Ishida et al., 2008), as well as determining the root hair morphology (Bruex et al., 2012). The importance of TFs and the genes they regulate in taproot response under water deficit conditions, however, has not been investigated, and the specific role of TFs in enhancing drought resistance by promoting taproot growth, driven by ABA-regulated auxin transport, remains to be determined (Carlsbecker et al., 2010; Müller et al., 2016).

Role of Micro RNA in the Regulation of Root Growth and Development

MicroRNAs (miRNA), along with other growth regulators, form networks controlling gene expressions at a developmental and tissue level, being key for the regulation of root development (Jones-Rhoades et al., 2006; Couzigou and Combier, 2016), also in deciduous and coniferous trees such as *Pinus tabuliformis*, *Larix olgensis*, and *Poncirus trifoliate* (Song et al., 2009; Zhang et al., 2013, 2019; Niu et al., 2015). Particularly, miRNAs play an important role in root morphogenesis, contributing to the regulation of meristem establishment and maintenance, vasculature differentiation, lateral and adventitious root formation, and the regulation of symbiotic interactions (Couzigou and Combier, 2016). The multitude of functional roles played by miRNAs, both in model, annual, and perennial plant species, confirms their integral role in root development (**Figure 3**). Little is known, however, about the role of miRNAs in the development of taproots in trees. Thus, understanding the role of these RNAs and their interactions with other molecular components, such as genes, TFs, and plant hormones, will assist in the elucidation of the complex pathways that control taproot development and function during foraging for water and nutrients, as overexpression of specific miRNAs increase tolerance to many abiotic stresses by changing root architecture and its adaptive responses to stressful conditions (Zhang, 2015). MicroRNAs and their interactions with other molecular components effectively regulate RAM size and the differentiation of vascular tissue in root, thus, represent a mechanism that could be applied to taproots growth (Khan et al., 2011). A comparison of PHV (PHAVOLUTA) and PHB (PHABULOSA) gene expression in long and short growing roots in miR165/166-resistant mutants indicated that these mutants have a reduced RAM size and a lower level of vascular differentiation than wild-type plants. Hence, miR165/166 regulates root development by controlling RAM size, organ polarity, differentiation of vascular elements, and shape of the root system architecture (Carlsbecker et al., 2010; Couzigou and Combier, 2016).

Hormone signal transduction pathways are also affected by miRNAs. For example, miR390 mediates the *miR390–TAS3–AUXIN RESPONSE FACTOR 2/ARF3/ARF4* regulatory pathway, which is involved in auxin signaling, and miR393 represses auxin signaling mediated by its downstream F-box auxin receptor targets, namely, TRANSPORT INHIBITOR RESPONSE 1 (TIR1), as well as AUXIN SIGNALING F-BOX PROTEINS 2 (AFB2) and AFB3 (Yoon et al., 2010; Meng et al., 2011). A negative regulation of ARF TFs by miR160 contributes to the maintenance of adequate auxin homeostasis and further lateral root formation (Wang et al., 2005; Meng et al., 2011), for example. Mutants resistant to miR160, however, exhibited reduced root branching (Couzigou and Combier, 2016). Another miRNA, miR390, expressed in cells located in the region of lateral root initiation downregulates *ARF2*, *ARF3*, and *ARF4*, resulting in the inhibition of lateral root growth (Marin et al., 2010). Furthermore, miR164 acts on the NAC1 TF acts downstream of TIR1 transmitting auxin signals, promotes lateral root emergence and controls lateral root elongation (miR167 acts on *ARF7* and *ARF19*) (Xie et al., 2004; Guo et al., 2005). The modulation of both the primary root and the lateral roots by miRNAs reveals the broad spectrum of action of these growth regulators in root development and function (Gutierrez et al., 2009).

The regulatory function of miRNAs may also affect drought resistance in roots enabling through the expression of drought-responsive genes. In this regard, some miRNAs, such as ABA responsive genes, auxin signaling genes, genes encoding osmolytes, and antioxidant defense-related genes, can promote an accumulation of target mRNAs associated with enhanced stress tolerance (Ding et al., 2013). Notably, many of the miRNAs that respond to drought stress have only been identified in trees such as poplar and larch, and have not been detected in annual plants, such as Arabidopsis or rice. This may indicate a specific role for miRNA in woody plant species with long-term root systems, whether they are broadleaf or coniferous tress. Accordingly, the ability of miRNAs to regulate gene expression in response to drought, may facilitate tree growth and survival under adverse conditions on a long-term basis (Osakabe et al., 2014). The regulation of both, lateral and primary roots growth (Gutierrez et al., 2009), increases the ability to explore of deeper soil layers. Nevertheless, our understanding of the mechanisms and genes controlling taproot growth, development,

differentiation, function, and architecture, especially in response to adverse conditions, such as drought, is far from complete.

CONCLUSION

The interaction of external and internal factors influences the growth and physiology of the taproot. The tips of a taproot consist of meristematic cells in the RAM. Assuming that the RAM is the main regulatory center responsible for taproot growth and cessation, a better understanding of the factors regulating the function of the RAM in taproots will provide fundamental information on the mechanisms that influence the development of the taproot. It is therefore necessary to understand the interactions between internal factors in the regulation of taproot growth and development, and to determine how these factors are related to external factors, e.g., drought. This raises the question of whether water restriction regulates and/or induces root growth in plants not only to maintain but also to accelerate root growth into deeper soil layers in response to water stress, and what internal factors are responsible for taproot development under drought stress. However, it is difficult to determine which one of these factors has a dominant effect on root growth, because the paths of dependence between external and internal factors are closely related and dependent on each other.

In the long term, understanding the regulatory role of genes, hormones, and microRNAs will help to improve the quality of nursery seedling production, including the development of effective management strategies that will allow the restoration of taproots in container cuttings. Unfortunately, the selection of specific strategies to improve the elongation of taproots in tree seedlings is challenging due to the variability of the reactions of roots to multiple internal and external influences. Under changing climate, manifested by high temperatures and reduced precipitation, the formation of a deep root system is crucial for the survival of seedlings, saplings and maturing tree.

AUTHOR CONTRIBUTIONS

PK drafted the manuscript. MZ sought funding for it. All authors contributed to the article review and editing, and approved the submitted version.

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REFERENCES

Aida, M., Beis, D., Heidstra, R., Willemsen, V., Blilou, I., Galinha, C., et al. (2004). The PLETHORA genes mediate patterning of the *Arabidopsis* root stem cell niche. *Cell* 119, 109–120. doi: 10.1016/j.cell.2004.09.018

Allen, C. D., Breshears, D. D., and McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6:55. doi: 10.1890/es15-00203.1

Arend, M., Kuster, T., Gunthardt-Goerg, M. S., and Dobbertin, M. (2011). Provenance-specific growth responses to drought and air warming in three European oak species (*Quercus robur*, *Q.petraea* and *Q.pubescens*). *Tree Physiol.* 31, 287–297. doi: 10.1093/treephys/tpr004

Atkinson, T. J., and Halfon, M. S. (2014). Regulation of gene expression in the genomic context. *Comp. Struct. Biotechnol. J.* 9:e201401001. doi: 10.5936/csbj.201401001

Baesso, B., Chiatante, D., Terzaghi, M., Zenga, D., Nieminen, K., Mahonen, A. P., et al. (2018). Transcription factors PRE3 and WOX11 are involved in the formation of new lateral roots from secondary growth taproot in *A.thaliana*. *Plant Biol.* 20, 426–432. doi: 10.1111/plb.12711

Baesso, B., Terzaghi, M., Chiatante, D., Scippa, G. S., and Montagnoli, A. (2020). WOX genes expression during the formation of new lateral roots from secondary structures in *Populus nigra* (L.) taproot. *Sci. Rep.* 10:6. doi: 10.1038/s41598-020-75150-1

Baluška, F., Mancuso, S., Volkmann, D., and Barlow, P. W. (2010). Root apex transition zone: a signalling-response nexus in the root. *Trends Plant Sci.* 15, 402–408. doi: 10.1016/j.tplants.2010.04.007

Bao, F., Shen, J. J., Brady, S. R., Muday, G. K., Asami, T., and Yang, Z. B. (2004). Brassinosteroids interact with auxin to promote lateral root development in *Arabidopsis*. *Plant Physiol.* 134, 1624–1631. doi: 10.1104/pp.103.036897

Barbeta, A., and Peñuelas, J. (2017). Relative contribution of groundwater to plant transpiration estimated with stable isotopes. *Sci. Rep.* 7:10. doi: 10.1038/s41598-017-09643-x

Beemster, G. T. S., and Baskin, T. I. (2000). Mediates effects of cytokinin, but not of auxin, on cell division and expansion in the root of *Arabidopsis*. *Plant Physiol.* 124, 1718–1727. doi: 10.1104/pp.124.4.1718

Benková, E., and Hejatko, J. (2009). Hormone interactions at the root apical meristem. *Plant Mol. Biol.* 69, 383–396. doi: 10.1007/s11103-008-9393-6

Berleth, T., and Jurgens, G. (1993). The role of the monopteros gene in organizing the basal body region of the *Arabidopsis* embryo. *Development* 118, 575–587.

Bleby, T. M., McElrone, A. J., and Jackson, R. B. (2010). Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. *Plant Cell Environ.* 33, 2132–2148. doi: 10.1111/j.1365-3040.2010.02212.x

Blilou, I., Xu, J., Wildwater, M., Willemsen, V., Paponov, I., Friml, J., et al. (2005). The PIN auxin efflux facilitator network controls growth and patterning in *Arabidopsis* roots. *Nature* 433, 39–44. doi: 10.1038/nature03184

Bonke, M., Thitamadee, S., Mähönen, A. P., Hauser, M. T., and Helariutta, Y. (2003). APL regulates vascular tissue identity in *Arabidopsis*. *Nature* 426, 181–186. doi: 10.1038/nature02100

Bréda, N., Huc, R., Granier, A., and Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann. For. Sci.* 63, 625–644. doi: 10.1051/forest:2006042

Bruex, A., Kainkaryam, R. M., Wieckowski, Y., Kang, Y. H., Bernhardt, C., Xia, Y., et al. (2012). A gene regulatory network for root epidermis cell differentiation in *Arabidopsis*. *PLoS Genet.* 8:20. doi: 10.1371/journal.pgen.1002446

Brunner, I., Herzog, C., Dawes, M. A., Arend, M., and Sperisen, C. (2015). How tree roots respond to drought. *Front. Plant Sci.* 6:16. doi: 10.3389/fpls.2015.00547

Calvo-Polanco, M., Ruiz-Lozano, J. M., Azcón, R., Molina, S., Beuzon, C. R., García, J. L., et al. (2019). Phenotypic and molecular traits determine the tolerance

of olive trees to drought stress. *Plant Physiol. Biochem.* 139, 521–527. doi: 10.1016/j.plaphy.2019.04.017

Carlsbecker, A., Lee, J. Y., Roberts, C. J., Dettmer, J., Lehesranta, S., Zhou, J., et al. (2010). Cell signalling by microRNA165/6 directs gene dose-dependent root cell fate. *Nature* 465, 316–321. doi: 10.1038/nature08977

Casson, S. A., and Lindsey, K. (2003). Genes and signalling in root development. *New Phytol.* 158, 11–38. doi: 10.1046/j.1469-8137.2003.00705.x

Chapman, K., Groot, E. P., Nichol, S. A., and Rost, T. L. (2002). Primary root growth and the pattern of root apical meristem organization are coupled. *J. Plant Growth Regul.* 21, 287–295. doi: 10.1007/s00344-002-0036-x

Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R., and Medlyn, B. E. (2018). Triggers of tree mortality under drought. *Nature* 558, 531–539. doi: 10.1038/s41586-018-0240-x

Clowes, F. A. L. (2000). Pattern in root meristem development in angiosperms. *New Phytol.* 146, 83–94. doi: 10.1046/j.1469-8137.2000.00614.x

Couzigou, J. M., and Combier, J. P. (2016). Plant microRNAs: key regulators of root architecture and biotic interactions. *New Phytol.* 212, 22–35. doi: 10.1111/nph.14058

David, T. S., Pinto, C. A., Nadezhdina, N., Kurz-Besson, C., Henriques, M. O., Quilhó, T., et al. (2013). Root functioning, tree water use and hydraulic redistribution in *Quercus suber* trees: a modeling approach based on root sap flow. *For. Ecol. Manage.* 307, 136–146. doi: 10.1016/j.foreco.2013.07.012

Dello Ioio, R., Linhares, F. S., Scacchi, E., Casamitjana-Martinez, E., Heidstra, R., Costantino, P., et al. (2007). Cytokinins determine *Arabidopsis* root-meristem size by controlling cell differentiation. *Curr. Biol.* 17, 678–682. doi: 10.1016/j.cub.2007.02.047

Di Iorio, A., Lasserre, B., Scippa, G. S., and Chiatante, D. (2005). Root system architecture of *Quercus pubescens* trees growing on different sloping conditions. *Ann. Bot.* 95, 351–361. doi: 10.1093/aob/mci033

Di Mambro, R., De Ruvo, M., Pacifici, E., Salvi, E., Sozzani, R., Benfey, P. N., et al. (2017). Auxin minimum triggers the developmental switch from cell division to cell differentiation in the *Arabidopsis* root. *Proc. Natl. Acad. Sci. U.S.A.* 114, E7641–E7649. doi: 10.1073/pnas.1705833114

DiLaurenzio, L., Wysocka-Diller, J., Malamy, J. E., Pysh, L., Helariutta, Y., Freshour, G., et al. (1996). The *SCARECROW* gene regulates an asymmetric cell division that is essential for generating the radial organization of the *Arabidopsis* root. *Cell* 86, 423–433. doi: 10.1016/s0092-8674(00)80115-4

Ding, Y. F., Tao, Y. L., and Zhu, C. (2013). Emerging roles of microRNAs in the mediation of drought stress response in plants. *J. Exp. Bot.* 64, 3077–3086. doi: 10.1093/jxb/ert164

Dolan, L., Janmaat, K., Willemsen, V., Linstead, P., Poethig, S., Roberts, K., et al. (1993). Cellular-organization of the *Arabidopsis thaliana* root. *Development* 119, 71–84.

Domec, J. C., Warren, J. M., Meinzer, F. C., Brooks, J. R., and Coulombe, R. (2004). Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution. *Oecologia* 141, 7–16. doi: 10.1007/s00442-004-1621-4

Drisch, R. C., and Stahl, Y. (2015). Function and regulation of transcription factors involved in root apical meristem and stem cell maintenance. *Front. Plant Sci.* 6:8. doi: 10.3389/fpls.2015.00505

Dubrovsky, J. G., and Gómez-Lomelí, L. F. (2003). Water deficit accelerates determinate developmental program of the primary root and does not affect lateral root initiation in a Sonoran Desert cactus (*Pachycereus pringlei*. Cactaceae). *Am. J. Bot.* 90, 823–831. doi: 10.3732/ajb.90.6.823

Eklof, S., Astot, C., Blackwell, J., Moritz, T., Olsson, O., and Sandberg, G. (1997). Auxin-cytokinin interactions in wild-type and transgenic tobacco. *Plant Cell Physiol.* 38, 225–235. doi: 10.1093/oxfordjournals.pcp.a029157

Fàbregas, N., Lozano-Elena, F., Blasco-Escámez, D., Tohge, T., Martínez-Andújar, C., Albacete, A., et al. (2018). Overexpression of the vascular brassinosteroid receptor BRL3 confers drought resistance without penalizing plant growth. *Nat. Commun.* 9:13. doi: 10.1038/s41467-018-06861-3

Forzani, C., Aichinger, E., Sornay, E., Willemsen, V., Laux, T., Dewitte, W., et al. (2014). WOX5 suppresses CYCLIN D activity to establish quiescence at the center of the root stem cell niche. *Curr. Biol.* 24, 1939–1944. doi: 10.1016/j.cub.2014.07.019

Freschet, G. T., Roumet, C., Comas, L. H., Weemstra, M., Bengough, A. G., Rewald, B., et al. (2021a). Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytol.* 232, 1123–1158. doi: 10.1111/nph.17072

Freschet, G. T., Pagès, L., Iversen, C. M., Comas, L. H., Rewald, B., Roumet, C., et al. (2021b). A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. *New Phytol.* 232, 973–1122. doi: 10.1111/nph.17572

Galinha, C., Hofhuis, H., Luijten, M., Willemsen, V., Blilou, I., Heidstra, R., et al. (2007). PLETHORA proteins as dose-dependent master regulators of *Arabidopsis* root development. *Nature* 449, 1053–1057. doi: 10.1038/nature06206

Guo, H. S., Xie, Q., Fei, J. F., and Chua, N. H. (2005). MicroRNA directs mRNA cleavage of the transcription factor NAC1 to downregulate auxin signals for *Arabidopsis* lateral root development. *Plant Cell* 17, 1376–1386. doi: 10.1105/tpc.105.030841

Gupta, A., Rico-Medina, A., and Caño-Delgado, A. I. (2020). The physiology of plant responses to drought. *Science* 368, 266–269. doi: 10.1126/science.aaz7614

Gutierrez, L., Bussell, J. D., Păcurar, D. I., Schwambach, J., Păcurar, M., and Bellini, C. (2009). Phenotypic plasticity of adventitious rooting in *Arabidopsis* is controlled by complex regulation of AUXIN RESPONSE FACTOR transcripts and microrna abundance. *Plant Cell* 21, 3119–3132. doi: 10.1105/tpc.108.064758

Hamann, T., Benková, E., Bäurle, I., Kientz, M., and Jürgens, G. (2002). The *Arabidopsis BODENLOS* gene encodes an auxin response protein inhibiting MONOPTEROS-mediated embryo patterning. *Genes Dev.* 16, 1610–1615. doi: 10.1101/gad.229402

Harris, J. M. (2015). Abscisic acid: hidden architect of root system structure. *Plants-Basel* 4, 548–572. doi: 10.3390/plants4030548

Hu, X., and Xu, L. (2016). Transcription factors WOX11/12 directly activate *WOX5/7* to promote root primordia initiation and organogenesis. *Plant Physiol.* 172, 2363–2373. doi: 10.1104/pp.16.01067

Ishida, T., Adachi, S., Yoshimura, M., Shimizu, K., Umeda, M., and Sugimoto, K. (2010). Auxin modulates the transition from the mitotic cycle to the endocycle in *Arabidopsis*. *Development* 137, 63–71. doi: 10.1242/dev.035840

Ishida, T., Kurata, T., Okada, K., and Wada, T. (2008). A genetic regulatory network in the development of trichomes and root hairs. *Annu. Rev. Plant Biol.* 59, 365–386. doi: 10.1146/annurev.arplant.59.032607.092949

Jiang, K., and Feldman, L. J. (2010). Positioning of the auxin maximum affects the character of cells occupying the root stem cell niche. *Plant Signal. Behav.* 5, 202–204. doi: 10.4161/psb.5.2.11188

Jones-Rhoades, M. W., Bartel, D. P., and Bartel, B. (2006). MicroRNAs and their regulatory roles in plants. *Annu. Rev. Plant Biol.* 57, 19–53. doi: 10.1146/annurev.arplant.57.032905.105218

Jung, J. K. H., and McCouch, S. (2013). Getting to the roots of it: genetic and hormonal control of root architecture. *Front. Plant Sci.* 4:32. doi: 10.3389/fpls.2013.00186

Khan, G. A., Declerck, M., Sorin, C., Hartmann, C., Crespi, M., and Lelandais-Brière, C. (2011). MicroRNAs as regulators of root development and architecture. *Plant Mol. Biol.* 77, 47–58. doi: 10.1007/s11103-011-9793-x

Kuderova, A., Urbankova, I., Valkova, M., Malbeck, J., Brzobohaty, B., Nemethova, D., et al. (2008). Effects of conditional IPT-Dependent cytokinin overproduction on root architecture of *Arabidopsis* seedlings. *Plant Cell Physiol.* 49, 570–582. doi: 10.1093/pcp/pcn029

Laplaze, L., Benková, E., Casimiro, I., Maes, L., Vanneste, S., Swarup, R., et al. (2007). Cytokinins act directly on lateral root founder cells to inhibit root initiation. *Plant Cell* 19, 3889–3900. doi: 10.1105/tpc.107.055863

Liu, J. C., Sheng, L. H., Xu, Y. Q., Li, J. Q., Yang, Z. N., Huang, H., et al. (2014). WOX11 and *12* are involved in the first-step cell fate transition during de novo root organogenesis in *Arabidopsis*. *Plant Cell* 26, 1081–1093. doi: 10.1105/tpc.114.122887

Löf, M., and Welander, N. T. (2004). Influence of herbaceous competitors on early growth in direct seeded *Fagus sylvatica* L. and *Quercus robur* L. *Ann. For. Sci.* 61, 781–788. doi: 10.1051/forest:2004075

Lynch, J., Marschner, P., and Rengel, Z. (2012). *Effect of Internal and External Factors on Root Growth and Development*. San Diego, CA: Elsevier Academic Press Inc.

Mackay, D. S., Savoy, P. R., Grossiord, C., Tai, X. N., Pleban, J. R., Wang, D. R., et al. (2020). Conifers depend on established roots during drought: results from

a coupled model of carbon allocation and hydraulics. *New Phytol.* 225, 679–692. doi: 10.1111/nph.16043

Marin, E., Jouannet, V., Herz, A., Lokerse, A. S., Weijers, D., Vaucheret, H., et al. (2010). miR390, *Arabidopsis* TAS3 tasiRNAs, and their AUXIN RESPONSE factor targets define an autoregulatory network quantitatively regulating lateral root growth. *Plant Cell* 22, 1104–1117. doi: 10.1105/tpc.109.072553

McCormack, M. L., Dickie, I. A., Eissenstat, D. M., Fahey, T. J., Fernandez, C. W., Guo, D. L., et al. (2015). Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytol.* 207, 505–518. doi: 10.1111/nph.13363

McCormack, M. L., Guo, D. L., Iversen, C. M., Chen, W. L., Eissenstat, D. M., Fernandez, C. W., et al. (2017). Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes. *New Phytol.* 215, 27–37. doi: 10.1111/nph.14459

Meng, Y., Shao, C., Wang, H., and Chen, M. (2011). The regulatory activities of plant microRNAs: a more dynamic perspective. *Plant Physiol.* 157, 1583–1595. doi: 10.1104/pp.111.187088

Mira, M. M., Huang, S. L., Kapoor, K., Hammond, C., Hill, R. D., and Stasolla, C. (2017). Expression of *Arabidopsis* class 1 phytoglobin (AtPgb1) delays death and degradation of the root apical meristem during severe PEG-induced water deficit. *J. Exp. Bot.* 68, 5653–5668. doi: 10.1093/jxb/erx371

Mitsis, T., Efthimiadou, A., Bacopoulou, F., Vlachakis, D., Chrousos, G. P., and Eliopoulos, E. (2020). Transcription factors and evolution: an integral part of gene expression (Review). *World Acad. Sci. J.* 2, 3–8. doi: 10.3892/wasj.2020.32

Montagnoli, A., Dumroese, R. K., Terzaghi, M., Onelli, E., Scippa, G. S., and Chiatante, D. (2019). Seasonality of fine root dynamics and activity of root and shoot vascular cambium in a *Quercus ilex L.* forest (Italy). *For. Ecol. Manage.* 431, 26–34. doi: 10.1016/j.foreco.2018.06.044

Motte, H., Vanneste, S., and Beeckman, T. (2019). "Molecular and environmental regulation of root development," in *Annual Review of Plant Biology*, Vol. 70, ed. S. S. Merchant (Palo Alto, CA: Annual Reviews), 465–488.

Mucha, J., Jagodziński, A. M., Bułaj, B., Łakomy, P., Talaśka, A. M., Oleksyn, J., et al. (2018). Functional response of *Quercus robur* L. to taproot pruning: a 5-year case study. *Ann. For. Sci.* 75:12. doi: 10.1007/s13595-018-0708-8

Müller, C. J., Valdés, A. E., Wang, G., Ramachandran, P., Beste, L., Uddenberg, D., et al. (2016). PHABULOSA mediates an auxin signaling loop to regulate vascular patterning in *Arabidopsis*. *Plant Physiol.* 170, 956–970. doi: 10.1104/pp.15.01204

Nakashima, K., and Yamaguchi-Shinozaki, K. (2013). ABA signaling in stress-response and seed development. *Plant Cell Rep.* 32, 959–970. doi: 10.1007/s00299-013-1418-1

Negi, S., Sukumar, P., Liu, X., Cohen, J. D., and Muday, G. K. (2010). Genetic dissection of the role of ethylene in regulating auxin-dependent lateral and adventitious root formation in tomato. *Plant J.* 61, 3–15. doi: 10.1111/j.1365-313X.2009.04027.x

Niu, S. H., Liu, C., Yuan, H. W., Li, P., and Li, W. (2015). Identification and expression profiles of sRNAs and their biogenesis and action-related genes in male and female cones of *Pinus tabuliformis*. *BMC Genomics* 16:13. doi: 10.1186/s12864-015-1885-6

Nordstrom, A., Tarkowski, P., Tarkowska, D., Norbaek, R., Astot, C., Dolezal, K., et al. (2004). Auxin regulation of cytokinin biosynthesis in *Arabidopsis thaliana*: a factor of potential importance for auxin-cytokinin-regulated development. *Proc. Natl. Acad. Sci. U.S.A.* 101, 8039–8044. doi: 10.1073/pnas.0402504101

Osakabe, Y., Osakabe, K., Shinozaki, K., and Tran, L. S. (2014). Response of plants to water stress. *Front. Plant Sci.* 5:86. doi: 10.3389/fpls.2014.00086

Osonubi, O., and Davies, W. J. (1981). Root-growth and water relations of oak and birch seedlings. *Oecologia* 51, 343–350. doi: 10.1007/bf00540904

Palovaara, J., and Hakman, I. (2009). *WOX2* and polar auxin transport during spruce embryo pattern formation. *Plant Signal. Behav.* 4, 153–155. doi: 10.4161/psb.4.2.7684

Palovaara, J., Hallberg, H., Stasolla, C., and Hakman, I. (2010). Comparative expression pattern analysis of *WUSCHEL-related homeobox 2* (*WOX2*) and *WOX8/9* in developing seeds and somatic embryos of the gymnosperm *Picea abies*. *New Phytol.* 188, 122–135. doi: 10.1111/j.1469-8137.2010.03336.x

Pandey, B. K., Huang, G. Q., Bhosale, R., Hartman, S., Sturrock, C. J., Jose, L., et al. (2021). Plant roots sense soil compaction through restricted ethylene diffusion. *Science* 371, 276–280. doi: 10.1126/science.abf3013

Perilli, S., Di Mambro, R., and Sabatini, S. (2012). Growth and development of the root apical meristem. *Curr. Opin. Plant Biol.* 15, 17–23. doi: 10.1016/j.pbi.2011.10.006

Peters, W. S., and Tomos, A. D. (1996). The history of tissue tension. *Ann. Bot.* 77, 657–665. doi: 10.1006/anbo.1996.0082

Petricka, J. J., Winter, C. M., and Benfey, P. N. (2012). Control of *Arabidopsis* root development. *Annu. Rev. Plant Biol.* 63, 563–590. doi: 10.1146/annurev-arplant-042811-105501

Promchuea, S., Zhu, Y. J., Chen, Z. Z., Zhang, J., and Gong, Z. Z. (2017). ARF2 coordinates with PLETHORAs and PINs to orchestrate ABA-mediated root meristem activity in *Arabidopsis*. *J. Integr. Plant Biol.* 59, 30–43. doi: 10.1111/jipb.12506

Qi, L. Y., Chen, L., Wang, C. S., Zhang, S. L., Yang, Y. J., Liu, J. L., et al. (2020). Characterization of the auxin efflux transporter PIN proteins in pear. *Plants-Basel* 9:17. doi: 10.3390/plants9030349

Qin, H., He, L. N., and Huang, R. F. (2019). The coordination of ethylene and other hormones in primary root development. *Front. Plant Sci.* 10:8. doi: 10.3389/fpls.2019.00874

Rahman, A., Bannigan, A., Sulaman, W., Pechter, P., Blancaflor, E. B., and Baskin, T. I. (2007). Auxin, actin and growth of the *Arabidopsis thaliana* primary root. *Plant J.* 50, 514–528. doi: 10.1111/j.1365-313X.2007.03068.x

Ristova, D., Giovannetti, M., Metesch, K., and Busch, W. (2018). Natural genetic variation shapes root system responses to phytohormones in *Arabidopsis*. *Plant J.* 96, 468–481. doi: 10.1111/tpj.14034

Robbins, N. E., and Dinneny, J. R. (2018). Growth is required for perception of water availability to pattern root branches in plants. *Proc. Natl. Acad. Sci. U.S.A.* 115, E822–E831. doi: 10.1073/pnas.1710709115

Rowe, J. H., Topping, J. F., Liu, J. L., and Lindsey, K. (2016). Abscisic acid regulates root growth under osmotic stress conditions via an interacting hormonal network with cytokinin, ethylene and auxin. *New Phytol.* 211, 225–239. doi: 10.1111/nph.13882

Růžička, K., Ljung, K., Vanneste, S., Podhorská, R., Beeckman, T., Friml, J., et al. (2007). Ethylene regulates root growth through effects on auxin biosynthesis and transport-dependent auxin distribution. *Plant Cell* 19, 2197–2212. doi: 10.1105/tpc.107.052126

Sabatini, S., Heidstra, R., Wildwater, M., and Scheres, B. (2003). SCARECROW is involved in positioning the stem cell niche in the *Arabidopsis* root meristem. *Genes Dev.* 17, 354–358. doi: 10.1101/gad.252503

Sarkar, A. K., Luijten, M., Miyashima, S., Lenhard, M., Hashimoto, T., Nakajima, K., et al. (2007). Conserved factors regulate signalling in *Arabidopsis thaliana* shoot and root stem cell organizers. *Nature* 446, 811–814. doi: 10.1038/nature05703

Savina, M. S., Pasternak, T., Omelyanchuk, N. A., Novikova, D. D., Palme, K., Mironova, V. V., et al. (2020). Cell dynamics in WOX5-overexpressing root tips: the impact of local auxin biosynthesis. *Front. Plant Sci.* 11:13. doi: 10.3389/fpls.2020.560169

Schaller, G. E., and Kieber, J. J. (2002). Ethylene. *Arabidopsis Book* 1:e0071. doi: 10.1199/tab.0071

Scheres, B., Dilaurenzio, L., Willemsen, V., Hauser, M. T., Janmaat, K., Weisbeek, P., et al. (1995). Mutations affecting the radial organization of the *Arabidopsis* root display specific defects throughout the embryonic axis. *Development* 121, 53–62.

Schiefelbein, J., Huang, L., and Zheng, X. H. (2014). Regulation of epidermal cell fate in *Arabidopsis* roots: the importance of multiple feedback loops. *Front. Plant Sci.* 5:4. doi: 10.3389/fpls.2014.00047

Schlereth, A., Möller, B., Liu, W. L., Kientz, M., Flipse, J., Rademacher, E. H., et al. (2010). MONOPTEROS controls embryonic root initiation by regulating a mobile transcription factor. *Nature* 464, 913–U128. doi: 10.1038/nature08836

Sharp, R. E., LeNoble, M. E., Else, M. A., Thorne, E. T., and Gherardi, F. (2000). Endogenous ABA maintains shoot growth in tomato independently of effects on plant water balance: evidence for an interaction with ethylene. *J. Exp. Bot.* 51, 1575–1584. doi: 10.1093/jexbot/51.350.1575

Sharp, R. E., Poroyko, V., Hejlek, L. G., Spollen, W. G., Springer, G. K., Bohnert, H. J., et al. (2004). Root growth maintenance during water deficits: physiology to functional genomics. *J. Exp. Bot.* 55, 2343–2351. doi: 10.1093/jxb/erh276

Shishkova, S., Las Peñas, M. L., Napsucialy-Mendivil, S., Matvienko, M., Kozik, A., Montiel, J., et al. (2013). Determinate primary root growth as an adaptation to aridity in Cactaceae: towards an understanding of the evolution and genetic control of the trait. *Ann. Bot.* 112, 239–252. doi: 10.1093/aob/mct100

Shishkova, S., Rost, T. L., and Dubrovsky, J. G. (2008). Determinate root growth and meristem maintenance in angiosperms. *Ann. Bot.* 101, 319–340. doi: 10.1093/aob/mcm251

Skiadaresis, G., Schwarz, J. A., and Bauhus, J. (2019). Groundwater extraction in floodplain forests reduces radial growth and increases summer drought sensitivity of pedunculate oak trees (*Quercus robur* L.). *Front. For. Glob. Change* 2:16. doi: 10.3389/ffgc.2019.00005

Slovak, R., Ogura, T., Satbhai, S. B., Ristova, D., and Busch, W. (2016). Genetic control of root growth: from genes to networks. *Ann. Bot.* 117, 9–24. doi: 10.1093/aob/mcv160

Smart, D. R., Carlisle, E., Goebel, M., and Núñez, B. A. (2005). Transverse hydraulic redistribution by a grapevine. *Plant Cell Environ.* 28, 157–166. doi: 10.1111/j.1365-3040.2004.01254.x

Song, C. N., Fang, J. G., Li, X. Y., Liu, H., and Chao, C. T. (2009). Identification and characterization of 27 conserved microRNAs in citrus. *Planta* 230, 671–685. doi: 10.1007/s00425-009-0971-x

Sozzani, R., and Iyer-Pascuzzi, A. (2014). Postembryonic control of root meristem growth and development. *Curr. Opin. Plant Biol.* 17, 7–12. doi: 10.1016/j.pbi.2013.10.005

Stepanova, A. N., Robertson-Hoyt, J., Yun, J., Benavente, L. M., Xie, D. Y., DoleZal, K., et al. (2008). TAA1-mediated auxin biosynthesis is essential for hormone crosstalk and plant development. *Cell* 133, 177–191. doi: 10.1016/j.cell.2008.01.047

Stepanova, A. N., Yun, J., Likhacheva, A. V., and Alonso, J. M. (2007). Multilevel interactions between ethylene and auxin in *Arabidopsis* roots. *Plant Cell* 19, 2169–2185. doi: 10.1105/tpc.107.052068

Street, I. H., Mathews, D. E., Yamburkenko, M. V., Sorooshzadeh, A., John, R. T., Swarup, R., et al. (2016). Cytokinin acts through the auxin influx carrier AUX1 to regulate cell elongation in the root. *Development* 143, 3982–3993. doi: 10.1242/dev.132035

Su, Y. H., Liu, Y. B., and Zhang, X. S. (2011). Auxin-cytokinin interaction regulates meristem development. *Mol. Plant* 4, 616–625. doi: 10.1093/mp/ssr007

Sun, Y. F., Pri-Tal, O., Michaeli, D., and Mosquna, A. (2020). Evolution of abscisic acid signaling module and its perception. *Front. Plant Sci.* 11:9. doi: 10.3389/fpls.2020.00934

Tuberosa, R. (2012). Phenotyping for drought tolerance of crops in the genomics era. *Front. Physiol.* 3:26. doi: 10.3389/fphys.2012.00347

Ubeda-Tomás, S., Swarup, R., Coates, J., Swarup, K., Laplaze, L., Beemster, G. T. S., et al. (2008). Root growth in *Arabidopsis* requires gibberellin/DELLA signalling in the endodermis. *Nat. Cell Biol.* 10, 625–628. doi: 10.1038/ncb1726

van den Berg, T., Korver, R. A., Testerink, C., and ten Tusscher, K. (2016). Modeling halotropism: a key role for root tip architecture and reflux loop remodeling in redistributing auxin. *Development* 143, 3350–3362. doi: 10.1242/dev.135111

Vieten, A., Vanneste, S., Wisniewska, J., Benková, E., Benjamins, R., Beeckman, T., et al. (2005). Functional redundancy of PIN proteins is accompanied by auxindependent cross-regulation of PIN expression. *Development* 132, 4521–4531. doi: 10.1242/dev.02027

Vukašinović, N., Wang, Y. W., Vanhoutte, I., Fendrych, M., Guo, B. Y., Kvasnica, M., et al. (2021). Local brassinosteroid biosynthesis enables optimal root growth. *Nat. Plants* 7, 619–632. doi: 10.1038/s41477-021-00917-x

Wachsman, G., Sparks, E. E., and Benfey, P. N. (2015). Genes and networks regulating root anatomy and architecture. *New Phytol.* 208, 26–38. doi: 10.1111/nph.13469

Wang, J. W., Wang, L. J., Mao, Y. B., Cai, W. J., Xue, H. W., and Chen, X. Y. (2005). Control of root cap formation by microRNA-targeted auxin response factors in *Arabidopsis*. *Plant Cell* 17, 2204–2216. doi: 10.1105/tpc.105.033076

Wang, L. K., Chu, H. W., Li, Z. Y., Wang, J., Li, J. T., Qiao, Y., et al. (2014). Origin and development of the root cap in rice. *Plant Physiol.* 166, 603–U223. doi: 10.1104/pp.114.240929

Weijers, D., Schlereth, A., Ehrismann, J. S., Schwank, G., Kientz, M., and Jürgens, G. (2006). Auxin triggers transient local signaling for cell specification in *Arabidopsis* embryogenesis. *Dev. Cell* 10, 265–270. doi: 10.1016/j.devcel.2005.12.001

Werner, T., Motyka, V., Strnad, M., and Schmülling, T. (2001). Regulation of plant growth by cytokinin. *Proc. Natl. Acad. Sci. U.S.A.* 98, 10487–10492. doi: 10.1073/pnas.171304098

Woeste, K. E., Ye, C., and Kieber, J. J. (1999). Two *Arabidopsis* mutants that overproduce ethylene are affected in the posttranscriptional regulation of 1-aminocyclopropane-1-carboxylic acid synthase. *Plant Physiol.* 119, 521–530. doi: 10.1104/pp.119.2.521

Xie, Z. X., Johansen, L. K., Gustafson, A. M., Kasschau, K. D., Lellis, A. D., Zilberman, D., et al. (2004). Genetic and functional diversification of small RNA pathways in plants. *PLoS Biol.* 2:E104. doi: 10.1371/journal.pbio.0020104

Xuan, W., Band, L. R., Kumpf, R. P., Van Damme, D., Parizot, B., De Rop, G., et al. (2016). Cyclic programmed cell death stimulates hormone signaling and root development in *Arabidopsis*. *Science* 351, 384–387. doi: 10.1126/science.aad2776

Yang, L., Zhang, J., He, J. N., Qin, Y. Y., Hua, D. P., Duan, Y., et al. (2014). ABA-mediated ROS in mitochondria regulate root meristem activity by controlling *PLETHORA* expression in *Arabidopsis*. *PLoS Genet.* 10:18. doi: 10.1371/journal.pgen.1004791

Yoon, E. K., Yang, J. H., and Lee, W. S. (2010). Auxin and abscisic acid responses of auxin response factor 3 in *Arabidopsis* lateral root development. *J. Plant Biol.* 53, 150–154. doi: 10.1007/s12374-010-9100-4

Zadworny, M., Jagodziński, A. M., Łakomy, P., Mucha, J., Oleksyn, J., Rodríguez-Calcerrada, J., et al. (2019). Regeneration origin affects radial growth patterns preceding oak decline and death - insights from tree-ring δC-13 and δO-18. *Agricult. Forest Meteorol.* 278:12. doi: 10.1016/j.agrformet.2019.107685

Zadworny, M., Jagodziński, A. M., Łakomy, P., Ufnalski, K., and Oleksyn, J. (2014). The silent shareholder in deterioration of oak growth: common planting practices affect the long-term response of oaks to periodic drought. *For. Ecol. Manage.* 318, 133–141. doi: 10.1016/j.foreco.2014.01.017

Zadworny, M., Mucha, J., Jagodziński, A. M., Kościelniak, P., Łakomy, P., Modrzejewski, M., et al. (2021). Seedling regeneration techniques affect root systems and the response of Quercus robur seedlings to water shortages. *For. Ecol. Manage.* 479:11. doi: 10.1016/j.foreco.2020.118552

Zhang, B. (2015). MicroRNA: a new target for improving plant tolerance to abiotic stress. *J. Exp. Bot.* 66, 1749–1761. doi: 10.1093/jxb/erv013

Zhang, S. F., Yan, S. S., Zhao, J. L., Xiong, H. H., An, P. Q., Wang, J. H., et al. (2019). Identification of miRNAs and their target genes in *Larix olgensis* and verified of differential expression miRNAs. *BMC Plant Biol.* 19:20. doi: 10.1186/s12870-019-1853-4

Zhang, W. J., Swarup, R., Bennett, M., Schaller, G. E., and Kieber, J. J. (2013). Cytokinin induces cell division in the quiescent center of the *Arabidopsis* root apical meristem. *Curr. Biol.* 23, 1979–1989. doi: 10.1016/j.cub.2013.08.008

Zhang, W. X., Fan, J. J., Tan, Q. Q., Zhao, M. M., Zhou, T., and Cao, F. L. (2017). The effects of exogenous hormones on rooting process and the activities of key enzymes of *Malus hupehensis* stem cuttings. *PLoS One* 12:13. doi: 10.1371/journal.pone.0172320

Zobel, R. W. (2011). A developmental genetic basis for defining root classes. *Crop Sci.* 51, 1410–1413. doi: 10.2135/cropsci2010.11.0652

Zobel, R. W., and Waisel, Y. (2010). A plant root system architectural taxonomy: a framework for root nomenclature. *Plant Biosyst.* 144, 507–512. doi: 10.1080/11263501003764483

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OakRootRNADB—a consolidated RNA-seq database for coding and noncoding RNA in roots of pedunculate oak (*Quercus robur*)

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Abstract

The degree to which roots elongate is determined by the expression of genes that regulate root growth in each developmental zone of a root. Most studies have, however, focused on the molecular factors that regulate primary root growth in annual plants. In contrast, the relationship between gene expression and a specific pattern of taproot development and growth in trees is poorly understood. However, the presence of a deeply located taproot, with branching lateral roots, can especially mitigate the effect of insufficient water availability in long-lived trees, such as pedunculated oak. In the present article, we integrated the ribonucleic acid (RNA) sequencing data on roots of oak trees into a single comprehensive database, named OakRootRNADB that contains information on both coding and noncoding RNAs. The sequences in the database also enclose information pertaining to transcription factors, transcriptional regulators and chromatin regulators, as well as a prediction of the cellular localization of a transcript. OakRootRNADB has a user-friendly interface and functional tools that increase access to genomic information. Integrated knowledge of molecular patterns of expression, specifically occurring within and between root zones and within root types, can elucidate the molecular mechanisms regulating taproot growth and enhanced root soil exploration.

Database URL: https://oakrootrnadb.idpan.poznan.pl/

Introduction

Several adaptations are required to optimize root architecture to efficiently acquire water from either deep or shallow soil layers. This is especially true for long-lived *Quercus robur* in order to overcome water deficit challenges (1). The ability to develop a root system that enables foraging for water from deep soil layers that have higher water content for much longer periods of time than shallow, subsurface layers of the soil, is crucial to the survival of some long-lived tree species (2–7). This adaptation is of particular importance given increasing frequency of insufficient precipitation and long-lasting, extending cycles of drought (5, 9). The development of long taproots that enhance water acquisition and supply it to above-ground organs requires endogenous mechanisms that regulate root growth toward deep soil layers with high water content (10, 11). Mechanisms directing root growth toward wet soil layers include (i) taproot apical zone molecular pathways driving the ability of root tips to grow deeper and (ii) a molecular network coordinating root tip growth in response to moisture deficit and growth in the elongation zone to optimize water uptake.

The ability of roots to grow deeper beginning at the early stages of tree growth is determined by molecular drivers that coordinate and mediate root growth through long-distance signaling (12). Some of these factors include genes that control plant growth at every stage of tree development, as well as factors that control the transcription and translation of these genes, such as transcription factors (TFs) and noncoding ribonucleic acids (ncRNAs), in response to a variety of molecular and environmental signals (13, 14). Although ncRNAs are nonprotein coding molecules, they play a significant role in controlling root system architecture by regulating transcription, alternative splicing, microRNA (miRNA) activity, transcript stability and the translation of messenger RNA (15). Identifying root-related coding and ncRNAs and their function is crucial to elucidating regulatory mechanisms controlling deep taproot growth, as well as root system architecture overall, which not only determines root water absorption

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ability but also the pattern of root growth in response to root injury.

Taproots can be lost at early as well as at late developmental stages of a root system, as a result of biotic and abiotic stresses, as well as commonly used management procedures in container nurseries that injure taproots. Oaks deprived of taproots are more susceptible to water deficit, as they have a decreased ability to uptake water from deep soil layers (4, 5). The ability of containerized seedlings to foster the growth of fine roots to deeper soil layers and reconstitute taproot growth in a significant fraction of seedlings (5, 16, 17) suggests the capacity to restore taproot growth. Determining the factors that regulate taproot growth and enable regrowth of a taproot in container seedlings after they are planted in the field can provide a mechanistic understanding of the effect of nursery management practices on seedling growth and its potential impact on subsequently managed forest stands.

Despite the relatively good understanding of the processes regulating root growth in short-living annual plants, the same level of understanding of these processes in long-lived woody plants that have to face numerous episodes of drought during their lifespan and depend more heavily on deeply located water sources remains to be investigated or explored. Understanding the groups of genes and the factors regulating their expression used by oak trees to maintain taproot growth for many years requires the identification of root zone-specific gene expression that enables the maintenance and cessation of root growth when needed. The ability to access whole records of the global expression of coding sequence (CDS) and non-CDS expressed during root growth, rather than just bits of information, would help to identify and assess the role of signaling network–mediated taproot growth strategies, including the coordination that exists between root tip sensing and root elongation. This ability now exists due to the development of high-throughput sequencing technologies, such as next-generation sequencing, and the deposition of the acquired sequence data in publicly available databases, especially that a whole genome sequence for *Q. robur* is currently available on the Quercus Portal platform (https://quercusportal.pierroton.inra.fr/). This allows for more accurate transcript assembly and expression testing.

Existing databases for plant species typically contain information for only one type of RNA, coding or noncoding (12, 18). The QuercusMap database contains single tree genotypic and phenotypic data of offspring belonging to oak mapping pedigrees. The genotypic data comprise various markers (Amplified Fragment Length Polymorphism, Random Amplified Polymorphic DNA, Single - sequence repeats, Single Nucleotide Polymorphisms and Polymerase Chain Reaction - Restriction Fragment Length Polymorphism) traditionally used for mapping purposes (http://mapedigree.pierroton.inra.fr/qmap/). Another oak database CMAP contains genetic map data on oak pedigrees, and Quantitative Trait Loci positions for a variety of traits assessed in field tests (https://arachne.pierroton.inra.fr/cgi-bin/cmap), with limited specific information about genes or a group of genes regulating the traits. Another database expressed sequence tag (EST) contains files for three sets of unigenes constructed for the *Quercus* data related to oak pedigrees. This database also contains three versions (called Oakcontig). Version 1 (OCV1) (http://genotoul-contigbrowser.toulouse.inra.fr) contains a comprehensive collection of ESTs from oaks (19). The advanced version (OCV2) is a reference library that catalogs differential gene expression in *Q. robur* during controlled biotic interactions and is primarily used for quantitative transcriptomic profiling of oak roots in ectomycorrhizal symbiosis (20). OCV3 contains a *de novo* assembly of the oak transcriptome, focused on the molecular mechanisms involved in dormancy release in buds (21). The TreePop database contains passport, phenotypic and genotypic data of individual oaks within a single population, Instensive Study Plot or Instensive Study Sites (https://treepop.pierroton.inra.fr/). Unfortunately, there is a limited opportunity when using this database to determine the genes involved in the development of oak roots. Another database Oak provenance contains passport data and phenotypic assessments of *Quercus petraea* and *Q. robur* provenances and provenance tests established in Europe (https://oakprovenances.pierroton.inrae.fr/). Another available reference is the GD^2 database, which contains genetic and georeferenced passport data of different genetic units in natural populations (http://gd2.pierroton.inra.fr/). This is a georeferenced database, however, less convenient as a good gene identification tool. The SSR database containing deoxyribonucleic acid (DNA) sequences of microsatellite motifs and primer DNA sequences, as well as information on candidate genes and their single nucleotide polymorphisms, is very useful (http://ssrdatabase.pierroton.inra.fr/home). One of the most interesting databases is CorkOakDB released in 2018 by the GENOSUBER consortium that contains the first draft genome of *Quercus suber* and allows genome browsing and gene searches (22). The portal (https://corkoakdb.org/) provides the ability to search and explore curated genomic and transcriptomic data on *Q. suber* but only has limited use for obtaining information pertaining to primary root growth (23). Raw data deposited in publicly accessible databases often require specialized data processing software, as well as programming skills and computers with high processing power, which can significantly limit their utility. These limitations highlight the need to create databases containing data that are available to the user in a simple, direct and easy-to-understand manner. Therefore, we endeavored to create a database and user-friendly interface that provides the ability to conduct a detailed analysis of the available data, as well as a comprehensive examination of genes, transcripts, proteins and miRNAs both separately and in the context of an interrelated network.

The objective of the *Q. robur* oak root database (OakRootRNADB) was to integrate RNA sequencing (RNA-seq) data for genes, transcript RNA sequences encoding oak proteins, and long ncRNA (lncRNA) and miRNAs (based on pre-miRNAs). In addition to protein-encoding transcripts, OakRootRNADB contains information about known and new miRNAs, as well as lncRNAs. It provides a user-friendly interface that allows one to browse transcripts, genes and miRNAs involved in oak root growth. In addition, the identification of TFs, transcriptional regulators (TRs) and chromatin regulators (CRs), as well as the predicted cellular localization of transcripts, is also available. OakRootRNADB provides the opportunity to broaden our knowledge about the root system of trees and to assess the potential role of genes and non-CDSs in mechanisms that mediate growth and a variety of other processes during taproot and lateral root development. The portal for the database can be accessed at http://oakrootrnadb.idpan.poznan.pl.

Material and methods

Plant material and sample collection

Two-month-old seedlings of *Q. robur* were collected and used for RNA-seq. Plants were grown in a large, semi-closed, foil greenhouse located at the Arboretum of the Institute of Dendrology of the Polish Academy of Sciences in Kórnik, Poland. Roots were grown in a clear-walled rhizotron chamber (30 × 50 cm), filled with a growing medium of peat and perlite (proportions 5:1 volumetric proportion), deacidified with dolomite and enriched with 2.5 kg/m^3 slow-release fertilizer (Osmocote 15-9-12-2 N-P-K-Mg, with trace nutrients). The rhizotrons were constructed using two transparent plexiglass plates held 2–3 cm apart by thick-walled plastic tubing to provide adequate space for the growing roots. Waterlogging was prevented by providing drainage in the bottom of each rhizotron. The rhizotrons allowed us to record root growth measurements in the same seedlings over time without disturbing the root system. Additionally, one acorn was sown per container (180 mm high, 5 mm wide, 0.275 dm^3) in the same growing medium under similar growth conditions that were used for the acorns that were sown in the rhizotrons. The containerized seedlings were subjected to root growth inhibition by air pruning. In the spring of the following year, 1-year-old containerized seedlings were transplanted to a rhizotron (one per rhizotron), without cutting the roots to monitor factors involved in the regrowth of a taproot in container seedlings. These samples were designated as transplanted seedlings.

Seven- and eight-week-old seedlings growing in each system (rhizotron or container) were harvested in three replicate time points (early spring and summer in 2019). Each taproot was classified at its time of harvest based on its length: short (5–9 cm), medium (9.5–15 cm) and long (>15.5 cm), as well as on its morphology: normal or thick (taproots that were thicker than normal taproots and still actively growing), and vitality: active or dying (typically container taproots that had reached the bottom of the container). The same root classification approach was used for oak seedlings that had been initially grown in a container and were then transplanted to a rhizotron in 2020. In the case of transplanted seedlings, roots were harvested 8 weeks after transplantation.

The root system of harvested seedlings was gently washed with deionized, autoclaved water (ddH_2O) to remove adhering soil, and then the meristematic and elongation zones of taproots and lateral roots were separated and immediately frozen in liquid nitrogen and stored at −80°C until RNA extraction.

The samples were combined into two sets. The material in Dataset 1 (Table 1) was from the meristematic zone of all classes *Q. robur* taproots and lateral roots of seedlings grown in a container or a rhizotron system in 2019. The samples were labeled: 1K_kr_NN_kon_1 according to the formula, Harvest date → Type of root → Root length → Root vitality → Type of cultivation → Biological replicates as detailed in Table 1.

The material in Dataset 2 (Table 2) was from the meristematic and elongation zones of taproots and lateral roots of *Q. robur* growing in either a container or a rhizotron system as the acorns grown in 2019 (with the exception that 2-year-old acorns were sown, derived from the same lot of acorns that had been used in the previous year), and oak seedlings that had been initially grown in a container in 2019 and then transferred to a rhizotron in 2020. The samples were labeled: K_kr_NN_kon1 according to the formula, Type of root → Root length → Type of cultivation → Biological replicates as detailed in Table 2.

RNA isolation, library preparation and RNA-seq

Total RNA was extracted from 100 mg root tissue of each sample using Ribospin (GeneAll Biotechnology, Seoul, South Korea), with a DNAse treatment, according to the manufacturer's instructions. RNA quality was assessed on 1% agarose gels. The quality and quantity of RNA were further verified prior to library constructions using a NanoDrop 1000 spectrophotometer (Thermo Scientific, Wilmington, DE,

Table 1. Classification of samples in Dataset 1

Harvest date 1/2/3	Type of root K/KB	Root length kr/sr/dl	Root morphology/vitality NN/NT/TN/TT	Type of cultivation kon/rh
1—first harvest date: 7 weeks old plant (sown in early spring)	K—meristematic zone of the taproot	kr—short root (5–9 cm)	NN—normal roots	kon—growing in containers
2—second harvest date: 8 weeks old plant (sown in early spring)	KB—lateral root	sr—medium root (9.5–15 cm)	NT—dying root	rh—growing in rhizotron
3—third harvest date: 8 weeks old plant (sown in early summer)		dl—long root (>15.5 cm)	TN—thick root	
			TT—thick and dying root	

Table 2. Classification of samples in Dataset 2

Type of root K/KB/SW	Root length kr/sr/dl	Root morphology/vitality NN/NT/TN/TT	Type of cultivation kon/rh/krh
K—meristematic zone of the taproot	kr—short root (5–9 cm)	NN—normal condition roots	kon—growing in containers
SW—elongation zone of taproot	sr—medium root (9.5–15 cm)	NT—dying root	rh—growing in rhizotron
KB—lateral root	dl—long root (>15.5 cm)	TN—thick root	krh—growing in a container and then transplanted to a rhizotron
		TT—thick and dying root	

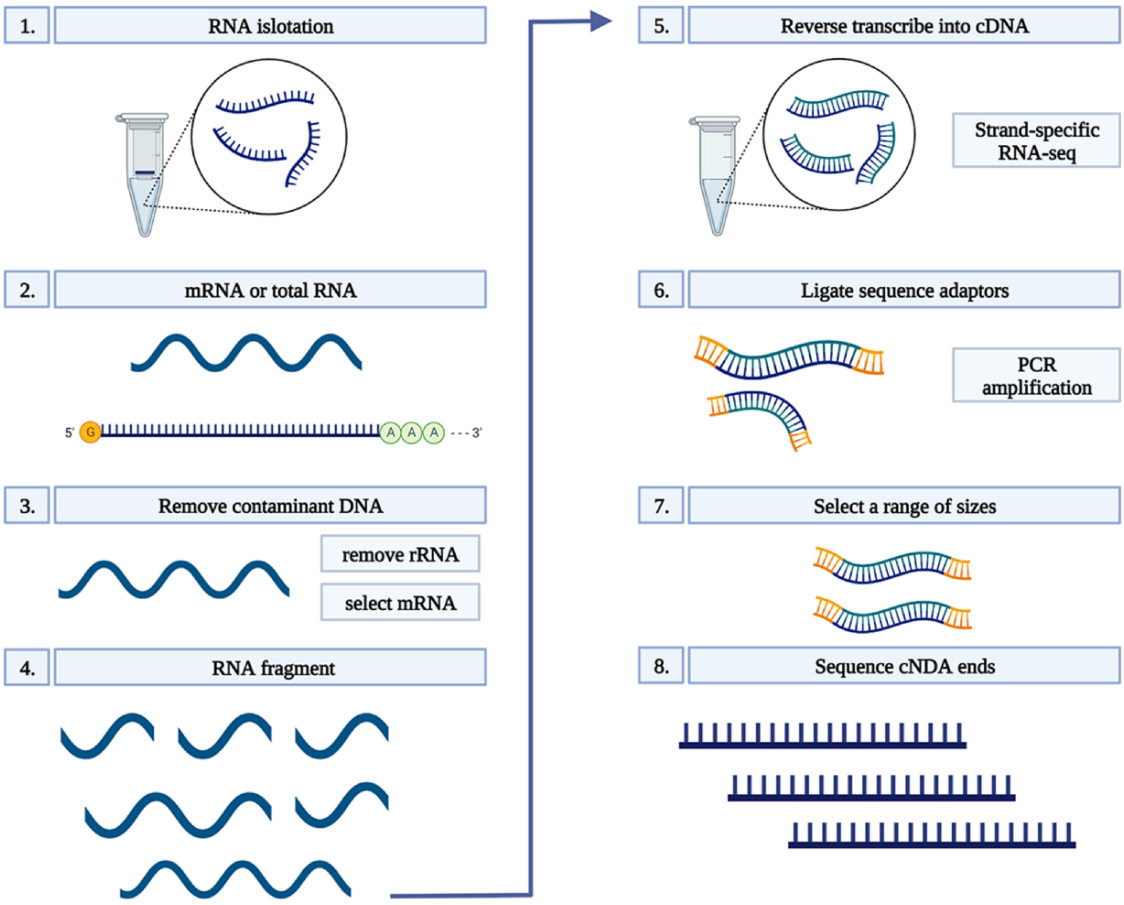

Figure 1. RNA-seq workflow. 1) Isolate the mRNA or total RNA from root tissue; 2) Quality and quantity control of mRNA or total RNA; 3) Eliminate DNA contamination from RNA samples using DNase; 4) Choose an appropriate kit for library preparation based on the type of RNA. For mRNA with poly-A tail, a mRNA purification kit was used to isolate mRNA with a poly-A tail; 5) Random fragment purified RNA for short read sequencing; 6) Reverse transcribe fragmented RNA into cDNA; 7) Ligate adapters onto both ends of the cDNA fragments. 8) PCR amplification of cDNA and selection of fragment sizes between 200-400 bp. Conduct paired-end sequencing of the cDNA libraries (Martin and Wang 2011).

USA), and an RNA integrity number (RIN) was determined using a 2100 Bioanalyzer (Agilent, Santa Clara, CA, USA) and a small RNA kit (Agilent Santa Clara, CA, USA). Only RNA samples with a RIN of $\geq$8.5 were used for complementary DNA (cDNA) conversion. Each cDNA library was constructed using a TruSeq Stranded mRNA LT Sample Prep Kit and sequenced on a NovaSeq platform (Illumina, San Diego, CA, USA) in the 150-bp PE mode. Sequencing was conducted by Macrogen (South Korea). All libraries were constructed using three biological replicates which resulted in a total number of 75 libraries in Dataset 1 and 90 in Dataset 2 (Figure 1) (24).

Quality control and preprocessing of raw sequence data

Quality reports were generated with FastQC v0.11.5. The reads were then subjected to quality filtering and adapter trimming using BBDUK 2 v38.41 with the following settings: qtrim = w, trimq = 20, maq = 10, k = 23, mink = 11, hdist = 1, tbo, tpe, minlength = 50, removeifeitherbad = t. This was followed by removal of reads that mapped to *A. thaliana* ribosomal RNAs using Bowtie 2 v2.3.5.1.

RNA-seq: *ab initio* transcriptome assembly and estimation of transcript expression

Reads were mapped against the *Q. robur* genome Qrob_PM1N.fa using Spliced Transcripts Alignment to a Reference (STAR) 2.5.3a using the settings described in the STAR manual (https://github.com/alexdobin/STAR) (25). The resulting BAM files, one per sample, were then subjected to *ab initio* transcriptome assembly using StringTie v1.3.3b, observing the reads strandedness. The resulting The Gene transfer format (GTF) files, one per sample, were then merged using StringTie into a single oak transcriptome in a GTF format. RNAs with no genomic strand assigned were discarded. Each transcript was given an ID of the type MSTRG.1.1. This designation indicates that it is a transcript of a MSTRG.1 gene. The first number is the gene identifier, and the second number is the identifier for the specific transcript that had been assigned to that gene. Expression values were obtained using RNA-Seq by Expectation- Maximization with Bowtie 2 as a mapper and observing the reads strandedness. The resulting files refer to expression on the gene level and the transcript level. The expression values are shown in three ways: expected count, the number of paired reads mapped to a given gene/transcript; transcripts per million (TPM), the number of paired reads mapped to a gene/transcript and normalized to the size of

sequenced data and transcript/gene length; and fragments per kilobase of exon per million fragments mapped, the number of paired reads mapped to a gene/transcript and normalized to the size of sequenced data and transcript/gene length (a different formula is used there as compared to the case of TPM values).

RNA-seq: transcript annotation

Annotation of the assembled transcripts was performed with Trinotate v 3.0.2. In the first step, the transcript sequence was searched against Swiss-Prot proteins, a nonredundant and manually curated set of proteins in the UniProt database. BLASTX in the Basic Local Alignment Search Tool (BLAST) package was utilized, with -max_target_seqs 1 option. Open reading frames (ORFs) were predicted with TransDecoder v 5.0.1, and the predicted protein sequences were searched against Swiss-Prot using BLASTP in the BLAST package (-max_target_seqs 1 option was used). Next, the transcripts were searched against protein domains in the PFAM database using hmmscan with default settings. Trinotate v 3.0.2 was also used to annotate the transcripts using the Kyoto Encyclopedia of Genes and Genomes (KEGG) database. The results obtained from BLAST and PFAM were used to further annotate the transcripts using the Gene Ontology (GO) database.

Identification of ncRNAs

Transcript sequences in FASTA format were extracted from the oak genome, based on the GTF file data of the assembled oak transcriptome. lncRNA identification was performed using the following settings as implemented in in-house Python scripts (26, 27). Transcripts shorter than 200 bases were first removed. Next, transcripts containing ORFs as identified using TransDecoder v5.0.2 with -m 100 (minimum protein length; default: 100) and -S (strand-specific) options were discarded. Transcripts classified as coding by coding potential calculator (version 0.9-r2) with default settings were also discarded.

Pre-miRNA sequences were downloaded from miRBase 22, and Us in the sequences were converted to Ts. A BLASTN search conducted, using the transcriptome as a database and the downloaded pre-miRNAs as a query. An *E*-value threshold of 1e-5 was set, and an "-m 8" parameter was used to obtain a tab-delimited output file. The output file was then parsed and filtered with an in-house Python script. Hits were required to be in a sense orientation. An *E*-value of <1e-8 was also required (manual inspection of the results indicated that a threshold of 1e-5 was too liberal, as a substantial number of hits against animals were obtained). For each transcript, only the best hits, in terms of *E*-value, were kept. Finally, to filter hits against animal pre-miRNAs, which were relatively scarce, only hits against plants were retained (Viridiplantae). This was accomplished using the organismstxt file downloaded from miRBase that links species code (like ath for *Arabidopsis thaliana*) to species names and clades.

Identification of TFs, TRs and CRs

Identification of TFs, TRs and CRs was accomplished using PlantTFcat with default settings. The prediction was done for protein sequences predicted with TransDecoder. The resulting list is available in the database annotation directory and contains the following fields: (i) Family, such as C2H2, WD40-like and SET; (ii) Family_type, such as TF and chromatin remodeling; (iii) Sequence_Acc: ID of input protein sequence; (iv) Domains, such as IPR001214 (protein domain IDs from InterPro database) and (v) Sequence_Annotation: an extended name for the input protein sequence.

Prediction of cellular localization of the transcripts

mRNALoc was used for predicting the cellular localization of transcripts. Default settings were used with the exception of threshold for "Prediction score", which was set to 0.0. Lower thresholds result in lower specificity of the predictions, but higher thresholds did not produce any output predictions for a number of RNAs. The data are grouped into predicted localization categories (cytoplasm, nucleus, endoplasmic reticulum, extracellular or mitochondria); however, if the prediction score is below the threshold (<0.0), a "No Localization Found" designation is provided.

Validation of gene expression by reverse transcription-quantitative polymerase chain reaction

First-strand cDNAs were synthesized using 1 μg of total RNAs as a template and SuperScript III Reverse Transcriptase (Invitrogen, Carlsbad, CA, USA). Total RNA and oligo d(T) primers were then subjected to heat at 65°C for 5 min, incubated at 50°C for 60 min and extension at 70°C for 15 min. Synthesized cDNA samples were diluted five times prior to the reverse transcription-quantitative polymerase chain reaction (RT-qPCR). RT-qPCR analysis was used to validate the RNA-seq results on gene expression.

The RT-qPCR was conducted using a SensiFAST Probe No-ROX Kit (Bioline, UK) following the manufacturer's protocol. The volume of the reaction mixture was 11 μl, consisting of 5.2 μl of 2x SensiFAST qPCR Master Mix, 0.02 μM of each primer, 0.1 μM of a specific Universal Probe Library (UPL) probe and 5 μl of diluted cDNA. The RT-qPCR analysis was carried out on a LightCycler480 (Roche, Switzerland) under the following conditions: 95°C for 10 min, 45 cycles of 95°C for 10 s, 58°C for 30 s and 72°C for 1 s. Two biological and three technical replicates were used for each gene in each sample group. *Ubiquitin* and *elongation factor* were used as reference genes for normalization. Primers and UPL probes used in the RT-qPCR analysis were designed using the Universal Probe Library Assay Design Center (Roche, Switzerland) and are listed in Supplementary Table S1. Expression levels in the RT-qPCR analyses were determined using LightCycler480 software (Roche, Switzerland).

Database implementation and testing

The OakRootRNADB interactive database was constructed using the relational database management system MariaDB (https://mariadb.org/), PHP 7.4. (https://www.php.net/), Bootstrap 4 framework (https://getbootstrap.com/), HTML 5, CSS 3, JavaScript and jQuery 3.6.0 (https://jquery.com/). The interactive JavaScript Chart.js library (https://www.chartjs.org/) was used for visualization of the expression data. National Center for Biotechnology Information (NCBI) BLAST+ 2.8.1 was employed as a local alignment search tool

(28, 29). The database was tested, and it was determined that it could be successfully run on several different web browsers, including Google Chrome, Mozilla Firefox, Microsoft Edge, Vivaldi and Opera. The responsive web design facilitates the use of the database on mobile devices (https://www.ncbi.nlm.nih.gov/books/NBK131777/).

Results

Utilization of the database

Data sources and generation in OakRootRNADB

OakRootRNADB was created based on transcriptomes of pedunculate oak roots. Two different zones of the taproots (meristematic and elongation) and lateral roots were sampled. Taproots were classified according to their length (short 5–9 cm, medium 9.5–15 cm and long >15.5 cm) to determine the molecular networks associated with root elongation. The experimental design was designed (i) to determine the global changes in gene expression at the postemergence steps of root development, (ii) provide information on the potential regulation of taproot and lateral root growth, as well as similarities/differences in molecular mechanisms regulating growth in both root types, and (iii) identify the genes being expressed during root establishment at different time points. Three independent samples (biological replicates) of taproots and lateral roots were collected separately in early spring and summer to determine if sowing date had an impact on root development, and how the postemergent stage of growth (i.e. roots of different lengths) affects the profile of gene expression. We also took into account root morphology, as we observed that root elongation was inhibited in some of the roots growing in the container system but continued to increase in thickness. We assume that ceasing growth before reaching the bottom of container would prevent them from dying, which occurs as a result of air pruning. The experimental design allowed us to determine factors responsible for the cessation of growth, and factors determining the restoration of taproot growth after air pruning occurred in container-grown seedlings which were subsequently planted in the field. In addition, our approach also provided information pertaining to the molecular processes involved in root dieback.

After sequencing and preliminary data analysis, data corresponding to coding RNAs and ncRNAs were deposited as raw sequences in the NCBI Gene Expression Omnibus (GEO) database, after which analysis-ready data were uploaded to the OakRootRNADB database. Supplementary Table S2 lists details of the data deposited in NCBI's GEO and the OakRootRNADB.

The final transcriptomes obtained after sequencing, filtering, assembly and analysis comprised 145 538 transcripts belonging to 35 397 genes. Additionally, 24 593 lncRNAs and 225 miRNAs (based on pre-miRNA) were identified in the dataset. This level of ncRNAs is expected for higher organisms, such as plants. The transcripts were evenly mapped to the reference genome. Transcript assembly was accomplished using the *ab initio* (reference-based) method. The statistics on the transcriptome assembly are presented in Table 3. Over 900 000 transcripts and proteins, including over 16 000 unique transcripts, were annotated to PFAM, KEGG and GO databases using BLASTX and BLASTP (Table 3).

Table 3. Summary of protein-coding transcripts deposited to date in OakRootRNADB and annotated using various open access databases

Public database	Number of annotated Differential Gene Expression (DEGs)
BLASTP	60 769
BLASTX	70 861
GO_BLAST	8490
GO_PFAM	305 261
KEGG	56 153
PFAM	150 302

Figure 2. Distribution of transcripts on chromosomes.

The advantage of the *ab initio* approach is that it provides information pertaining to the localization of the transcripts, on paralogs and splicing forms, and exon-intron structure of genes. The downside of this approach is that some genes may be missing due to an incomplete genome. The transcript density on chromosomes was visualized using the karyoploteR library in the R environment (Figure 2). The shortest contours were omitted in the illustration to improve its clarity.

A total of 5349 TFs were identified in the dataset, belonging to major TF families, such as C2H2, WD40-like, MYB-HB-like, AP2-EREBP, bHLH and others (Table 4). A total of 39 of the TFs have been identified as transcription regulators, belonging to the SAP and Homeodomain-LIKE families, and 316 of the TFs have been classified as CRs. The identification of the cellular localization indicated that the identified transcripts were potentially localized to the cytoplasm, nucleus, endoplasmic reticulum, extracellular and mitochondria.

Table 4. Transcripts identified as TFs

Family type	Number
C2H2	900
WD40-like	647
MYB-HB-like	328
AP2-EREBP	187
bHLH	164
C3H	149
Hap3/NF-YB	129
bZIP	126
GRAS	95
NAM	95
WRKY	90
Homobox-WOX	82
FAR	72
B3-Domain	53
HSF-type-DNA-binding	52
MYB/SANT	46
C2C2-CO-like	36
C2C2-Dof	33
AS2-LOB	31
MADS-MIKC	30
TCP	30
TIFY	29
SBP	28
MYB	27
ARF	26
C2C2-GATA	26
GRF	22
TUBBY	22
Homeodomain-TALE-KNOX	19
Homeodomain-TALE-BEL	18
GARP-G2-like	16
HD-ZIP	15
GAGA-Binding-like	13
Nin-like	13
BES/BZR	12
ZF-HD	12
CG1-CAMTA	11
Hap2/NF-YA	11
GeBP	10
E2F-DP	9
Znf-LSD	9
STY-LRP1	8
MADS-type1	6
RAV	6
ssDNA-binding-TF	6
C2C2-YABBY	4
EIL	4
S1Fa-like	2
MYB-related	1
STAT	1

Database organization

The OakRootRNADB database was designed with a user-friendly interface that allows one to view data directly in the database and download the data from the website in various formats. On the main page, there is a quick search (Search) of the deposited sequences (transcript, gene or miRNA). Below that, there is a description of the database which includes a description of the data contained in it (Datasets 1 and 2) and relevant information pertaining the project (Project). Information on all persons involved in the creation of OakRootRNADB (People), as well as project financing (Funding) and contact information for the corresponding author (Contact), is also provided. Accessing the main components of the database is possible using tabs located at the top of the main page. The tabs are labeled: Transcript, Gene, miRNA, BLAST and Download (Supplementary Figure S1).

A total of 72 769 records have been deposited in the transcript section that can be filtered by gene name, cellular localization, chromosome localization, strand, biotype (other or lncRNA), peptide, regulation or miRNA (if found). The Gene tab can be accessed directly from the Gene page through a hyperlink provided in the name of the gene. There is also a filter for annotation derived from the following databases: PFAM and KEGG (including the hierarchy), BLASTP and BLASTX (Symbol and Description). The Transcript name also includes a hyperlink to a page with more information about the transcript. In the Transcript tab, you can find more information about the transcript (Summary), the sequence of the transcript and the protein it encodes (if available), along with the ability to download the data in FASTA format. The Regulation tab provides the gene family to which the transcript belongs (if found) with a reference. The Expression tab provides information on the expression of the transcript in each of the sequenced libraries used to generate the database along with a legend. The data on transcript expression can also be downloaded in the form of a table. The Cross-ref tab provides annotation information from databases such as PFAM, PFAM GO, BLASTP, BLASTX, BLAST GO and KEGG, along with hyperlinks to each database. If the transcript was a ncRNA transcript, the miRNA tab provides information on the miRNA (if found) with a hyperlink to the miRBase database. The Download tabs provide the ability to download the nucleotide or amino acid sequence in FASTA format and information on the expression level in the libraries used to generate the database (Figure 3).

In the Gene section, as in the Transcript section, the data can be filtered by chromosome, start and end, and strand. The Gene section contains 35 397 records, corresponding to the number of identified genes. Genes are also annotated to the following databases: BLASTP, BLASTX and PFAM. The gene name also contains a hyperlink to a page with more information about the gene (Summary) along with a hyperlink to the transcript. The Sequence tab provides the sequence of a gene

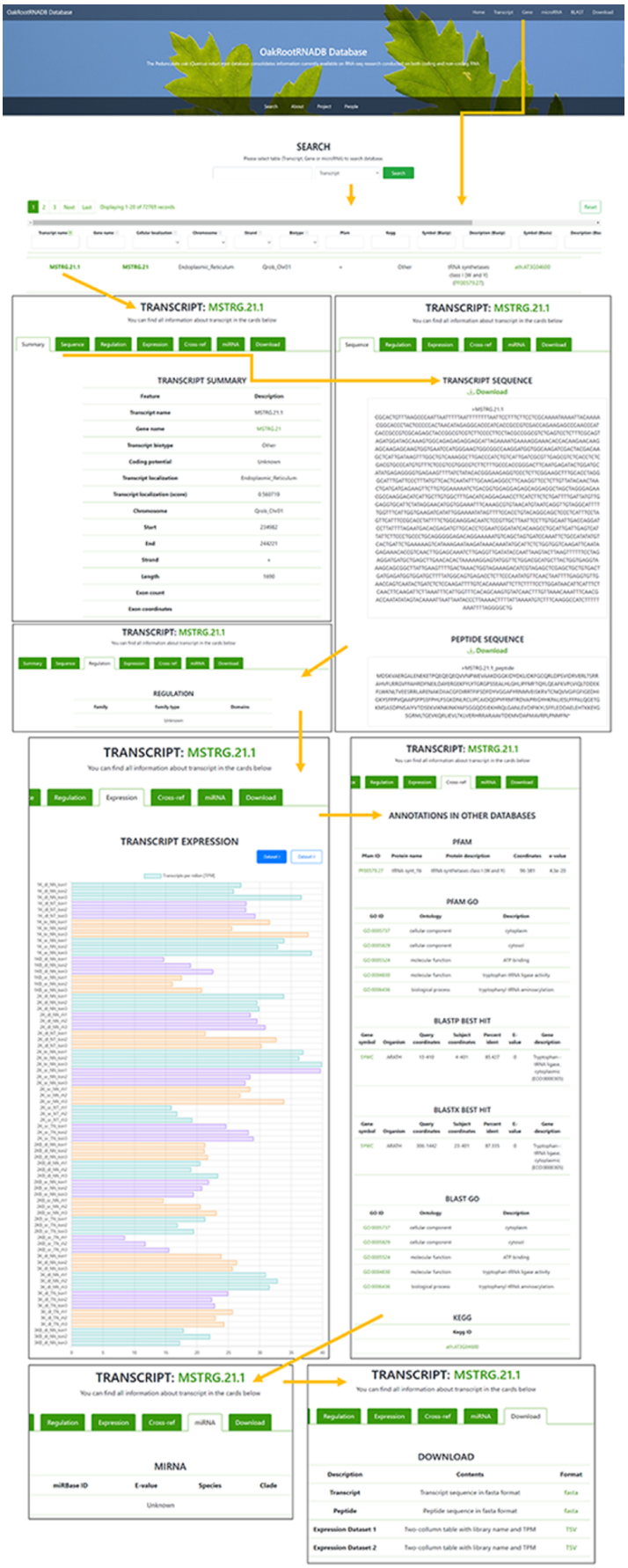

Figure 3. Screenshot of the information provided on the Transcript page of the OakRootRNADB.

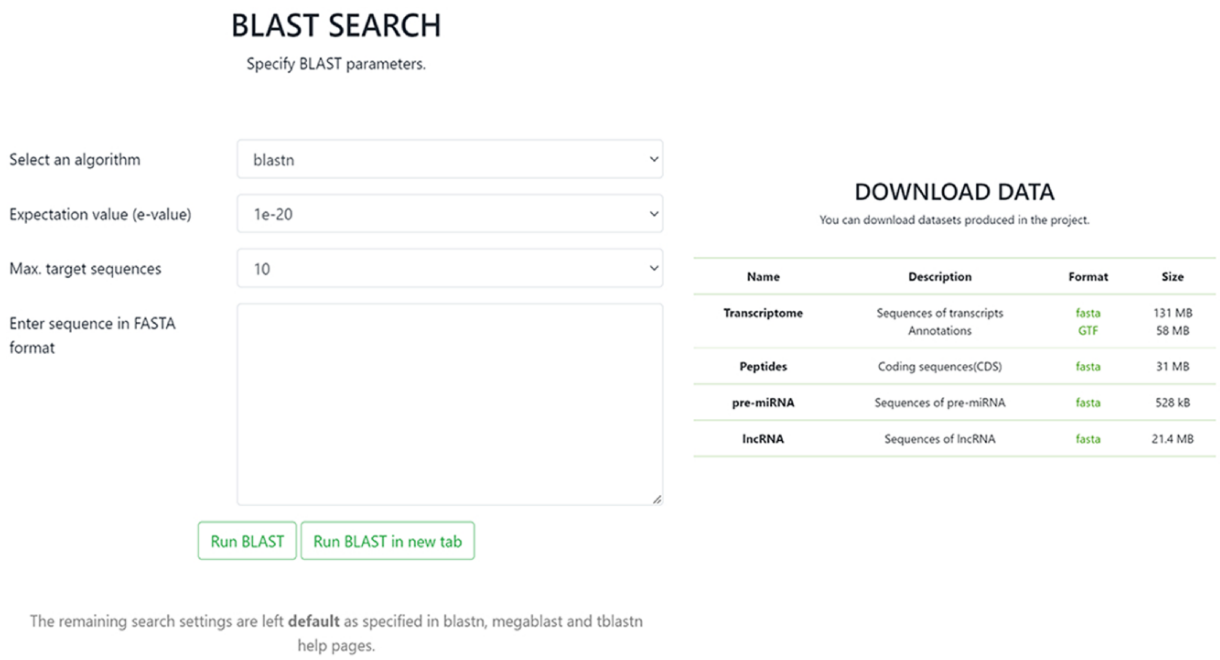

Figure 4. Screenshot of BLAST and Download pages in the OakRootRNADB.

and the protein it encodes in FASTA format, which can be downloaded. The Expression tab displays information on the level of gene expression in each of the libraries used to construct the database, along with the legend. The data on gene expression can also be retrieved as a table. The Download tab allows one to quickly download the nucleotide sequence of all the gene transcripts or the amino acid sequence for the proteins encoded by the transcripts in a FASTA format, as well as the expression level of the deposited transcripts (Supplementary Figure S2).

Two hundred twenty-five records were deposited in the miRNA section, based on the number of miRNAs that were identified (based on pre-miRNA). The list of identified miRNAs can be searched by sequence identifier (miRNA), RNA sequence (Transcript name and Gene name), *E*-value, Species and Clade. A hyperlink is provided in the miRNA identifier to the miRBase database where detailed information about a given miRNA in other organisms can be found. This part of the database is the least comprehensive due to the limited data obtained in our miRNA analysis (Supplementary Figure S3).

In the BLAST section, it is possible to conduct a BLAST query by sequence with the option to set specific BLAST parameters. The Download tab allows one to download in FASTA format any of the data contained in the database, including sequences of transcripts with annotations, CDSs of peptides, sequences of pre-miRNA and sequences of lncRNA (Figure 4).

In addition to its user-friendly interface, the OakRootRNADB database provides the ability to conduct a data analysis through the website directly or by downloading the data from the database. Hyperlinks to other annotated databases enable a sequence to be quickly identified. Each transition to other pages in the database or other databases is simply done by opening a new tab, which prevents readers from losing the visible information already obtained.

Validation of the RNA-seq results deposited in OakRootRNADB

We assessed the expression of 9 genes selected from 15 samples using RT-qPCR to validate the expression results obtained in the analysis of the RNA-seq data. Overall, the RT-qPCR analysis were similar to the results obtained in the RNA-seq analysis. Figure 5 illustrates the relationship between the RNA-seq and RT-qPCR data, showing the similarity between the data obtained in the two analyses. Figure 5A illustrates the level of correlation between the RNA-seq and RT-qPCR data, which exhibited and $R^2 = 0.86$, and Figure 5B illustrates the similarity in expression levels of individual genes as determined from the RNA-seq data or the RT-qPCR data.

Discussion

Suggested use of the data contained in the OakRootRNADB

The constructed database and web page user interface provide the ability to investigate in-depth the molecular mechanisms regulating postemergence taproot growth and similarities in gene expression and regulatory mechanisms in taproots roots versus lateral. It provides the ability to systematically analyze both CDS and non-CDS and to identify targets of soluble RNAs or miRNA. This information can provide essential knowledge on the molecular network regulating taproot and lateral development, determining the root architecture in pedunculate oak trees. The data available in OakRootRNADB can also be used by root research community to explore how the seedling root system of pedunculate oaks will respond to environmental cues. A comparison of the genes involved in root development in a long-lived, perennial tree species versus an annual plant, such as *Arabidopsis*, can help to determine how life cycle shapes the transcript profiles of roots. Our database provides a broad transcriptomic

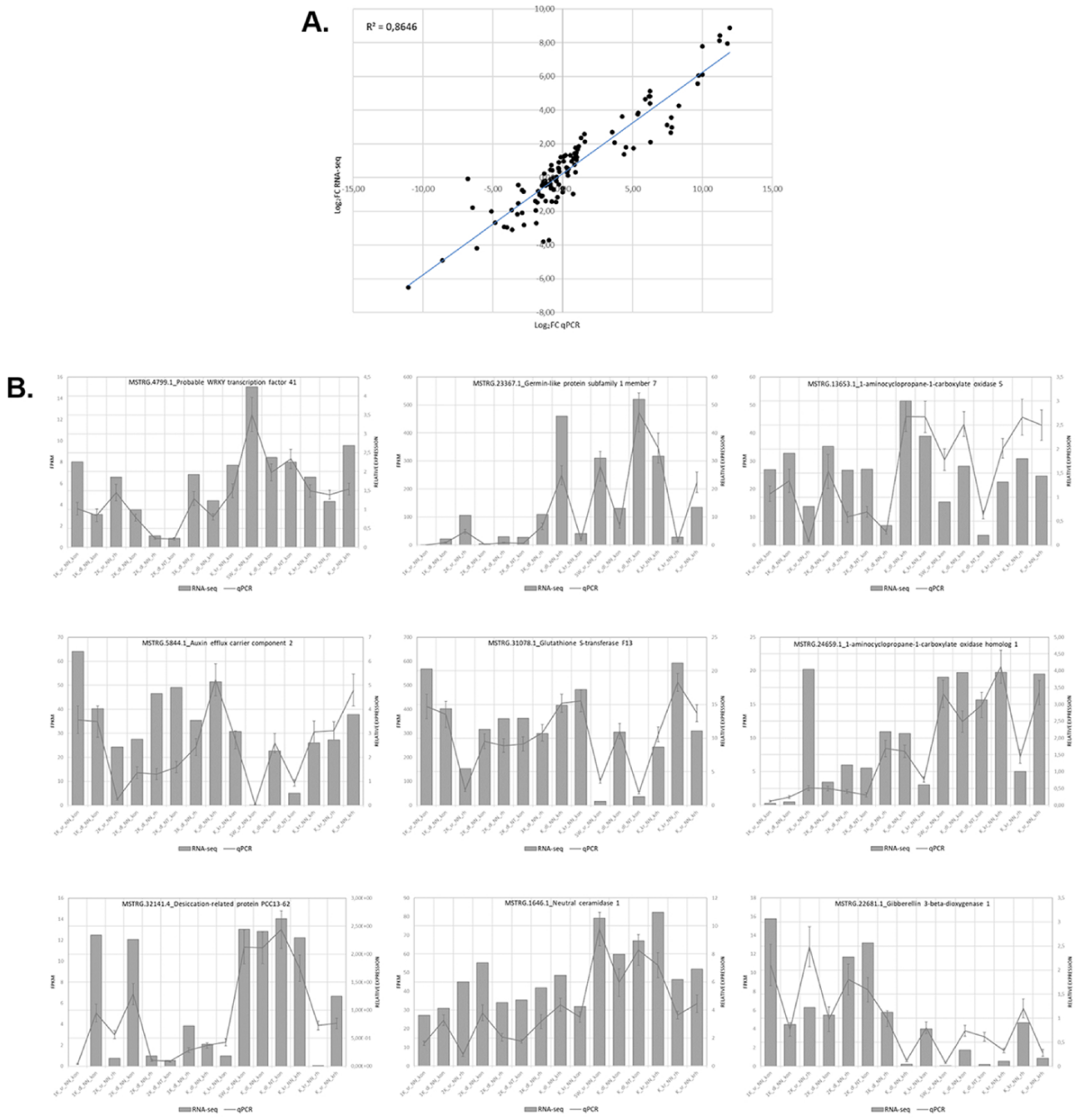

Figure 5. Relationship between levels of expression obtained by RNA-seq and RT-qPCR. (A) Log2 fold change in gene expression determined by plotting RNA-seq data against log2 fold change in gene expression assessed by qPCR. (B) Graphs showing similar trends in the expression levels of individual genes determined by RNA-seq and RT-qPCR analyses.

perspective that will enable biologists the function of specific genes in relation to other parameters (root type, season, etc.). The database will be extremely useful for researchers who want to predict root growth in tree nurseries and root response to water shortage.

Conclusion

The constructed OakRootRNADB database is provided with a user-friendly and intuitive interface that provides the ability to analyze the RNA-seq data deposited in the database. We illustrate how to use the OakRootRNADB database and how it facilitates the analysis of both CDS and non-CDS involved in the regulation of taproot and lateral root growth. The OakRootRNADB database contains both CDS and non-CDS obtained from an RNA-seq analysis of pedunculate oak and enables one, for the first time, to obtain a broad picture of the genes involved in regulating the growth and development of a long-lived root system comprised of both a taproot and lateral roots. The database can be used as a starting point for research on mRNA and ncRNA associated with pedunculate oak, as well as other perennial plant species, especially trees.

Supplementary data

Supplementary data are available at *Database* Online.

Data availability

The data discussed in this publication have been deposited in NCBI's GEO (30) and are accessible through GEO Series accession number GSE181860 (https://www.ncbi.nlm.nih.gov/geo/query/acc.cgi?acc=GSE181860).

Author contributions

P.K. drafted the manuscript. P.K. and P.G. conducted the analyses. M.Z. conceived the project and sought funding for it. All authors contributed to the article editing and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

1. Köstler,J., Brückner,E. and Bibelriether,H. (1968) Die Wurzeln der Waldbäume: Untersuchungen zur Morphologie der Waldbäume in Mitteleuropa. P. Parey.
2. Gessler,A., Cailleret,M., Joseph,J. *et al.* (2018) Drought induced tree mortality—a tree-ring isotope based conceptual model to assess mechanisms and predispositions. *New Phytol.*, **219**, 485–490.
3. Barbeta,A. and Penuelas,J. (2017) Increasing carbon discrimination rates and depth of water uptake favor the growth of Mediterranean evergreen trees inthe ecotone with temperate deciduous forests. *Glob. Chang. Biol.*, **23**, 5054–5068.
4. Zadworny,M., Jagodziński,A.M., Łakomy,P. *et al.* (2014) The silent shareholder in deterioration of oak growth: common planting practices affect the long-term response of oaks to periodic drought. *For. Ecol. Manage.*, **318**, 133–141.
5. Zadworny,M., Mucha,J., Jagodziński,A.M. *et al.* (2021) Seedling regeneration techniques affect root systems and the response of *Quercus robur* seedlings to water shortages. *For. Ecol. Manage.*, **479**, 118552.
6. Rodriguez-Calcerrada,J., Sancho-Knapik,D., Martin-stpaul,N.K. *et al.* (2017) Drought-induced oak decline-factors involved, physiological dysfunctions, and potential attenuation by forestry practices. In: GilPelegrin E, PegueroPina JJ, SanchoKnapik D (eds). *Oaks Physiological Ecology. Exploring the Functional Diversity of Genus Quercus L.* Springer International Publishing Ag, Cham, pp. 419–451.
7. Zadworny,M., Jagodziński,A.M., Łakomy,P. *et al.* (2019) Regeneration origin affects radial growth patterns preceding oak decline and death - insights from tree-ring δC-13 and δO-18. *Agric. For. Meteorol.*, **278**, 107685.
8. Brown,P.T. and Caldeira,K. (2017) Greater future global warming inferred from Earth's recent energy budget. *Nature*, **552**, 45–50.
9. Hari,V., Rakovec,O., Markonis,Y. *et al.* (2020) Increased future occurrences of the exceptional 2018-2019 Central European drought under global warming. *Sci. Rep.*, **10**, 12207.
10. Kościelniak,P., Glazińska,P., Kęsy,J. *et al.* (2021) Formation and development of taproots in deciduous tree species. *Front. Plant Sci.*, **12**, 772567.
11. Skiadaresis,G., Schwarz,J.A. and Bauhus,J. (2019) Groundwater extraction in floodplain forests reduces radial growth and increases summer drought sensitivity of pedunculate oak trees (*Quercus robur* L.). *Front. For. Glob. Change*, **2**, 5.
12. Gupta,A., Rico-Medina,A. and Caño-Delgado,A.I. (2020) The physiology of plant responses to drought. *Science*, **368**, 266–269.
13. Drisch,R.C. and Stahl,Y. (2015) Function and regulation of transcription factors involved in root apical meristem and stem cell maintenance. *Front. Plant Sci.*, **6**, 505.
14. Mitsis,T., Efthimiadou,A., Bacopoulou,F. *et al.* (2020) Transcription factors and evolution: an integral part of gene expression (review). *World Acad. Sci. J.*, **2**, 3–8.
15. Bazin,J. and Bailey-Serres,J. (2015) Emerging roles of long noncoding RNA in root developmental plasticity and regulation of phosphate homeostasis. *Front. Plant Sci.*, **6**, 400.
16. Nilsson,U. and Orlander,G. (1995) Effects of regeneration methods on drought damage to newly planted Norway spruce seedlings. *Can. J. For. Res.*, **25**, 790–802.
17. Pernot,C., Thiffault,N. and DesRochers,A. (2019) Influence of root system characteristics on black spruce seedling responses to limiting conditions. *Plants-Basel*, **8**, 70.
18. Robbins,N.E. and Dinneny,J.R. (2018) Growth is required for perception of water availability to pattern root branches in plants. *Proc. Natl Acad. Sci. U.S.A.*, **115**, E822–E831.
19. Ueno,S., Le Provost,G., Léger,V. *et al.* (2010) Bioinformatic analysis of ESTs collected by Sanger and pyrosequencing methods for a keystone forest tree species: oak. *BMC Genom.*, **11**, 650.
20. Tarkka,M.T., Herrmann,S., Wubet,T. *et al.* (2013) OakContigDF159.1, a reference library for studying differential gene expression in *Quercus robur* during controlled biotic interactions: use for quantitative transcriptomic profiling of oak roots in ectomycorrhizal symbiosis. *New Phytol.*, **199**, 529–540.
21. Lesur,I., Le Provost,G., Bento,P. *et al.* (2015) The oak gene expression atlas: insights into Fagaceae genome evolution and the discovery of genes regulated during bud dormancy release. *BMC Genom.*, **16**, 112.
22. Ramos,A.M., Usié,A., Barbosa,P. *et al.* (2018) The draft genome sequence of cork oak. *Sci. Data*, **5**, 180069.
23. Arias-Baldrich,C., Silva,M.C., Bergeretti,F. *et al.* (2020) CorkOakDB—the cork oak genome database portal. *Database*, **2020**, baaa114.
24. Martin,J.A. and Wang,Z. (2011) Next-generation transcriptome assembly. *Nat. Rev. Genet.*, **12**, 671–682.
25. Dobin,A., Davis,C.A., Schlesinger,F. *et al.* (2013) STAR: ultrafast universal RNA-seq aligner. *Bioinformatics*, **29**, 15–21.
26. Haas,B.J., Papanicolaou,A., Yassour,M. *et al.* (2013) De novo transcript sequence reconstruction from RNA-seq using the Trinity platform for reference generation and analysis. *Nat. Protoc.*, **8**, 1494–1512.

27. Kong,L., Zhang,Y., Ye,Z.-Q. *et al.* (2007) CPC: assess the protein-coding potential of transcripts using sequence features and support vector machine. *Nucleic Acids Res.*, **35**, W345–W349.
28. Altschul,S.F., Madden,T.L., Schäffer,A.A. *et al.* (1997) Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. *Nucleic Acids Res.*, **25**, 3389–3402.
29. Camacho,C., Coulouris,G., Avagyan,V. *et al.* (2009) BLAST+: architecture and applications. *BMC Bioinform.*, **10**, 421.
30. Edgar,R., Domrachev,M. and Lash,A.E. (2002) Gene expression omnibus: NCBI gene expression and hybridization array data repository. *Nucleic Acids Res.*, **30**, 207–210.

Supplementary Table 1. Primers and UPL (Universal Probe Library) probes used in the RT-qPCR analysis.

Gene	Gene ID	Primer	Sequence (5’ → 3’)	UPL probe
CERD	MSTRG.1646	forward	TTGCTGCTGGAACAACAGAT	31
		reverse	TTCCCTTGTCATCTCCTTGC	
G3OX	MSTRG.22681	forward	CGGACCCGTTATCGTTTATC	20
		reverse	TTTTGAGAGTGGAGAGATTTGGA	
WRKY	MSTRG.4799	forward	CCCACGCTACCAATTTGATT	9
		reverse	TGCTGTTGTTGTTGTGTTTCTG	
GST	MSTRG.31078	forward	TGAATCTAGGGCAATTACAGCA	5
		reverse	GAGATCAGTTCCAGTTTCCTTGA	
PIN2	MSTRG.5844	forward	TCTTCACACCAGACCAGTGC	5
		reverse	GGAAGGAAAGTAATGGAACTGC	
GERL1	MSTRG.23367	forward	CCAACCCTCCCATTAATCCT	97
		reverse	CTCTTCAACCACATTTTTGTCG	
ACO5	MSTRG.13653	forward	CGGCAAGTTGGAGAATGTG	88
		reverse	GCTGGCCACTCGTTATTGTC	
ACO1	MSTRG.24659	forward	GTAAGTAATTCCATTTTGACAATCCA	31
		reverse	CCTACACTAGAAGTGAGATCCATCC	
PCC13	MSTRG.32141	forward	CTCTATGAGAGAGCCGAAGAAAA	145
		reverse	CGAGAGATATAGTCTGTGAACTGTGC	
UBQ	MSTRG.26207	forward	CTTTCCCAAATTTATTCGTTGG	9
		reverse	TCTATTGACAAGCCACTGTTTCA	
EF	MSTRG.28793	forward	CACCTCTTGGTCGTTTTGCT	5
		reverse	TTCTCAACACTCTTGATGACACC	

Supplementary Table 2. Data deposited in NCBI GEO and the OakRootRNADB.

Sample name	title	source name	organism	molecule	description
1K_dl_NN_kon_rep_1	1K_dl_NN_kon_rep_1	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, meristematic zone of the taproot, short root, growing in containers
1K_dl_NN_kon_rep_2	1K_dl_NN_kon_rep_2	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, meristematic zone of the taproot, short root, growing in containers
1K_dl_NN_kon_rep_3	1K_dl_NN_kon_rep_3	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, meristematic zone of the taproot, short root, growing in containers
1K_dl_NT_kon_rep_1	1K_dl_NT_kon_rep_1	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, meristematic zone of the taproot, long root, dying root, growing in containers
1K_dl_NT_kon_rep_2	1K_dl_NT_kon_rep_2	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, meristematic zone of the taproot, long root, dying root, growing in containers
1K_dl_NT_kon_rep_3	1K_dl_NT_kon_rep_3	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, meristematic zone of the taproot, long root, dying root, growing in containers
1K_kr_NN_kon_rep_1	1K_kr_NN_kon_rep_1	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, meristematic zone of the taproot, short root, growing in containers
1K_kr_NN_kon_rep_2	1K_kr_NN_kon_rep_2	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, meristematic zone of the taproot, short root, growing in containers
1K_kr_NN_kon_rep_3	1K_kr_NN_kon_rep_3	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, meristematic zone of the taproot, short root, growing in containers
1K_sr_NN_kon_rep_1	1K_sr_NN_kon_rep_1	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, meristematic zone of the taproot, medium root, growing in containers
1K_sr_NN_kon_rep_2	1K_sr_NN_kon_rep_2	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, meristematic zone of the taproot, medium root, growing in containers
1K_sr_NN_kon_rep_3	1K_sr_NN_kon_rep_3	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, meristematic zone of the taproot, medium root, growing in containers
1KB_dl_NN_kon_rep_1	1KB_dl_NN_kon_rep_1	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, lateral root, long root, growing in containers
1KB_dl_NN_kon_rep_2	1KB_dl_NN_kon_rep_2	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, lateral root, long root, growing in containers

1KB_dl_NN_kon_rep_3	1KB_dl_NN_kon_rep_3	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, lateral root, long root, growing in containers
1KB_sr_NN_kon_rep_1	1KB_sr_NN_kon_rep_1	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, lateral root, medium root, growing in containers
1KB_sr_NN_kon_rep_2	1KB_sr_NN_kon_rep_2	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, lateral root, medium root, growing in containers
1KB_sr_NN_kon_rep_3	1KB_sr_NN_kon_rep_3	root	Quercus robur	total RNA	First harvest date - 7-weeks old plant, lateral root, medium root, growing in containers
2K_dl_NN_kon_rep_1	2K_dl_NN_kon_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, long root, growing in containers
2K_dl_NN_kon_rep_2	2K_dl_NN_kon_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, long root, growing in containers
2K_dl_NN_kon_rep_3	2K_dl_NN_kon_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, long root, growing in containers
2K_dl_NN_rh_rep_1	2K_dl_NN_rh_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, long root, growing in rhizotron
2K_dl_NN_rh_rep_2	2K_dl_NN_rh_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, long root, growing in rhizotron
2K_dl_NN_rh_rep_3	2K_dl_NN_rh_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, long root, growing in rhizotron
2K_dl_NT_kon_rep_1	2K_dl_NT_kon_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, long root, dying root, growing in containers
2K_dl_NT_kon_rep_2	2K_dl_NT_kon_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, long root, dying root, growing in containers
2K_dl_NT_kon_rep_3	2K_dl_NT_kon_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, long root, dying root, growing in containers
2K_kr_NN_kon_rep_1	2K_kr_NN_kon_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, short root, growing in containers
2K_kr_NN_kon_rep_2	2K_kr_NN_kon_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, short root, growing in containers
2K_kr_NN_kon_rep_3	2K_kr_NN_kon_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, short root, growing in containers

2K_sr_NN_kon_rep_1	2K_sr_NN_kon_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, medium root, growing in containers
2K_sr_NN_kon_rep_2	2K_sr_NN_kon_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, medium root, growing in containers
2K_sr_NN_kon_rep_3	2K_sr_NN_kon_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, medium root, growing in containers
2K_sr_NN_rh_rep_1	2K_sr_NN_rh_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, medium root, growing in rhizotron
2K_sr_NN_rh_rep_2	2K_sr_NN_rh_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, medium root, growing in rhizotron
2K_sr_NN_rh_rep_3	2K_sr_NN_rh_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, medium root, growing in rhizotron
2K_sr_NT_rh_rep_1	2K_sr_NT_rh_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, medium root, dying root, growing in rhizotron
2K_sr_NT_rh_rep_2	2K_sr_NT_rh_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, medium root, dying root, growing in rhizotron
2K_sr_NT_rh_rep_3	2K_sr_NT_rh_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, medium root, dying root, growing in rhizotron
2K_sr_TN_kon_rep_1	2K_sr_TN_kon_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, medium root, thick root, growing in containers
2K_sr_TN_kon_rep_2	2K_sr_TN_kon_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, medium root, thick root, growing in containers
2K_sr_TN_kon_rep_3	2K_sr_TN_kon_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, meristematic zone of the taproot, medium root, thick root, growing in containers
2KB_dl_NN_kon_rep_1	2KB_dl_NN_kon_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, long root, growing in containers
2KB_dl_NN_kon_rep_2	2KB_dl_NN_kon_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, long root, growing in containers
2KB_dl_NN_kon_rep_3	2KB_dl_NN_kon_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, long root, growing in containers
2KB_dl_NN_rh_rep_1	2KB_dl_NN_rh_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, long root, growing in rhizotron

2KB_dl_NN_rh_rep_2	2KB_dl_NN_rh_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, long root, growing in rhizotron
2KB_dl_NN_rh_rep_3	2KB_dl_NN_rh_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, long root, growing in rhizotron
2KB_sr_NN_kon_rep_1	2KB_sr_NN_kon_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, medium root, growing in containers
2KB_sr_NN_kon_rep_2	2KB_sr_NN_kon_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, medium root, growing in containers
2KB_sr_NN_kon_rep_3	2KB_sr_NN_kon_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, medium root, growing in containers
2KB_sr_NN_rh_rep_1	2KB_sr_NN_rh_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, medium root, growing in rhizotron
2KB_sr_NN_rh_rep_2	2KB_sr_NN_rh_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, medium root, growing in rhizotron
2KB_sr_NN_rh_rep_3	2KB_sr_NN_rh_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, medium root, growing in rhizotron
2KB_sr_TN_kon_rep_1	2KB_sr_TN_kon_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, medium root, thick root, growing in containers
2KB_sr_TN_kon_rep_2	2KB_sr_TN_kon_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, medium root, thick root, growing in containers
2KB_sr_TN_kon_rep_3	2KB_sr_TN_kon_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, medium root, thick root, growing in containers
2KB_sr_TN_rh_rep_1	2KB_sr_TN_rh_rep_1	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, medium root, thick root, growing in rhizotron
2KB_sr_TN_rh_rep_2	2KB_sr_TN_rh_rep_2	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, medium root, thick root, growing in rhizotron
2KB_sr_TN_rh_rep_3	2KB_sr_TN_rh_rep_3	root	Quercus robur	total RNA	Second harvest date - 8-weeks old plant, lateral root, medium root, thick root, growing in rhizotron
3K_dl_NN_kon_rep_1	3K_dl_NN_kon_rep_1	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, meristematic zone of the taproot, long root, growing in containers
3K_dl_NN_kon_rep_2	3K_dl_NN_kon_rep_2	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, meristematic zone of the taproot, long root, growing in containers

3K_dl_NN_kon_rep_3	3K_dl_NN_kon_rep_3	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, meristematic zone of the taproot, long root, growing in containers
3K_dl_NN_rh_rep_1	3K_dl_NN_rh_rep_1	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, meristematic zone of the taproot, long root, growing in rhizotron
3K_dl_NN_rh_rep_2	3K_dl_NN_rh_rep_2	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, meristematic zone of the taproot, long root, growing in rhizotron
3K_dl_NN_rh_rep_3	3K_dl_NN_rh_rep_3	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, meristematic zone of the taproot, long root, growing in rhizotron
3K_dl_TN_kon_rep_1	3K_dl_TN_kon_rep_1	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, meristematic zone of the taproot, long root, thick root, growing in containers
3K_dl_TN_kon_rep_2	3K_dl_TN_kon_rep_2	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, meristematic zone of the taproot, long root, thick root, growing in containers
3K_dl_TN_kon_rep_3	3K_dl_TN_kon_rep_3	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, meristematic zone of the taproot, long root, thick root, growing in containers
3K_dl_TN_rh_rep_1	3K_dl_TN_rh_rep_1	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, meristematic zone of the taproot, long root, thick root, growing in rhizotron
3K_dl_TN_rh_rep_2	3K_dl_TN_rh_rep_2	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, meristematic zone of the taproot, long root, thick root, growing in rhizotron
3K_dl_TN_rh_rep_3	3K_dl_TN_rh_rep_3	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, meristematic zone of the taproot, long root, thick root, growing in rhizotron
3KB_dl_NN_kon_rep_1	3KB_dl_NN_kon_rep_1	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, lateral root, long root, growing in containers
3KB_dl_NN_kon_rep_2	3KB_dl_NN_kon_rep_2	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, lateral root, long root, growing in containers
3KB_dl_NN_kon_rep_3	3KB_dl_NN_kon_rep_3	root	Quercus robur	total RNA	Third harvest date – 8-weeks old plant, lateral root, long root, growing in containers
K_dl_NN_kon_rep_1	K_dl_NN_kon_rep_1	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, growing in containers
K_dl_NN_kon_rep_2	K_dl_NN_kon_rep_2	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, growing in containers
K_dl_NN_kon_rep_3	K_dl_NN_kon_rep_3	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, growing in containers

K_dl_NN_krh_rep_1	K_dl_NN_krh_rep_1	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, grown in a container and then transferred to a rhizotron
K_dl_NN_krh_rep_2	K_dl_NN_krh_rep_2	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, grown in a container and then transferred to a rhizotron
K_dl_NN_krh_rep_3	K_dl_NN_krh_rep_3	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, grown in a container and then transferred to a rhizotron
K_dl_NN_rh_rep_1	K_dl_NN_rh_rep_1	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, growing in rhizotron
K_dl_NN_rh_rep_2	K_dl_NN_rh_rep_2	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, growing in rhizotron
K_dl_NN_rh_rep_3	K_dl_NN_rh_rep_3	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, growing in rhizotron
K_dl_NT_kon_rep_1	K_dl_NT_kon_rep_1	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, dying root, growing in containers
K_dl_NT_kon_rep_2	K_dl_NT_kon_rep_2	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, dying root, growing in containers
K_dl_NT_kon_rep_3	K_dl_NT_kon_rep_3	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, dying root, growing in containers
K_dl_NT_krh_rep_1	K_dl_NT_krh_rep_1	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, grown in a container and then transferred to a rhizotron
K_dl_NT_krh_rep_2	K_dl_NT_krh_rep_2	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, grown in a container and then transferred to a rhizotron
K_dl_NT_krh_rep_3	K_dl_NT_krh_rep_3	root	Quercus robur	total RNA	meristematic zone of the taproot, long root, grown in a container and then transferred to a rhizotron
K_kr_NN_kon_rep_1	K_kr_NN_kon_rep_1	root	Quercus robur	total RNA	meristematic zone of the taproot, short root, growing in containers
K_kr_NN_kon_rep_2	K_kr_NN_kon_rep_2	root	Quercus robur	total RNA	meristematic zone of the taproot, short root, growing in containers
K_kr_NN_kon_rep_3	K_kr_NN_kon_rep_3	root	Quercus robur	total RNA	meristematic zone of the taproot, short root, growing in containers
K_kr_NN_krh_rep_1	K_kr_NN_krh_rep_1	root	Quercus robur	total RNA	meristematic zone of the taproot, short root, grown in a container and then transferred to a rhizotron

K_kr_NN_krh_rep_2	K_kr_NN_krh_rep_2	root	Quercus robur	total RNA	meristematic zone of the taproot, short root, grown in a container and then transferred to a rhizotron
K_kr_NN_krh_rep_3	K_kr_NN_krh_rep_3	root	Quercus robur	total RNA	meristematic zone of the taproot, short root, grown in a container and then transferred to a rhizotron
K_kr_NN_rh_rep_1	K_kr_NN_rh_rep_1	root	Quercus robur	total RNA	meristematic zone of the taproot, short root, growing in rhizotron
K_kr_NN_rh_rep_2	K_kr_NN_rh_rep_2	root	Quercus robur	total RNA	meristematic zone of the taproot, short root, growing in rhizotron
K_kr_NN_rh_rep_3	K_kr_NN_rh_rep_3	root	Quercus robur	total RNA	meristematic zone of the taproot, short root, growing in rhizotron
K_sr_NN_kon_rep_1	K_sr_NN_kon_rep_1	root	Quercus robur	total RNA	meristematic zone of the taproot, medium root, growing in containers
K_sr_NN_kon_rep_2	K_sr_NN_kon_rep_2	root	Quercus robur	total RNA	meristematic zone of the taproot, medium root, growing in containers
K_sr_NN_kon_rep_3	K_sr_NN_kon_rep_3	root	Quercus robur	total RNA	meristematic zone of the taproot, medium root, growing in containers
K_sr_NN_krh_rep_1	K_sr_NN_krh_rep_1	root	Quercus robur	total RNA	meristematic zone of the taproot, medium root, grown in a container and then transferred to a rhizotron
K_sr_NN_krh_rep_2	K_sr_NN_krh_rep_2	root	Quercus robur	total RNA	meristematic zone of the taproot, medium root, grown in a container and then transferred to a rhizotron
K_sr_NN_krh_rep_3	K_sr_NN_krh_rep_3	root	Quercus robur	total RNA	meristematic zone of the taproot, medium root, grown in a container and then transferred to a rhizotron
K_sr_NN_rh_rep_1	K_sr_NN_rh_rep_1	root	Quercus robur	total RNA	meristematic zone of the taproot, medium root, growing in rhizotron
K_sr_NN_rh_rep_2	K_sr_NN_rh_rep_2	root	Quercus robur	total RNA	meristematic zone of the taproot, medium root, growing in rhizotron
K_sr_NN_rh_rep_3	K_sr_NN_rh_rep_3	root	Quercus robur	total RNA	meristematic zone of the taproot, medium root, growing in rhizotron
K_sr_TT_krh_rep_1	K_sr_TT_krh_rep_1	root	Quercus robur	total RNA	meristemaric zone of the taproot, medium root, thick root, dying root, grown in a container and then transferred to a rhizotron

K_sr_TT_krh_rep_2	K_sr_TT_krh_rep_2	root	Quercus robur	total RNA	meristemaric zone of the taproot, medium root, thick root, dying root, grown in a container and then transferred to a rhizotron
K_sr_TT_krh_rep_3	K_sr_TT_krh_rep_3	root	Quercus robur	total RNA	meristemaric zone of the taproot, medium root, thick root, dying root, grown in a container and then transferred to a rhizotron
K_sr_TT_rh_rep_1	K_sr_TT_rh_rep_1	root	Quercus robur	total RNA	meristematic zone of the taproot, medium root, thick root, dying root, growing in rhizotron
K_sr_TT_rh_rep_2	K_sr_TT_rh_rep_2	root	Quercus robur	total RNA	meristematic zone of the taproot, medium root, thick root, dying root, growing in rhizotron
K_sr_TT_rh_rep_3	K_sr_TT_rh_rep_3	root	Quercus robur	total RNA	meristematic zone of the taproot, medium root, thick root, dying root, growing in rhizotron
KB_dl_NN_kon_rep_1	KB_dl_NN_kon_rep_1	root	Quercus robur	total RNA	lateral root, long root, growing in containers
KB_dl_NN_kon_rep_2	KB_dl_NN_kon_rep_2	root	Quercus robur	total RNA	lateral root, long root, growing in containers
KB_dl_NN_kon_rep_3	KB_dl_NN_kon_rep_3	root	Quercus robur	total RNA	lateral root, long root, growing in containers
KB_dl_NN_krh_rep_1	KB_dl_NN_krh_rep_1	root	Quercus robur	total RNA	lateral root, long root, grown in a container and then transferred to a rhizotron
KB_dl_NN_krh_rep_2	KB_dl_NN_krh_rep_2	root	Quercus robur	total RNA	lateral root, long root, grown in a container and then transferred to a rhizotron
KB_dl_NN_krh_rep_3	KB_dl_NN_krh_rep_3	root	Quercus robur	total RNA	lateral root, long root, grown in a container and then transferred to a rhizotron
KB_dl_NN_rh_rep_1	KB_dl_NN_rh_rep_1	root	Quercus robur	total RNA	lateral root, long root, growing in rhizotron
KB_dl_NN_rh_rep_2	KB_dl_NN_rh_rep_2	root	Quercus robur	total RNA	lateral root, long root, growing in rhizotron
KB_dl_NN_rh_rep_3	KB_dl_NN_rh_rep_3	root	Quercus robur	total RNA	lateral root, long root, growing in rhizotron
KB_dl_NT_kon_rep_1	KB_dl_NT_kon_rep_1	root	Quercus robur	total RNA	lateral root, long root, dying root, growing in containers
KB_dl_NT_kon_rep_2	KB_dl_NT_kon_rep_2	root	Quercus robur	total RNA	lateral root, long root, dying root, growing in containers
KB_dl_NT_kon_rep_3	KB_dl_NT_kon_rep_3	root	Quercus robur	total RNA	lateral root, long root, dying root, growing in containers
KB_sr_NN_kon_rep_1	KB_sr_NN_kon_rep_1	root	Quercus robur	total RNA	lateral root, medium root, growing in containers
KB_sr_NN_kon_rep_2	KB_sr_NN_kon_rep_2	root	Quercus robur	total RNA	lateral root, medium root, growing in containers
KB_sr_NN_kon_rep_3	KB_sr_NN_kon_rep_3	root	Quercus robur	total RNA	lateral root, medium root, growing in containers
KB_sr_NN_rh_rep_1	KB_sr_NN_rh_rep_1	root	Quercus robur	total RNA	lateral root, medium root, growing in rhizotron
KB_sr_NN_rh_rep_2	KB_sr_NN_rh_rep_2	root	Quercus robur	total RNA	lateral root, medium root, growing in rhizotron

KB_sr_NN_rh_rep_3	KB_sr_NN_rh_rep_3	root	Quercus robur	total RNA	lateral root, medium root, growing in rhizotron
KB_sr_TT_krh_rep_1	KB_sr_TT_krh_rep_1	root	Quercus robur	total RNA	lateral root, medium root, thick root, dying root, grown in a container and then transferred to a rhizotron
KB_sr_TT_krh_rep_2	KB_sr_TT_krh_rep_2	root	Quercus robur	total RNA	lateral root, medium root, thick root, dying root, grown in a container and then transferred to a rhizotron
KB_sr_TT_krh_rep_3	KB_sr_TT_krh_rep_3	root	Quercus robur	total RNA	lateral root, medium root, thick root, dying root, grown in a container and then transferred to a rhizotron
SW_dl_NN_kon_rep_1	SW_dl_NN_kon_rep_1	root	Quercus robur	total RNA	elongation zone of the taproot, long root, growing in containers
SW_dl_NN_kon_rep_2	SW_dl_NN_kon_rep_2	root	Quercus robur	total RNA	elongation zone of the taproot, long root, growing in containers
SW_dl_NN_kon_rep_3	SW_dl_NN_kon_rep_3	root	Quercus robur	total RNA	elongation zone of the taproot, long root, growing in containers
SW_dl_NN_krh_rep_1	SW_dl_NN_krh_rep_1	root	Quercus robur	total RNA	elongation zone of the taproot, long root, grown in a container and then transferred to a rhizotron
SW_dl_NN_krh_rep_2	SW_dl_NN_krh_rep_2	root	Quercus robur	total RNA	elongation zone of the taproot, long root, grown in a container and then transferred to a rhizotron
SW_dl_NN_krh_rep_3	SW_dl_NN_krh_rep_3	root	Quercus robur	total RNA	elongation zone of the taproot, long root, grown in a container and then transferred to a rhizotron
SW_dl_NN_rh_rep_1	SW_dl_NN_rh_rep_1	root	Quercus robur	total RNA	elongation zone of the taproot, long root, growing in rhizotron
SW_dl_NN_rh_rep_2	SW_dl_NN_rh_rep_2	root	Quercus robur	total RNA	elongation zone of the taproot, long root, growing in rhizotron
SW_dl_NN_rh_rep_3	SW_dl_NN_rh_rep_3	root	Quercus robur	total RNA	elongation zone of the taproot, long root, growing in rhizotron
SW_dl_NT_kon_rep_1	SW_dl_NT_kon_rep_1	root	Quercus robur	total RNA	elongation zone of the taproot, long root, dying root, growing in containers
SW_dl_NT_kon_rep_2	SW_dl_NT_kon_rep_2	root	Quercus robur	total RNA	elongation zone of the taproot, long root, dying root, growing in containers
SW_dl_NT_kon_rep_3	SW_dl_NT_kon_rep_3	root	Quercus robur	total RNA	elongation zone of the taproot, long root, dying root, growing in containers
SW_dl_NT_krh_rep_1	SW_dl_NT_krh_rep_1	root	Quercus robur	total RNA	elongation zone of the taproot, long root, dying root, grown in a container and then transferred to a rhizotron
SW_dl_NT_krh_rep_2	SW_dl_NT_krh_rep_2	root	Quercus robur	total RNA	elongation zone of the taproot, long root, dying root, grown in a container and then transferred to a rhizotron
SW_dl_NT_krh_rep_3	SW_dl_NT_krh_rep_3	root	Quercus robur	total RNA	elongation zone of the taproot, long root, dying root, grown in a container and then transferred to a rhizotron

SW_sr_NN_kon_rep_1	SW_sr_NN_kon_rep_1	root	Quercus robur	total RNA	elongation zone of raproot, medium root, growing in containers
SW_sr_NN_kon_rep_2	SW_sr_NN_kon_rep_2	root	Quercus robur	total RNA	elongation zone of raproot, medium root, growing in containers
SW_sr_NN_kon_rep_3	SW_sr_NN_kon_rep_3	root	Quercus robur	total RNA	elongation zone of raproot, medium root, growing in containers
SW_sr_NN_rh_rep_1	SW_sr_NN_rh_rep_1	root	Quercus robur	total RNA	elongation zone of the taproot, medium root, growing in rhizotron
SW_sr_NN_rh_rep_2	SW_sr_NN_rh_rep_2	root	Quercus robur	total RNA	elongation zone of the taproot, medium root, growing in rhizotron
SW_sr_NN_rh_rep_3	SW_sr_NN_rh_rep_3	root	Quercus robur	total RNA	elongation zone of the taproot, medium root, growing in rhizotron
SW_sr_NT_rh_rep_1	SW_sr_NT_rh_rep_1	root	Quercus robur	total RNA	elongation zone of the taproot, medium root, dying root, growing in rhizotron
SW_sr_NT_rh_rep_2	SW_sr_NT_rh_rep_2	root	Quercus robur	total RNA	elongation zone of the taproot, medium root, dying root, growing in rhizotron
SW_sr_NT_rh_rep_3	SW_sr_NT_rh_rep_3	root	Quercus robur	total RNA	elongation zone of the taproot, medium root, dying root, growing in rhizotron
SW_sr_TN_krh_rep_1	SW_sr_TN_krh_rep_1	root	Quercus robur	total RNA	elongation zone of the taproot, medium root, thick root, grown in a container and then transferred to a rhizotron
SW_sr_TN_krh_rep_2	SW_sr_TN_krh_rep_2	root	Quercus robur	total RNA	elongation zone of the taproot, medium root, thick root, grown in a container and then transferred to a rhizotron
SW_sr_TN_krh_rep_3	SW_sr_TN_krh_rep_3	root	Quercus robur	total RNA	elongation zone of the taproot, medium root, thick root, grown in a container and then transferred to a rhizotron
SW_sr_TT_krh_rep_1	SW_sr_TT_krh_rep_1	root	Quercus robur	total RNA	elongation zone of the taproot, medium root, thick root, dying root, grown in a container and then transferred to a rhizotron
SW_sr_TT_krh_rep_2	SW_sr_TT_krh_rep_2	root	Quercus robur	total RNA	elongation zone of the taproot, medium root, thick root, dying root, grown in a container and then transferred to a rhizotron
SW_sr_TT_krh_rep_3	SW_sr_TT_krh_rep_3	root	Quercus robur	total RNA	elongation zone of the taproot, medium root, thick root, dying root, grown in a container and then transferred to a rhizotron

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Kościelniak P., Glazińska P., Zadworny M. (2023) Early stages in the formation of *Quercus robur* root system: variation in gene expression is linked to the functional type of roots.

Early stages in the formation of *Quercus robur* root system: variation in gene expression is linked to the functional type of roots.

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Keywords: gene, oak, RNA-Seq, root, transcriptome

Abbreviations:

TR – taproot with standard morphology

TTR – thick taproot

DTR – dying taproot

TDTR –thick and dying taproot

STR – short taproot characterized by standard morphology

MTR – medium taproot characterized by standard morphology

LTR – long taproot characterized by standard morphology

LR – lateral roots

MLR – lateral roots harvested from a medium taproot of standard morphology

LLR – lateral roots harvested from a long taproot of standard morphology

Abstract

Primary root development is well-recognized in annual plants. However, the time-dependent contribution of specific molecular mechanisms controlling taproot elongation, a stable adaptation of *Quercus robur* to enhance water uptake during drought, remains poorly understood. Based on temporal changes in gene expression patterns within taproots and lateral roots at specific points of their elongation, we characterized regulators of oak root formation in the context of a temporal and functional approach. We demonstrated that the multidirectional control of root elongation at the genetic expression cascade is associated with growth points after root emergence, taproot morphology and vitality, and is also divergent among functionally different roots, such as taproots and lateral roots. Specific gene expression patterns were observed at different points during taproot elongation, with an abundance of genes encoding transcription factors and hormone-related factors required for formation. We revealed different mechanisms of lateral root formation and modes of growth, which include the generation of distinct molecular mechanisms within taproots, further signaling lateral root growth at specific points of taproot length. Expression of the *LRP* gene in medium taproots occurred simultaneously with lateral root growth emergence from these taproots, mirroring lateral root organogenesis. Moreover, we demonstrated that transcription factors contribute to growth restriction of taproots with thick morphology, and we recognized that the highest variation in expression within thick roots could be related to the sequence of gene activation when genes responsible for thickening are first activated. However, thick and healthy taproots exhibited enhanced expression of genes likely involved in transcription processes regulation, nucleic acid and ribosome stability, in contrast to taproots of standard morphology, resulting in the activation of processes responsible for high metabolic and developmental activity. Our study improves the understanding of molecular mechanisms of crucial taproot growth regulators.

1. Introduction

The high diversity within root system enables water and nutrient uptake and anchoring plants into the soil (Freschet et al. 2021a). This diversity enables plants to grow and survive in various environments, including water-rich and water-limited soils (Benfey and Schiefelbein 1994), due to internal and external factors that jointly control each root during complex root system development (Mitsis et al. 2020). Thus, the exploration of soil resources by root systems within diverse soil environments is a function of molecular regulators, regulating both long primary (i.e., taproots) formation and further lateral roots growth (Petricka et al. 2012). Nevertheless, it is unclear whether taproot and lateral root growth are similarly controlled by the same signaling

pathways, as straightforward long-distance growth towards deep soil layers of the radicle or primary roots (i.e., the first root emerging from the seed) should already be mediated at the embryonic stage to: (i) maintain a fast growth rate, (ii) overcome compacted soil, and (iii) regulate root architecture patterning. On the other hand, lateral roots (synonyms: secondary root or branch root) arise as branches from the pericycle of the taproot, and their initiation and further growth mechanisms may also be controlled by the taproot. The processes driving primary and lateral root formation may be universal or remarkably specific, and root type development can be linked to plant persistence in the environment (annual or perennial). Indeed, a regulatory signaling network of primary and lateral root formation has been generated for Arabidopsis, characterized by uncomplicated cellular organization. However, root development in perennial plants requires an integrated assessment to identify how these factors modulate primary roots (i.e., taproots) as they grow deeper into the soil, which becomes more compacted, and roots become longer (Jin et al. 2013). Thus, despite the importance of mechanisms underlying taproot and lateral root growth, our understanding of how endogenous factors foster or inhibit these roots' initiation and growth in trees remains incomplete, and many questions need to be addressed. Notably, the recognition of signaling pathways governing root growth and plasticity in Arabidopsis cannot be easily extrapolated to other plants with distinct ontogenic programs, such as long-lived oaks. Therefore, knowledge of how root growth is arranged at the genetic level, plays a fundamental role (Malamy 2005).

Although it has been demonstrated that successive root elongation correlates with factors contributing to the specification of root meristem size (Benková and Hejatko 2009), involving varied gene regulatory networks, transcription factors, and hormone distributions (Scheres et al. 2004; Svolacchia et al. 2020; Wendrich et al. 2017), the interactions between different factors that control meristems driving rapid longitudinal elongation in plants other than annuals and regulating root responses to environmental constraints (e.g., dry or compacted soil) remain unknown. Identifying and understanding the functions of genes promoting root elongation and growth in trees, which may have to activate and silence various genes and transduce cross-root zone signals many times, can provide valuable information regarding the factors and signal cascades playing central roles in root growth (Casson and Lindsey 2003; Chaiwanon et al. 2016; Slovak et al. 2016).

The initiation and rate of root penetration into the soil have been shown to be gene-inducible (Clowes 2000). Genetic, transcriptional, and hormonal factors are important for root patterning of deep root growth (e.g., primary roots) or high branching capacity (e.g., laterals)

(Casson and Lindsey 2003; Xuan et al. 2016). Expression of genes controlling BR actions leads to meristem formation with increased growth potential (González-García et al. 2011; Hacham et al. 2011). The influence of gene interplay is especially evident during the modulation of root growth under water shortage (Carlsbecker et al. 2010; Haswell and Verslues 2015; Müller et al. 2016), where it has been demonstrated that the stimulation or inhibition of primary root growth is controlled through regulation of PHOSPHATE-ISOPENTENYLTRANSFERASE expression affecting cytokinin content (Nishiyama et al. 2011). Consequently, the coordination of induction and growth maintenance based on a functional network of regulatory signaling, gene expression, and hormone production initiating and regulating long taproot growth in oaks should consider the effects of temporal dimensions of gene expression profiles and plant signaling molecules from a functional perspective.

However, the genetic mechanisms underlying the control of taproot versus lateral root growth on a temporal scale are not well understood. Nevertheless, it has been shown that an increase in *PINs* expression contributes to the initiation of primary root development, but PINs are not entirely responsible in the arrangement of lateral root elongation (Blilou et al. 2005; Vieten et al. 2005), confirming that characterizing the genetic basis of signals promoting root growth enables understanding of functional differences in pathways governing divergent root growth. The PIN family is indeed an important regulator of root growth. An analysis of PIN2 factors indicated a restriction of lateral but not primary root growth by increasing its sensitivity to auxin transport, enhanced by GAs signaling (Gou et al. 2010; Li et al. 2018; Waidmann et al. 2019). These studies suggest that the synergism of gene expression may coordinate the growth of both root types and regulates primary root growth orientation into wet areas located deeper in the soil profile (Pierret et al. 2016). However, the way of gene expression patterns during taproot elongation and the specific role of its meristem in lateral root initiation and growth maintenance (Atkinson and Halfon 2014) remains an open question in trees.

The need for remodeling in relation to a plant's life strategy must be addressed because genes may operate differently in annual herbaceous species and trees at different stages of root growth. It has been confirmed that dynamic soil exploration results from transcriptional signaling networks (Waidmann et al. 2019). Thus, a plant's ability to diversely modulate primary and lateral roots, whether it lives for one or many years, may be of special importance for shaping taproot system architecture (Smith and De Smet 2012) and may be attributed to the signaling components regulating gene expression during taproot growth. For instance, some miRNAs identified in tree roots that have not been identified in model plants such as

Arabidopsis may have a unique function in root development (Osakabe et al. 2014). Moreover, the sequential stages of primary root growth regulated by transcription factors (TFs) (Drisch and Stahl 2015; Kościelniak et al. 2021; Mitsis et al. 2020; Sarkar et al. 2007) and TFs driving auxin transport may regulate other auxin response genes (Weijers et al. 2006). These, together with WOX TFs (WOX 5/7 and WOX11), not only induce and sustain primary root growth but also regulate lateral root development arising from primary roots (Baesso et al. 2018; Hu and Xu 2016). The challenge is to assess how growth patterns enabling taproots to reach deep soil layers are regulated in trees and whether the molecular regulatory mechanisms involved in the growth of primary roots are also involved during the formation of lateral roots, as there is no evidence for the same transcriptomic pattern among both root types in perennial plants.

The aim of our study was to evaluate 1) the temporal changes in gene expression patterns during taproot elongation, 2) how the morphology of the apical meristem affected root transcriptome profiles, and 3) the specificity in expression profiles among taproots and lateral roots. To achieve these goals, we performed RNA-Seq to obtain a complete picture of the taproot (as well as different taproot morphologies) and lateral roots transcriptome. Expression analysis of differentially expressed hormone-associated genes and genes coding transcription factors allowed us to identify potential differences in the expression profiles of specific hormones and changes in the activity of genes encoding elements of signal transduction pathways, hormonal responses, and key transcription factors depending on the size and morphology of taproots and lateral roots. We report that differential gene expression patterns during root growth improve our understanding of taproot and lateral root development at a genetic expression cascade in long-lived trees, providing supportive evidence for our hypothesis that taproot regulators play a significant role in shaping the growth of oak roots.

2. Material and methods

2.1. Plant material cultivation and sample collection

For RNA-Seq analyses, we used two-month-old seedlings of *Quercus robur*. Briefly, the growth root tip containing the meristematic zone of the taproots (TR) and lateral roots (LR) from the taproots of seedlings growing in a clear-walled chamber called a rhizotron were collected (Figure 1). The roots were categorized according to their length into short (5-9cm), medium (9.5-15cm), and long (>15.5cm), marked as S-short, M-medium, and L-long, respectively. In addition to classification by root length, they were also classified by their morphology into roots with thick morphology (TTR, taproots that were thicker than standard taproots and still actively growing). Furthermore, roots were classified based on their vitality

into active (TR) or dying (DTR). RNA was isolated from the ground material using Ribospin from GeneAll Biotechnology in Seoul, South Korea. Subsequently, a cDNA library was created using a TruSeq Stranded mRNA LT Sample Prep Kit and the library was sequenced using a NovaSeq platform from Illumina in San Diego, CA, USA, in the 150bp paired-end mode. The assembled transcripts were mapped to the reference genome. Annotations were made to databases such as PFAM, PFAM GO, BLASTP, BLASTX, BLAST GO, and KEGG. Identification of TFs was accomplished using PlantTFcat with default settings. The information presented in this publication has been stored in NCBI GEO and can be accessed through the GEO Series accession number GSE181860. Expression of selected genes after NGS sequencing was validated by RT-qPCR reactions. More information about seedlings cultivation, sample collection, sequencing, and validation of sequencing results by RT-qPCR is described in detail by Kościelniak et al. (2022).

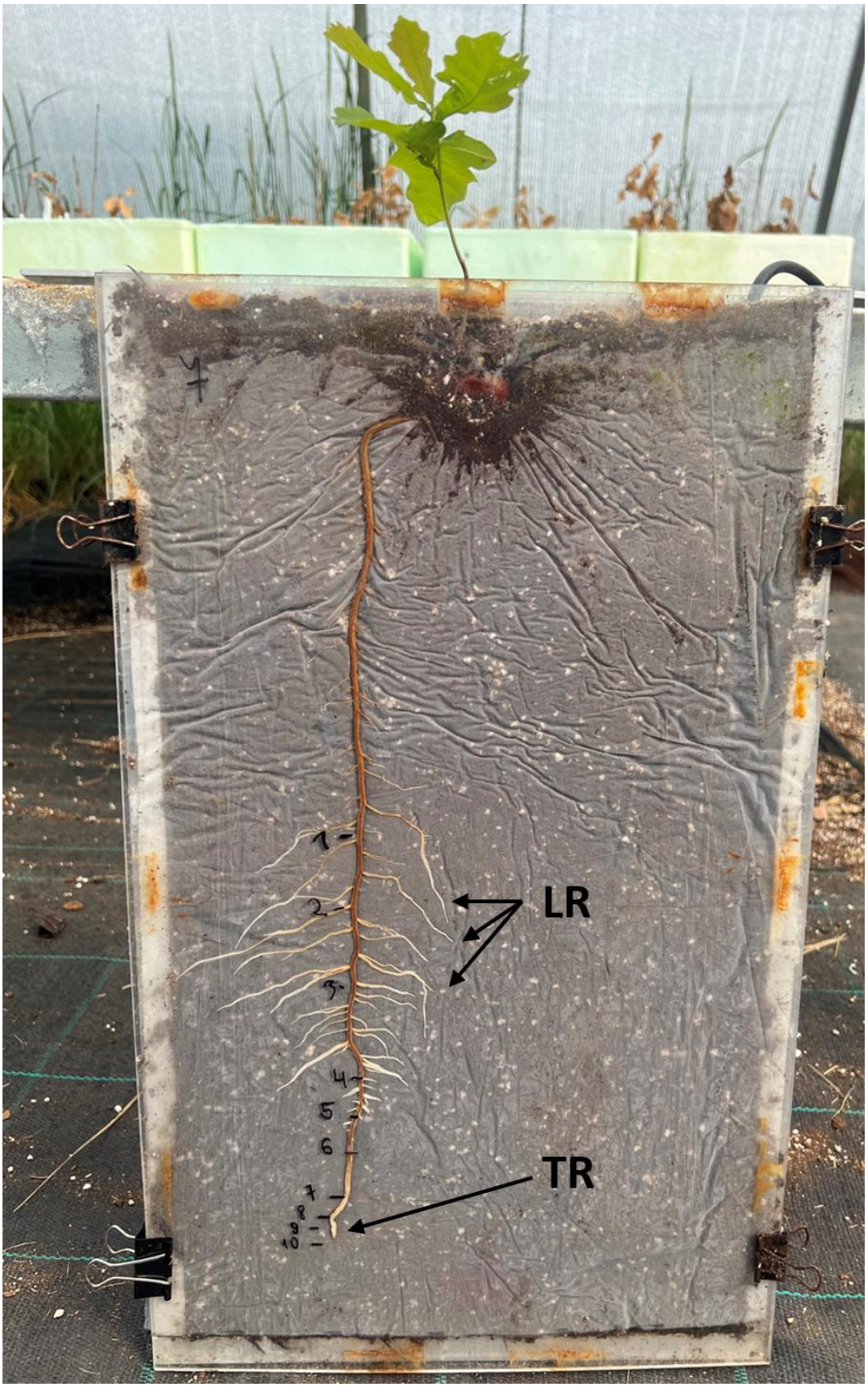

Figure 1. Sample image of well-established *Quercus robur* seedling growing in rhizotron system, TR – taproot, LR – lateral roots.

2.2.Identification of differentially expressed genes (DEGs)

Expression values were obtained with RSEM using Bowtie 2 as a mapper and observing the reads strandedness (Langmead and Salzberg 2012). Gene and single transcript expression levels were analyzed and presented in two different ways: expected count, TPM (Transcripts Per Million), and FPKM (Fragmentst Per Kilobase Of Exon Per Million Fragments Mapped). The expected count represents the number of paired reads that were mapped to a specific gene/transcript. TPM values indicate the number of paired reads mapped to a gene/transcript, normalized to the size of the sequenced data and transcript/gene length. FPKM values are also normalized to the size of the sequenced data and transcript/gene length, but using a different formula than TPM values. Differential analysis was performed with DESeq2 at the transcript level (Love et al. 2014). Genes whose expression changed at least 1.5 times (fold change > 1.5) with a statistical probability cut-off p-value <0.05 were considered to be differentially expressed.

2.3.Analysis of KEGG and GO

The analysis of GO term overrepresentation was performed using the script from the Trinotate-Trinotate-v3.2.2 package. GO analysis was conducted at two levels: ancestral (gene-level analysis taking into account the ancestral terms) and no_ancestral (similar to ancestral but not taking into account the ancestral terms). Obsolete terms were updated using data from the AmiGO database (amigo.geneontology.org). Some of the terms have an "obsolete" status in the database and were marked as "none" in the output. All identified genes obtained with Trinotate v 3.0.2 were used as background.

Ultimately, only the results obtained at the no_ancestral level were selected for the GO analysis. Expression values for each comparison were taken from the results of the edger program. Result files contained enriched terms or less frequent than statistically depleted terms with p-value <0.05. The same analysis was performed for the identified KEGG Pathways. The results were additionally filtered to include only terms derived from plants.

2.4.Anatomical analysis

The root systems of 2-month-old seedlings were gently washed with deionized water, after which the meristematic, elongation, and differentiation zones of short, medium, and long standard and thick taproots, as well as lateral roots, were excised. The samples were fixed immediately in a solution containing 2% formaldehyde and 2% glutaraldehyde in 0.05 M

phosphate-buffered saline, following the protocol outlined by Bagniewska-Zadworna et al. (2012). After a 24-hour fixation period, the roots were washed twice in 0.01 M phosphate-buffered saline and then twice in deionized water. The roots were dehydrated in a series of progressively increasing concentrations of ethyl alcohol (10%, 30%, 50%, 70%, 90%, 96%, and 100%) for 1 hour at each concentration, using ethyl alcohol obtained from Polish Chemical Reagents in Gliwice, Poland. The root samples were subsequently infiltrated with and embedded in Technovit 7100, a resin made by Heraeus Kulzer in Wehrheim, Germany. Cross-sections of roots with a thickness of 5 μm were prepared from the embedded samples using a rotary microtome (Leica RM2265), stained with a solution of 0.1% toluidine blue (Sigma, St. Louis, USA) dissolved in 1% sodium tetraborate (also from Sigma, St. Louis, USA). Cross-sections were observed at 5 to 20× magnification using a Carl Zeiss Axioskop 20 light microscope (Carl Zeiss, Germany), and photographs were taken using an Axiocam with AxioVision software, also from Carl Zeiss.

3. Results

3.1. Identification of Differentially Expressed Genes (DEGs)

Recognition of genes regulated growth and development of taproots and lateral roots, gene expression profiles was analyzed using RNA-Seq analysis. Furthermore, comparing the sequenced transcriptomes allowed us to identify genes (DEGs) engaged in the development of both root types. We compared transcriptomes of taproots and emerging lateral roots to determine the genetic landscape at different stages of root elongation and to define how changes in taproot meristem morphology contribute to root development. In this work, we concentrated primarily on the identification of DEGs encoding genes for transcription factors and plant hormones.

3.1.1. Gene expression changes within roots during elongation

Analyses were performed in four ways. First, we assessed whether temporal changes in DEGs contributed to the continuous elongation of roots with standard morphology when the roots were short (<9 cm long) and began to elongate, or if some DEGs contributed specifically to later stages of root elongation (>15.5 cm long). Evaluation of DEG expression revealed that 11,901 DEGs exhibited differential expression patterns during root elongation (Figure 3), including 9,071 down- and 2,830 up-regulated genes (Figure 2). These results demonstrated that the smallest differences (44.6% identical DEGs) in gene expression occurred between short and medium roots (2,802 differentially expressed genes). In contrast, in comparisons between

short and long roots, only 293 DEGs exhibited differential expression, while between medium and long roots, this number was 503. Only 140 differential genes were present in short, medium, and long roots simultaneously, indicating that the highest alteration in gene expression of root meristem was observed when lateral roots emerged from medium taproots but were initiated earlier in short roots. This observation was confirmed by the decrease in *LRP1* (*Protein LATERAL ROOT PRIMORDIUM 1*) in short roots and increased expression of this gene in medium and long taproots, and that very few genes are involved in regulating taproot growth consistently (Figure 3 A). In contrast, comparing lateral roots emerging from medium or long taproots displayed significant differences in expression, where only 215 DEGs (5.3%) were identical (Figure 3 B). For each of the selected comparisons, when sequences were ignored with unknown functions, genes with the most elevated and reduced expression patterns were able to be distinguished.

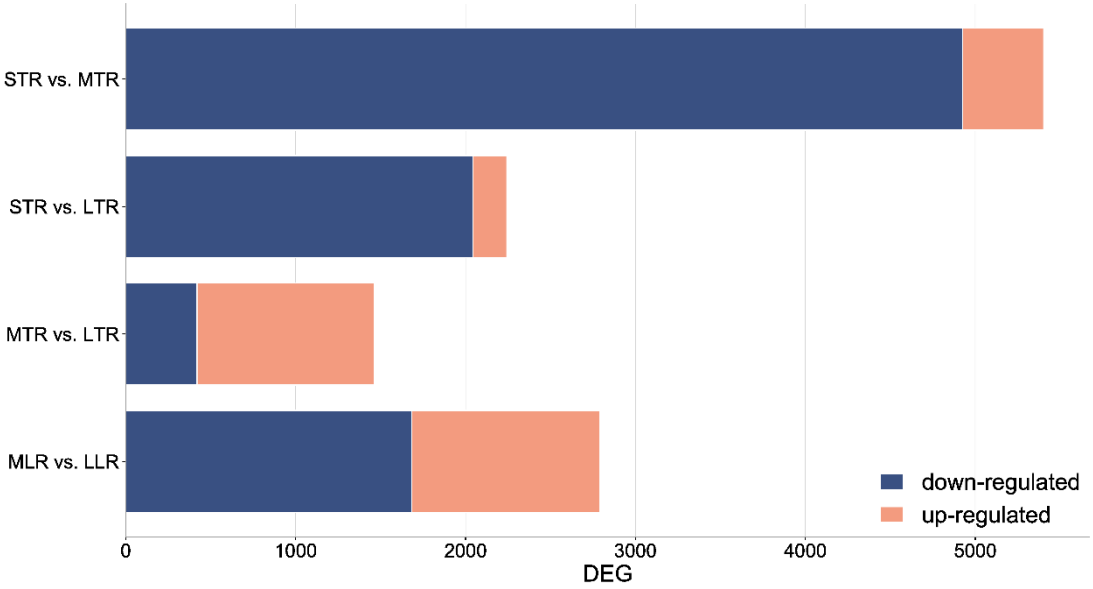

Figure 2. Number of differential DEGs in the taproot and lateral root at different stages of growth. STR – short taproot characterized by standard morphology; MTR – medium taproot characterized by standard morphology; MLR – lateral roots harvested from a medium taproot of standard morphology; LLR – lateral roots harvested from a long taproot of standard morphology.

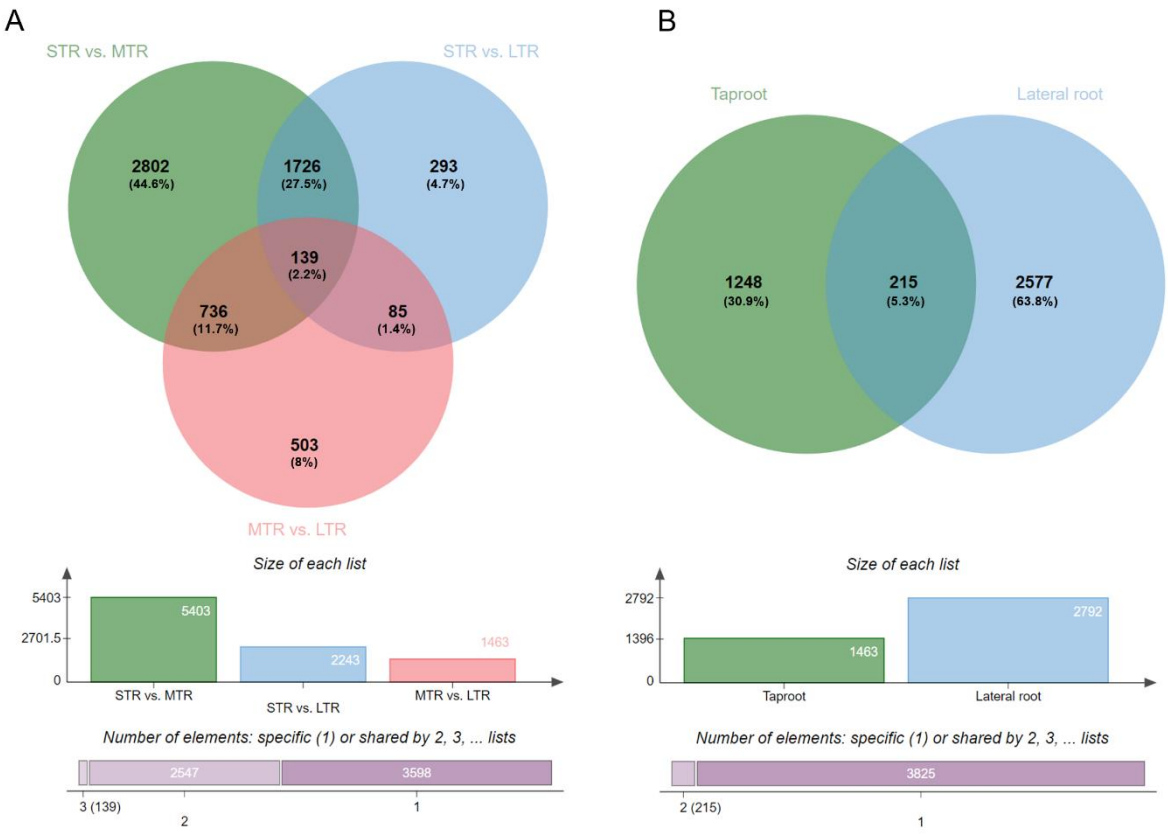

Figure 3. A) Venn diagrams of DEGs (in three comparisons: short vs. medium, short vs. long, and medium vs. long) display the number of genes with up- or down-regulated expression in short, medium, and long taproots for each comparison; B) Venn diagram of DEGs identified between medium and short roots in taproots and lateral roots based on Bardou et al. (2014). STR – short taproot characterized by standard morphology; MTR – medium taproot characterized by standard morphology; LTR – long taproot characterized by standard morphology.

3.1.1.1.Identification of transcription factors

The elongation stage had a strong effect on the number of DEGs and their regulation. The highest number of DEGs encoding transcription factors occurred within the comparison of short (STR) and long (LTR) taproots, with 145 DEGs, of which 142 were down-regulated. In long roots compared to short roots, their number decreased almost 4-fold (43 DEGs, of which 40 were down-regulated) and almost 5-fold within the medium (MTR) and short comparison (31 DEGs, of which 30 were upregulated). All transcription factors identified for this comparison are shown in Supplementary Table 1.

In comparison between STR and MTR, the expression of specific genes during root elongation was highly variable and dependent on root length. Pronounced down-regulation of transcription

factors from the *MYB* (*Myb family transcription factor MPH1*), *NAC* (*Transcription factor JUNGBRUNNEN 1*), and *WRKY* (*WRKY transcription factor 51*) families was observed in STR and MTR, as well as STR and LTR comparison, with only the latter family being down-regulated within the MTR and LTR comparison. DEGs TF gene family up-regulation was less uniform among comparisons, with the most pronounced effect manifested by the increased expression of *Ethylene-responsive transcription factors* (ERF022 and ERF013) at all steps of root elongation and *MYB* (*Transcription factor MYB1*) families exhibiting the highest expression when long roots were compared with short and medium ones. The highest levels of expression of genes coding transcription factors from *bHLH* (*Transcription factor bHLH120*) and *TCP* (*Transcription factor TCP15*) families were specific to the STR and MTR comparison. Enhanced levels of genes coding transcription factors *WER* (*Transcription factor WER*) expression were characteristic of STR and LTR roots, while *NF-Y* (*Nuclear transcription factor Y subunit A-3*) exhibited an increase in expression in the MTR and LTR comparison.

In contrast to taproots, comparative analysis between lateral roots of medium and long lengths exhibited only 8 DEGs encoding transcription factors with limited changes (i.e., 5 were down-regulated and 3 up-regulated). Similar to taproots, long lateral roots compared to medium ones showed down-regulation in *WRKY* (*WRKY transcription factor 51*) and *NAC* (*NAC transcription factor 56*) gene families, but contrarily, *ERF* (*Ethylene-responsive transcription factor 1A*) expression was reduced. Up-regulation of *TCP* (*Transcription factor TCP8*) and *MYB* (*Transcription factor MYB123*) families was consistent with the pattern observed in taproots, and up-regulation of genes coding transcription factors *AMS* (*Transcription factor ABORTED MICROSPORES*) was typical for lateral roots.

3.1.1.2. Identification of genes regulating hormone metabolism, signaling pathways, and responses

Since hormones initiate and coordinate root growth, we thoroughly analyzed DEGs related to hormone biosynthesis, conjugate synthesis, conjugate degradation, hormone transport, degradation/inactivation, and signal transduction-related processes. We analyzed DEGs associated with abscisic acid (ABA), brassinosteroid (BR), cytokinin (CK), ethylene (ET), gibberellin (GA), auxin (IAA), and jasmonic acid (JA) (Table 1). All DEGs related to hormones identified for this comparison are shown in Supplementary Table 2.

Overall, 59 down-regulated and 3 up-regulated DEGs related to hormone biosynthesis, conjugate synthesis, conjugate degradation, hormone transport, degradation/inactivation, and

signal transduction were identified in the STR between STR and MTR comparison in the transcriptome analysis. The most down-regulated DEGs in STR were identified among DEGs related to signal transduction in all analyzed hormones, with the highest numbers in ET (13 down-regulated) and IAA (12 down-regulated) hormones. These data indicate that these genes were up-regulated for MTR (Table 1).

Evaluations between STR and LTR revealed 18 down-regulated and 2 up-regulated DEGs related to conjugate degradation, hormone transport, degradation/inactivation, and signal transduction in STR. The most down-regulated DEGs in STR were identified among DEGs related to signal transduction in all hormones, with the highest numbers in ET and IAA. This implies that these genes were up-regulated for LTR (Table 1).

When MTR and LTR were compared, 6 down-regulated and 11 up-regulated DEGs related to hormone biosynthesis, hormone transport, degradation/inactivation, and signal transduction were identified in MTR. The most down-regulated gene was identified among DEGs related to signal transduction in GA, while the up-regulated genes were identified in hormone transport for IAA; indicating that these genes were up-regulated for LTR (Table 1).

In comparison between MLR and LLR, 17 down-regulated and 5 up-regulated DEGs were identified in DEGs related to hormone biosynthesis, synthesis, conjugate degradation, hormone transport, and signal transduction in MLR. The most down-regulated genes were identified in JA biosynthesis and conjugate degradation, and hormone transport in GA. This indicates that these genes were up-regulated for LLR (Table 1).

Table 1. Differential expression patterns of plant hormone metabolism, response and signaling-related genes in roots during elongation comparing short and medium taproots (STR vs. MTR), short and long taproots (STR vs. LTR), medium and long taproots (MTR vs. LTR) and lateral roots harvested from a medium taproot and long taproots (MLR vs. LTR) in relation to function. Please note that empty cells mean lack of the gene expression within a specific function

	STR vs. MTR			***STR vs. LTR***			***MTR vs. LTR***			***MLR vs. LTR***			
Hormone	Total no. of DEGs	down-regulated	up-regulated	Total no. of DEGs	down-regulated	up-regulated	Total no. of DEGs	down-regulated	up-regulated	Total no. of DEGs	down-regulated	up-regulated	Function
IAA	3	3	-	1	1	-							Conjugate synthesis
	2	2	-	1	-	1				3	3	-	Conjugate degradation
	4	3	1				5	-	5	3	3	-	Transport
	13	12	1	4	4	-	1	-	1	2	1	1	Signal transduction
CK	3	3	-	1	1	-	1	1	-				Degradation/Inactivation
	1	1	-	1	1	-							Signal transduction
ABA										2	2	-	Biosynthesis
	2	2	-	1	1	-	1	1	-				Degradation/Inactivation
	6	6	-	3	3	-				3	2	1	Signal transduction
ET	14	13	1	4	3	1	1	-	1	1	1	-	Signal transduction
JA	4	4	-				2	-	2	8	7	1	Biosynthesis
										1	1	-	Conjugate synthesis
	1	1	-	1	1	-	1	-	1				Degradation/Inactivation
	1	1	-				5	4	1				Signal transduction
GA	2	2	-										Biosynthesis
	3	3	-	1	1	-				3	1	2	Signal transduction
BR	1	1	-	1	1	-							Degradation/Inactivation
	2	2	-	1	1	-							Signal transduction

3.1.1.3. Functional annotation – GO and KEGG analysis

The selected genes were characterized by Gene Ontology (GO) terms. Genes exhibiting increased expression at different stages of taproot (small, medium, and long) and lateral roots (medium and long) were subsequently classified using a set of plant-specific GOs and grouped into following categories: biological process (BP), cellular component (CC), and molecular function (MF). Details of the GO analysis for differentially expressed genes (DEGs) are presented in Figure 4. The DEGs related to BP terms were predominantly enriched in oxidation-reduction and polysaccharide catabolic processes. The DEGs related to CC terms were mainly enriched in the extracellular region and matrix, apoplast, and cell wall. The DEGs related to MF terms were primarily enriched in heme binding, oxidoreductase activity, and chitinase activity.

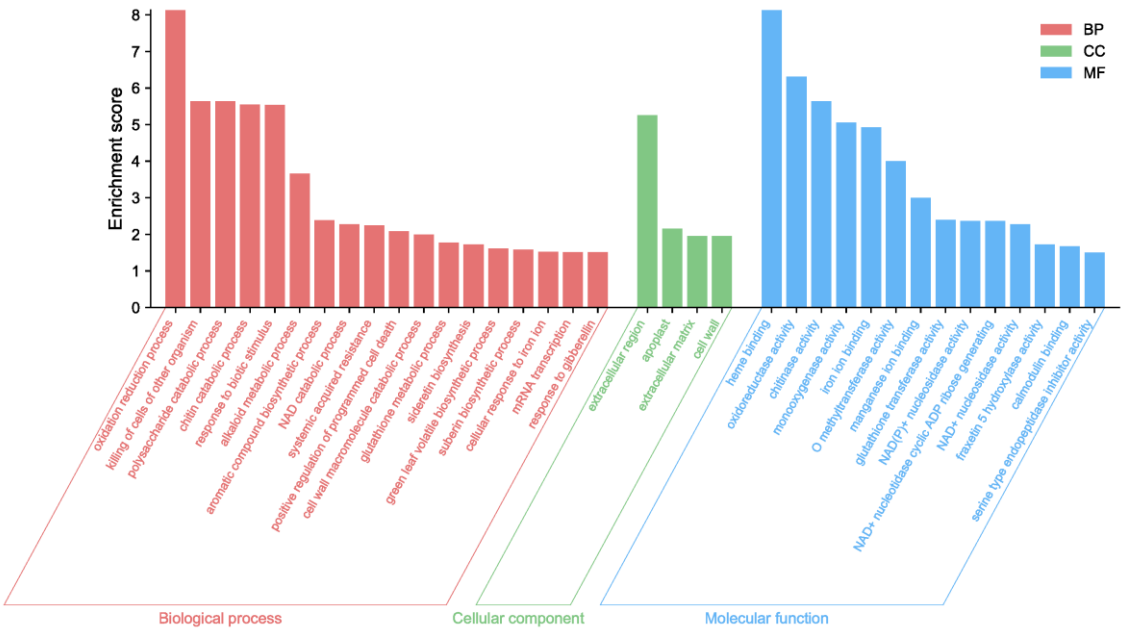

Figure 4. Gene Ontology (GO) term enrichment analysis for different stages of taproot and lateral roots. GO terms that were significantly enriched were chosen based on a false discovery rate (FDR) of < 1.5. Enrichment scores represent -log10(FDR). GO terms in the categories of Biological Processes, Cellular Components, and Molecular Functions are depicted in red, green, and blue, respectively.

To provide further insight into metabolic pathways and signal transduction pathways, Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway analysis of DEGs was performed. The most significantly enriched KEGG pathways are displayed in Figure 5. Among them, the

highest level of significance was observed for the metabolism of alpha-linolenic acid, linoleic acid, cysteine, methionine and amino and nucleotide sugars.

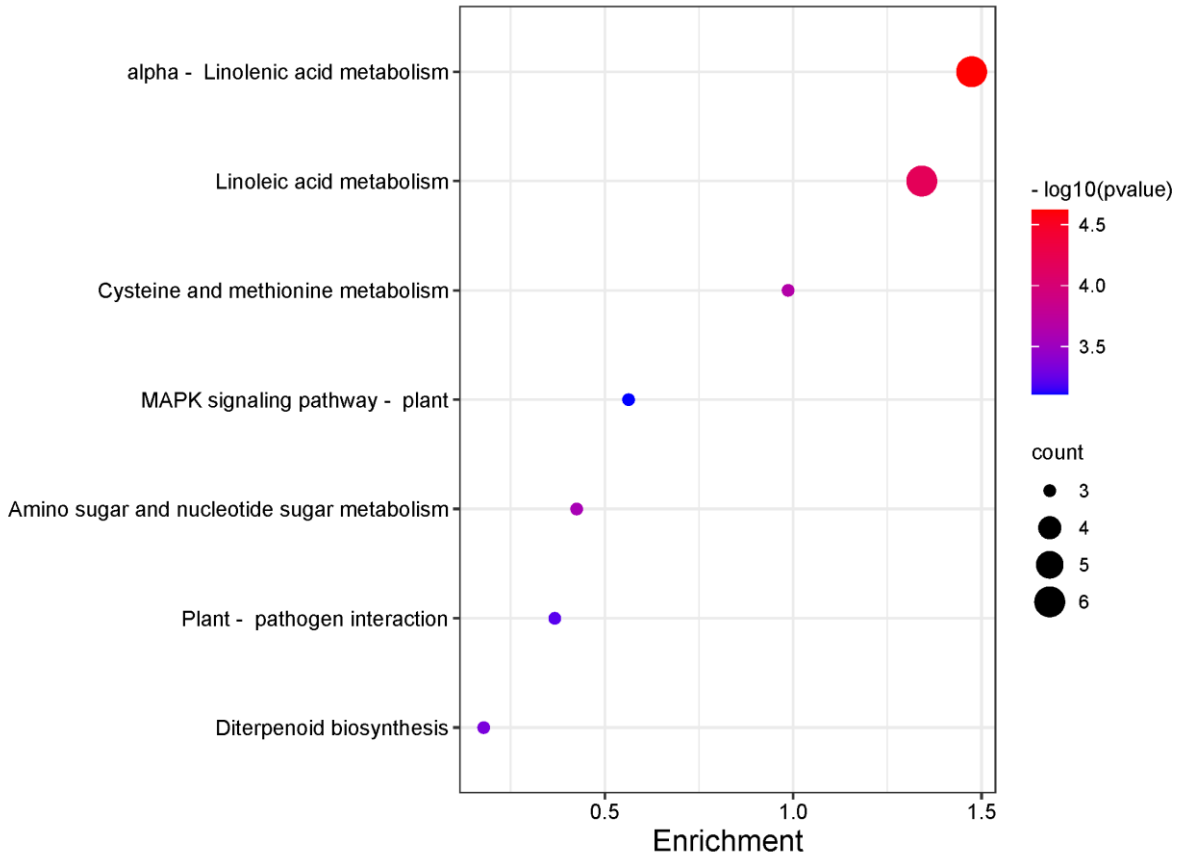

Figure 5. KEGG enrichment analysis for different stages of taproot and lateral roots. The figure displays KEGG metabolic pathways, where each circle represents a pathway, and the size of the circle corresponds to the number of genes enriched in that pathway. The degree of significance of the enrichment of differentially expressed genes (DEGs) in a pathway is indicated by -log10 (p-value). Low q-values are in blue, and high q-values are in red; the size of the circle is proportional to the number of enriched genes.

3.1.2. Gene expression changes within roots of different morphology

To better understand the interplay between variation in root tip morphology, vitality, and functional mechanisms engaged during root elongation, we conducted DEGs analysis within comparisons of a) standard taproot (MTR) and dying morphology (DTR); b) standard taproot (LTR_1) and thick (TTR) morphology; and c) standard taproot (MTR_1) and thick and dying taproot (TDTR) simultaneously. For the analysis between roots with standard morphology and thick and dying roots, we used a different notation for the tip of the taproot with standard

morphology, due to the difference in root length, as thick roots only occurred when the taproot was long. It is therefore reasonable to compare TTR to long taproots with standard morphology, which were the control for this comparison, named standard taproot (LTR_1) (Figure 6). We showed that, in total, 23,725 DEGs underwent differential expression in roots with differing morphology (Figure 7), with 11,459 down-regulated and 12,266 up-regulated (Figure 6). Briefly, the elongation of standard and thick taproots exhibited relatively high changes in the expression of DEGs (17.1%); the DEGs expression differentiated the declining pattern of both root types. Declining processes were related to the elevation of DEGs within tips of thick roots (47.1%), but the senescent tips of standard roots exhibited less variation in expression (7.5%). The highest number of DEGs was found between roots with standard morphology (MTR_1) and thick and dying roots (TDTR), reaching 12,869 DEGs, including 6,120 down-regulated and 6,749 up-regulated.

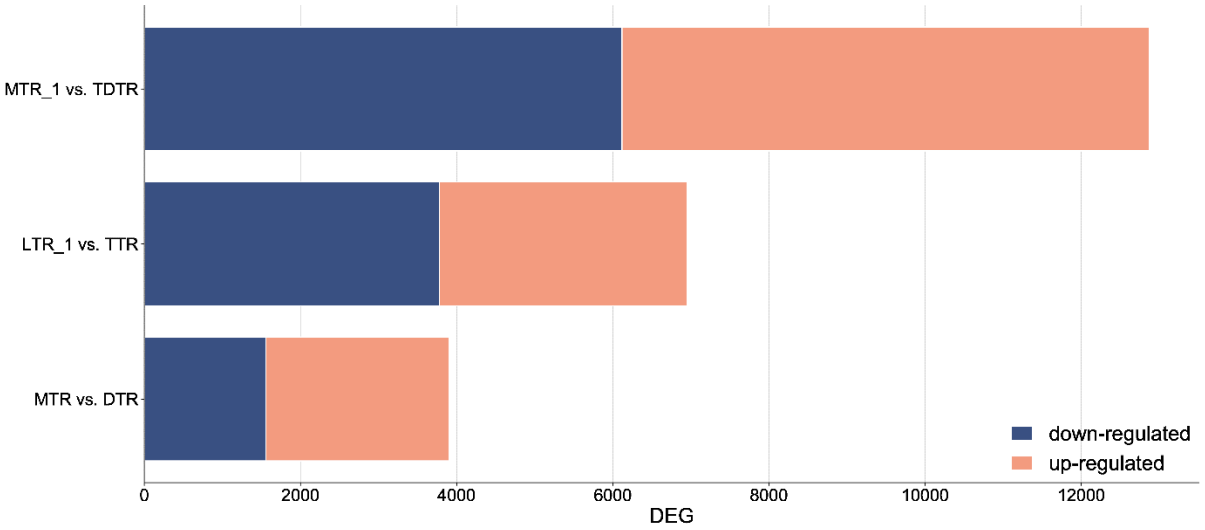

Figure 6. Number of differential DEGs in the taproot characterized by different morphology. MTR, MTR_1 – medium taproot characterized by standard morphology; TDTR – thick and dying taproot; LTR, LTR_1 – long taproot characterized by standard morphology; TTR – thick taproot; DTR – dying taproot.

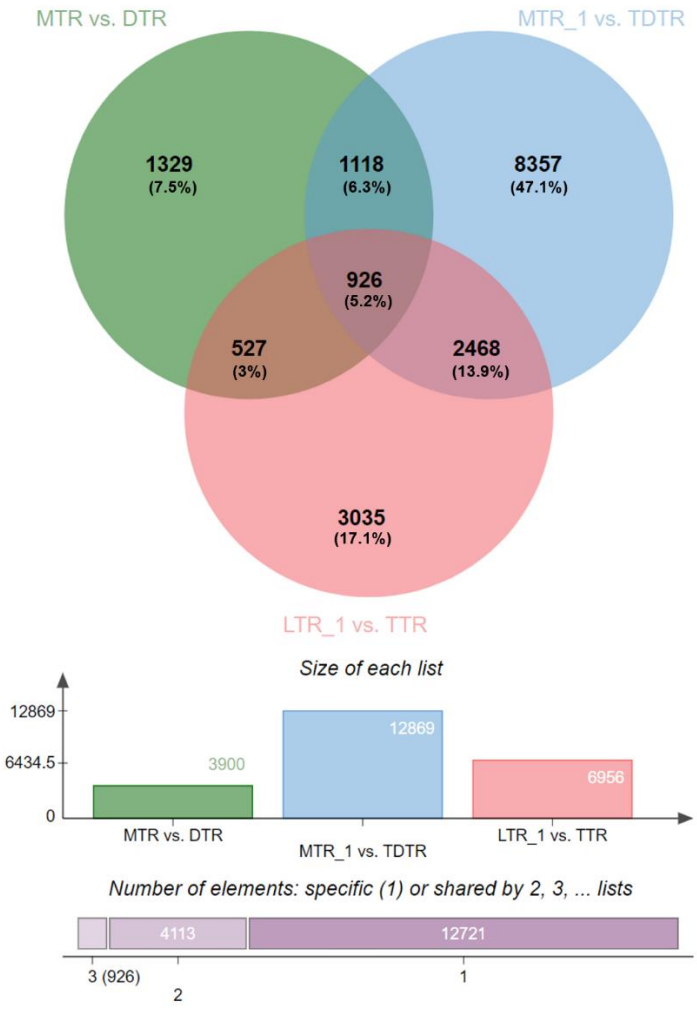

Figure 7. Venn diagrams of DEGs show the number of genes with up-regulated or down-regulated expression in normal, thick, and thick/dying taproots roots based on Bardou et al. (2014). MTR – medium taproot characterized by standard morphology; DTR – dying taproot; MTR – medium taproot characterized by standard morphology; TDTR –thick and dying taproot; LTR – long taproot characterized by standard morphology; TTR – thick taproot.

3.1.2.1.Identification of transcription factors

Specifically, we demonstrated that root thickness had a significant impact on the expression of 121 DEGs, encoding 85 down-regulated and 36 up-regulated transcription factors, when comparing TNTR and TTR. Furthermore, our results revealed that changes in 64 DEGs expression were limited in the tips of declining roots with standard morphology (21 down-regulated and 43 up-regulated). In contrast, the specific response was much more pronounced in thick, dying roots, inducing a 4-fold increase (265 DEGs, of which 126 were down-regulated and 139 up-regulated) compared to tips of standard roots. This indicates that declining was

manifested by a stronger signal within thick roots. All transcription factors identified for this comparison are presented in Supplementary Table 3.

We found that genes coding for transcription factors from the *AIL* (*AP2-like ethylene-responsive transcription factor AIL5*), *MYB* (*Transcription factor MYB59*), and *bHLH* (*Transcription factor bHLH154*) families enhanced transcript levels and were observed in the transcription factors' gene expression levels within tips differing in thickness, i.e., standard (TR) and thick (TTR). Conversely, the most down-regulated expression of *WRKY* (*WRKY transcription factor 51*), *ERF* (*Ethylene-responsive transcription factor ERF095*), and *ASIL* (*Trihelix transcription factor ASIL2*) gene families occurred when comparing tips of both root types. We observed *ERF (Ethylene-responsive transcription factor ERF115*, *87*, and *86*) as well as *WRKY* (*WRKY transcription factor 12*, *6*, and *71*) expression as characteristic for dying roots (DTR). Enhanced expression of *ERF115*, *98*, and *95* (*Ethylene-responsive transcription factor ERF115*, *98*, and *95*), *MYC2* (*Transcription factor MYC2*), *NAC42* (*Transcription factor JUNGBRUNNEN 1*), and *WRKY75* (*WRKY transcription factor 75*) was noted within thick and dying roots (TDTR).

3.1.2.2.Identification of genes involved in plant hormone metabolism, signaling pathways and response

Since hormones significantly contribute to the regulation of root development, we closely examined genes involved in various plant hormone-related processes in taproots with differing root morphology. The comparison of growth tips with varied morphology (thick - TTR, dying - DTR, and thick and dying - TDTR) to taproot tips of standard morphology (TR) revealed marked expression changes (primarily up-regulated in root tips with standard morphology) among hormone-related genes, not only regulated their biosynthesis but also related to their response (Table 2 and Supplementary Table 4).

The comparison between TR and TTR showed changes in DEGs, mainly genes related to GA, IAA (and conjugate synthesis), and JA biosynthesis. Conversely, when comparing TR and DTR, the expression of BR, CK, GA, IAA, and JA biosynthesis genes decreased. In contrast, changes in the activity of all hormone biosynthesis genes can be observed when comparing TR and TDTR (Table 2).

Similar to hormone biosynthesis genes, the most significant changes in the expression of hormone signal transduction pathway genes and responses to hormones occur in TDTR. All

studied hormones were affected, and the highest number of identified hormone-related DEGs in this category was in ET (15 down-regulated and 22 up-regulated DEGs) (Table 2).

Table 2. Differential expression patterns of plant hormone metabolism, response, and signaling-related genes in roots with different morphology comparing taproot with standard morphology (MTR, MTR_1 and LTR_1), dying taproot (DTR), thick and dying taproot (TDTR) and thick taproot (TTR) in relation to function. Please note that empty cells mean lack of the gene expression within a specific function.

	MTR vs. DTR			***MTR_1 vs. TDTR***			***LTR_1 vs. TTR***			
Hormone	Total no. of DEGs	down-regulated	up-regulated	Total no. of DEGs	down-regulated	up-regulated	Total no. of DEGs	down-regulated	up-regulated	Function
IAA	2	-	2	4	-	4	2	-	2	Biosynthesis
	1	-	1	5	2	3	2	1	1	Conjugate synthesis
	3	-	3	5	3	2	1	1	-	Conjugate degradation
	7	5	2	13	7	6	7	3	4	Transport
	8	3	5	22	7	15	17	8	9	Signal transduction
CK	2	1	1	5	1	4	4	2	2	Biosynthesis
	1	1	-	2	1	1	1	1	-	Degradation/Inactivatiom
	3	1	2	6	2	4	3	1	2	Signal transduction
ABA				2	1	1	2	1	1	Biosynthesis
				4	3	1	8	7	1	Degradation/Inactivation
	2	1	1	5	3	2				Signal transduction
ET	-	-	-	1	-	1				Biosynthesis
	9	5	4	37	15	22	11	5	6	Signal transduction
JA	6	1	5	13	8	5	3	2	1	Biosynthesis
				4	4	-	1	-	1	Degradation/Inactivation
				2	2	-	1	1	-	Signal transduction
GA	2	-	2	8	-	8	4	-	4	Biosynthesis
				2	2	-	1	1	-	Degradation/Inactivation
	2	-	2	10	-	10	8	2	6	Signal transduction
BR	3	-	3	5	-	5	1	-	1	Biosynthesis
	1	-	1	5	2	3	1	-	1	Degradation/Inactivation
				5	-	5	1	1	-	Signal transduction

3.1.2.3.Functional annotation – GO and KEGG analysis

The selected genes were described by GO terms. Genes exhibiting increased expression in different taproot tips (thick, dying, and thick and dying) compared to standard taproots were classified using a set of plant-specific GOs and grouped into three main categories (biological process – BP, cellular component – CC, and molecular function - MF). Details of the GO analysis for DEGs are presented in Figure 8. The DEGs related to BP terms were predominantly enriched in oxidation-reduction processes, hydrogen peroxide catabolic processes, and plant-type secondary cell wall biogenesis. DEGs related to CC terms were mainly enriched in the apoplast, extracellular region, and cell wall. DEGs related to MF terms were primarily enriched in heme binding, hydrolyzing O-glycosyl compounds, and peroxidase activity.

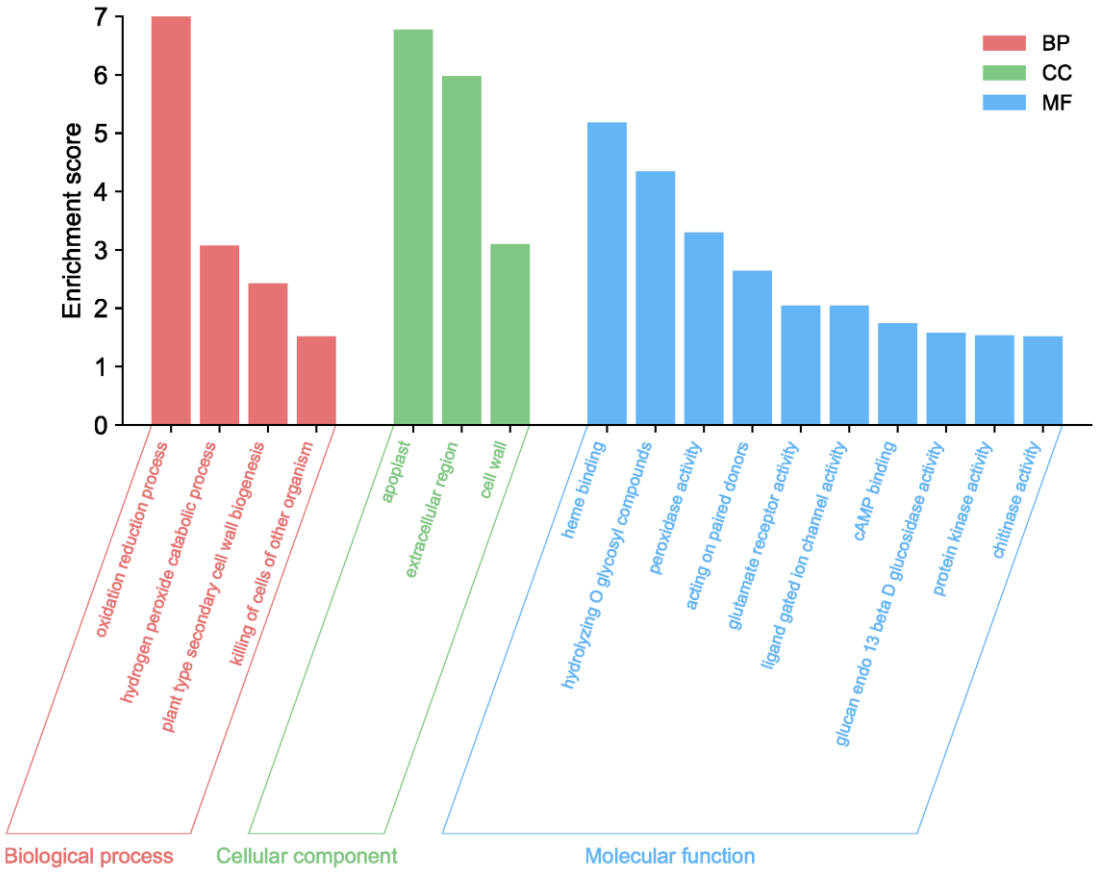

Figure 8. Gene Ontology (GO) Term Enrichment Analysis for Different Meristems in Taproots. GO terms that were significantly enriched were chosen based on a false discovery rate (FDR) of < 1.5. The enrichment score is presented as -log10(FDR). GO terms for the categories of Biological Processes, Cellular Components, and Molecular Functions are represented in red, green, and blue, respectively.

To gain further understanding of metabolic pathways and signal transduction in KEGG pathways, an analysis of differentially expressed genes (DEGs) was conducted. The most significantly enriched KEGG pathways are depicted in Figure 9. Among these, the highest level of significance was observed for Phenylpropanoid biosynthesis, Cyanoamino acid metabolism, Pentose and glucuronate interconversions, and Metabolic pathways.

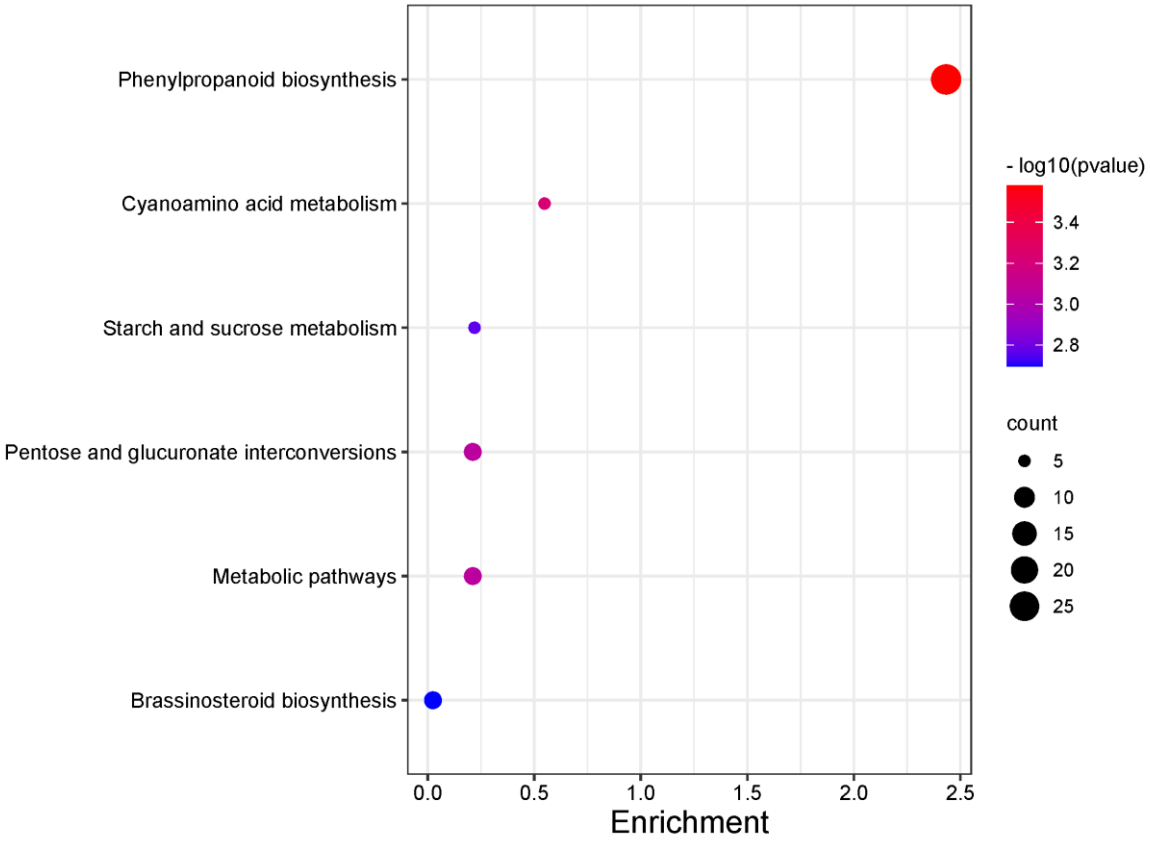

Figure 9. KEGG enrichment analysis for different meristems of taproots. The figure displays KEGG metabolic pathways, where each circle represents a pathway, and the size of the circle corresponds to the number of genes enriched in that pathway. The degree of significance of the enrichment of differentially expressed genes (DEGs) in a pathway is indicated by -log10 (p-value). Low q-values are in blue and high q-values are in red; the size of the circle is proportional to the number of enriched genes.

3.1.3. Gene expression changes within different types of roots

Production and elongation of lateral roots are enables soil exploration and transport absorbed minerals and water. Assessing the characteristics of taproots driven by DEG family expression in emerging lateral roots plays a central role in growth regulation. To monitor how sequential

steps of taproot elongation affect gene expression in lateral roots, we identified the difference in their expression within tips of medium and long taproots and lateral roots emerged among them (Figure 10). We revealed that along taproot elongation, the difference in gene expression (11,579 DEGs) increased, i.e., 40.7%. In contrast, when the taproots were of medium length, many more DEGs in tips of lateral roots showed similarity to the expression pattern occurring in tips of these taproots (81.1%; Fig. 11). Specifically, within lateral roots harvested from long taproots, 7,878 DEGs were down-regulated and 3,701 up-regulated. However, 40.4% of DEGs matched lateral roots harvested from medium and long taproots (Figure 11).

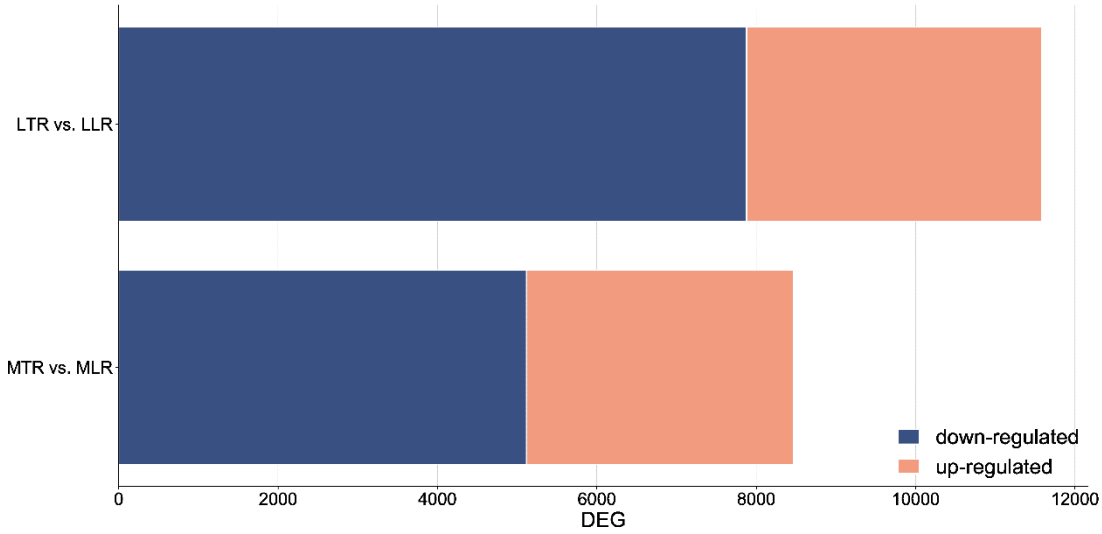

Figure 10. Number of differential DEGs in the taproot characterized by distinct morphology. LTR – long taproot characterized by standard morphology; LLR – lateral roots harvested from a long taproot of standard morphology; MTR – medium taproot characterized by standard morphology; MLR – lateral roots harvested from a medium taproot of standard morphology.

3.1.3.1 Identification of transcription factors

Comparative analysis of expression patterns indicated that a comparable number of DEGs occurred within lateral roots taken from medium and long taproots (249 and 289 DEGs, respectively), including 174 down-regulated and 75 up-regulated DEGs within the first comparison. Taproot elongation increased the percentage of down-regulated DEGs by 20% (259) and showed a 2 times lower expression level of up-regulated genes (30 in number) in LR and long TR comparisons. Reduced expression in taproots within both comparisons was found in *NF-Y* (*Nuclear transcription factor Y subunit B-4*), *MOF* (*Myb family transcription factor MOF1*), *ORG* (*Transcription factor ORG2*) families, and *TCP* (*Transcription factor TCP2*). In contrast, within both comparisons, we observed enhanced expression levels of *ABI* (*Ethylene-*

responsive transcription factor ABI4) and *bHLH* (*Transcription factor bHLH146* and *96*; medium and long, respectively) in LR. Within medium taproots, specific promotion of *MYB* (*Transcription factor MYB1*), *WER* (*Transcription factor WER*), and *WIN* (*Ethylene-responsive transcription factor WIN1*) families was observed. Taproot elongation activated the expression of certain transcription factors *ERF* (*Ethylene-responsive transcription factor 12*), *PRE* (*Transcription factor PRE6*), and *PLATZ* (*Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1*) families, and this gene had lowest transcript levels in LR. All transcription factors identified for this comparison are shown in Supplementary Table 5.

3.1.3.2. Identification of genes involved in plant hormone metabolism, signaling pathways, and responses

We further investigated whether the expression levels of hormone-related genes varied based on root type. Consequently, we conducted a differential expression gene (DEG) analysis for medium and long taproot apices in comparison with lateral roots derived from both medium and long taproots (Table 3, Supplementary Table 6).

A comparison of hormone-related gene activities between taproots (TR) and lateral roots (LR) derived from medium (MTR and MLR) and long (LTR and LLR) roots revealed similar trends (Table 3 and Supplementary Table 6). In both comparisons, the activities (including up- and down-regulation) of genes associated with the biosynthesis of all examined hormones changed. Among signal transduction and response pathway genes, DEGs related to all hormones, except for JA, were identified. The highest number of DEGs in this category were associated with ABA, ET, and IAA. Moreover, analyses demonstrated increased expression of genes linked to ABA, BR, CK, GA, and JA degradation/inactivation in lateral roots.

Gene expression of IAA transporters exhibited differential patterns depending on organ and root size. In medium roots, decreased expression in MLR was observed for genes from the *PILS* (*Protein PIN-LIKES 1*) family and the *PIN2* (Auxin efflux carrier component 2) gene, while increased expression was observed for genes from the *ABCB* family (*ABC transporter B family members 9, 11, 15, 21,* and *29*). In LLR, higher expression levels of *PIN5* (*Auxin efflux carrier component 5*) and *PIN6* (*Auxin efflux carrier component 6*), as well as *ABCB* genes (*Auxin efflux carrier components 2*, *8*, *9*, *11*, *15*, *21*, and *29*) were observed. Conversely, lower expression levels were detected for *PIN2* (*Auxin efflux carrier component 2*), *PID* (*Protein kinase PINOID*), and *ABCB19* (*ABC transporter B family member 19*) (Supplementary Table 6).

Table 3. Differential expression patterns of plant hormone metabolism, response, and signaling-related genes in in roots during elongation comparing medium taproots and lateral roots (MTR vs. LTR) and long taproot and lateral roots (LTR vs. LLR). Please note that empty cells mean lack of the gene expression within a specific function.

	MTR vs. MLR			***LTR vs. LLR***			
Hormone	Total no. of DEGs	down-regulated	up-regulated	Total no. of DEGs	down-regulated	up-regulated	Function
IAA	4	2	2	6	2	4	Biosynthesis
	5	4	1	2	2	-	Conjugate synthesis
	2	2	-	2	2	-	Conjugate degradation
	9	5	4	13	10	3	Transport
	27	14	13	29	20	9	Signal transduction
CK	2	2	-	4	2	2	Biosynthesis
	1	1	-	1	1	-	Conjugate synthesis
	4	3	1	4	4	-	Degradation/Inactivation
	2	2	-	3	3	-	Signal transduction
ABA	2	1	1	3	3	-	Biosynthesis
	1	1	-	2	2	-	Degradation/Inactivation
	27	17	10	41	34	7	Signal transduction
ET	8	4	4	13	10	3	Biosynthesis
	26	14	12	25	15	10	Signal transduction
JA	9	7	2	14	10	4	Biosynthesis
				1	1	-	Conjugate synthesis
	1	1	-	5	4	1	Degradation/Inactivation
GA	6	3	3	2	1	1	Biosynthesis
	2	2	-	1	1	-	Degradation/Inactivation
	6	3	3	4	3	1	Signal transduction
BR	3	-	3	3	-	3	Biosynthesis
	4	4	-	5	4	1	Degradation/Inactivation
	10	7	3	7	5	2	Signal transduction

3.1.3.3. Functional annotation – GO and KEGG analysis

The selected genes were characterized by Gene Ontology (GO) terms. We then classified genes exhibiting increased expression in different root types (medium and long taproots, and lateral roots) using a set of plant-specific GO terms. These genes were grouped into three primary categories: biological process (BP), cellular component (CC), and molecular function (MF). Detailed results of the GO analysis for differentially expressed genes (DEGs) are presented in Figure 12. DEGs associated with BP terms were predominantly enriched in oxidation-reduction processes, lignin catabolic processes, and plant-type secondary cell wall biogenesis. DEGs corresponding to CC terms were primarily enriched in the extracellular region, apoplast, and cell wall. Lastly, DEGs related to MF terms were mainly enriched in heme binding, acting on paired donors, and iron ion binding.

To gain further insights into metabolic pathways and signal transduction, we conducted a Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway analysis of DEGs. The most significantly enriched KEGG pathways are displayed in Figure 13. Among them, the highest levels of significance were observed for cyanoamino acid metabolism, phenylpropanoid biosynthesis, and metabolic pathways.

3.2.Heatmap

A heatmap was generated to examine the similarities in gene activity and identify the determinants of root growth patterns within the soil. Differentially expressed genes (DEGs) identified in taproots and lateral roots were clustered based on their expression dynamics (Figure 14), taking into account gene expression at different elongation stages (short, medium, and long, labeled STR, MTR, and LTR, respectively). We compared different stages (short, medium, and long taproots [STR, MTR, and LTR, respectively], lateral roots derived from medium or long taproots [MLR and LLR, respectively]) and considered meristems of various morphologies (standard-TR; dying-DTR and its control sample – MTR; thick-TTR and its control sample – LTR_1; and thick and dying-TDTR and its control sample standard root MTR_1). The list of genes represented in each cluster is provided in Supplementary Table 7. Genes were categorized into 10 clusters, each distinguished by individual gene groups.

Within these 10 clusters, cluster 1 exhibited the highest expression levels of DEGs in medium and long taproots (STR, MTR, MTR_1, LTR, and LTR_1) and in lateral roots (MLR and LLR), while the lowest expression levels were observed in thick and dying roots (TDTR), dying roots (DTR), and thick roots (TTR). Genes included in this group, such as *TIP* (*Aquaporin TIP1-3*),

are responsible for the precise regulation of not only water movement but also the transport of some small inert molecules, such as glycerol, urea, ammonia, hydrogen peroxide, and formamide (Liu et al. 2003). Additionally, *PER27* (*Peroxidase 27*) and *GSTF* (*Glutathione S-transferase*) participate in the biosynthesis and degradation of lignin, suberization, auxin catabolism, scavenging of reactive oxygen species such as H_2O_2, oxidation of toxic reductants, reactions to external stimuli like wounding, pathogen attack, and oxidative stress, as well as cell detoxification (Gullner et al. 2018; Yahong et al. 2001). This suggests that cluster 1 plays a crucial role not only in tissue development and elongation but also in cell detoxification, thus protecting cells from damage.

Gene expression levels in clusters 2 and 3 exhibit substantial variation across different stages of standard taproot growth (STR, MTR, and LTR), but less variation across taproots with different morphologies (TTR, DTR, and TDTR) and both lateral roots (MLR and LLR). Genes in cluster 2 primarily include groups such as *ERLI1* (*Lipid transfer protein EARLI 1*) and *DIRL1* (*Putative lipid-transfer protein DIR1*), which are responsible for lipid transport, as well as *TBB8* (*Tubulin beta-8 chain*) and *TBA* (*Tubulin alpha chain*). The proteins encoded by these latter genes are key components of microtubules and help construct the cytoskeleton, modulating cell shape and size (Hashimoto 2015; Lascombe et al. 2008; Maldonado et al. 2002; Shi et al. 2011; Xu et al. 2011). This cluster also contains *GASAE* and (*Gibberellin-regulated protein 14*), which exhibit high expression within STR and LTR, suggesting intensive developmental processes. Additionally, a gibberellin-related gene, *GASA6* (*Gibberellin-regulated protein 6*) in Cluster 2, likely regulates seed germination (Herzog et al. 1995). In contrast, higher expression levels in cluster 3 are associated with genes encoding oxidative enzymes that catalyze various reactions in plant metabolism, such as *ODD19* (*2-oxoglutarate-dependent dioxygenase 19*) and *BGL* (*Beta-glucosidase*) (Ahn et al. 2009; Wang et al. 2021).

Cluster 4 genes exhibit higher expression levels in lateral roots (MLR and LLR) and lower levels in standard roots, including short, medium, and long roots. This reveals a strong correlation between root functional types and expression patterns, as the high expression of aquaporin-related genes *PIP12*, *PIP21*, *PIP24*, and *PIP27* (*Aquaporin PIP1-2*, *PIP2-1*, *PIP2-4*, and *PIP2-7*) is consistent with the primary function of lateral roots, which is the absorption and water transport across cell membranes (Shibasaka et al. 2021).

Cluster 5 genes display the highest expression levels in lateral roots (MLR and LLR) and roots with variable morphologies (TTR, DTR, and TDTR). In contrast, the lowest expression levels of genes in this cluster are characteristic of early stages of taproot growth, i.e., STR, MTR, and

LTR. One of the genes, *CLE6* (*CLAVATA3*/*ESR (CLE)-related protein 6*), suppressing stem cell development in root and shoot development (Whitford et al. 2008). Moreover, many genes responsible for responding to biotic and abiotic stresses were upregulated in the TTR, DTR, and TDTR roots.

Higher expression of genes in clusters 6-7 is mainly characteristic of taproots with different morphologies (TTR, DTR, and TDTR), with the strongest increase in expression found in TDTR roots. This cluster contains numerous genes responsible for protecting the plant against pathogens. The low expression level of genes involved in plant defense against pathogens, biotic and abiotic stresses, and antioxidant protection such as *PER* (*Cationic peroxidase 1*), *CHI5* (*Endochitinase EP3*) and colonization by growth-promoting rhizobacteria (PGPR), represented by the *TLP1* (*Thaumatin-like protein 1*) and *KI104* (*Kunitz type trypsin inhibitor 104*) genes within STR, MLR, and LLR, but high in TTR, DTR, and especially TDTR, suggests that thick taproots protect themselves against biotic conditions more effectively than taproots of standard morphology (do Amaral et al. 2022; Léon-Kloosterziel et al. 2005; Vaghela et al. 2022). This cluster also contains many genes responsible for modifying the cell wall in response to pathogen attacks, such as *PRP* (*Repetitive proline-rich cell wall protein*) and *EPR1* (*Proline-rich extensin-like protein EPR1*), with increased expression levels in thick roots (TTR and TDTR), supporting the above hypothesis (Fowler et al. 1999; Kavi Kishor et al. 2015).

Specific to TTR, the highest expression of genes likely involved in transcription processes regulation, as well as nucleic acid and ribosome stability, i.e., *TAR1* (*Protein TAR1*), *RRT15* (*Regulator of rDNA transcription protein 15*), *ART2*, and *ART3* (*Putative uncharacterized proteins ART2 and ART3*), suggests high metabolic and developmental activity of TTR in cluster 8 (Bonawitz et al. 2008).

Clusters 9-10 primarily encode transcription factors that manifest plant response against pathogen invasion, with induced expression observed in dying root genes (DTR), slightly lower in thick roots (TTR), as well as STR and LTR. The lowest signal was detected in young and healthy MLR and LLR roots. Consistently, a key gene, *CPR38* (*Cysteine-rich repeat secretory protein 38*), which modulates host immunity in plant-pathogen interactions, exhibited increased expression (Hussain et al. 2022). Genes in cluster 10 also showed elevated expression levels mainly for DTR, and the lowest in LR. Results indicated significant overexpression of genes related to cell wall organization, such as *GP1* (*Polygalacturonase-1 non-catalytic subunit beta*), which depolymerizes and solubilizes cell wall polyuronides, a vital component of cell wall architecture. This can contribute to the restriction of dying root elongation (Watson et al. 1994).

In cluster 10, a clear separation was observed between gene expression in DTR and other analyzed root variants, with most genes being upregulated in the former root type.

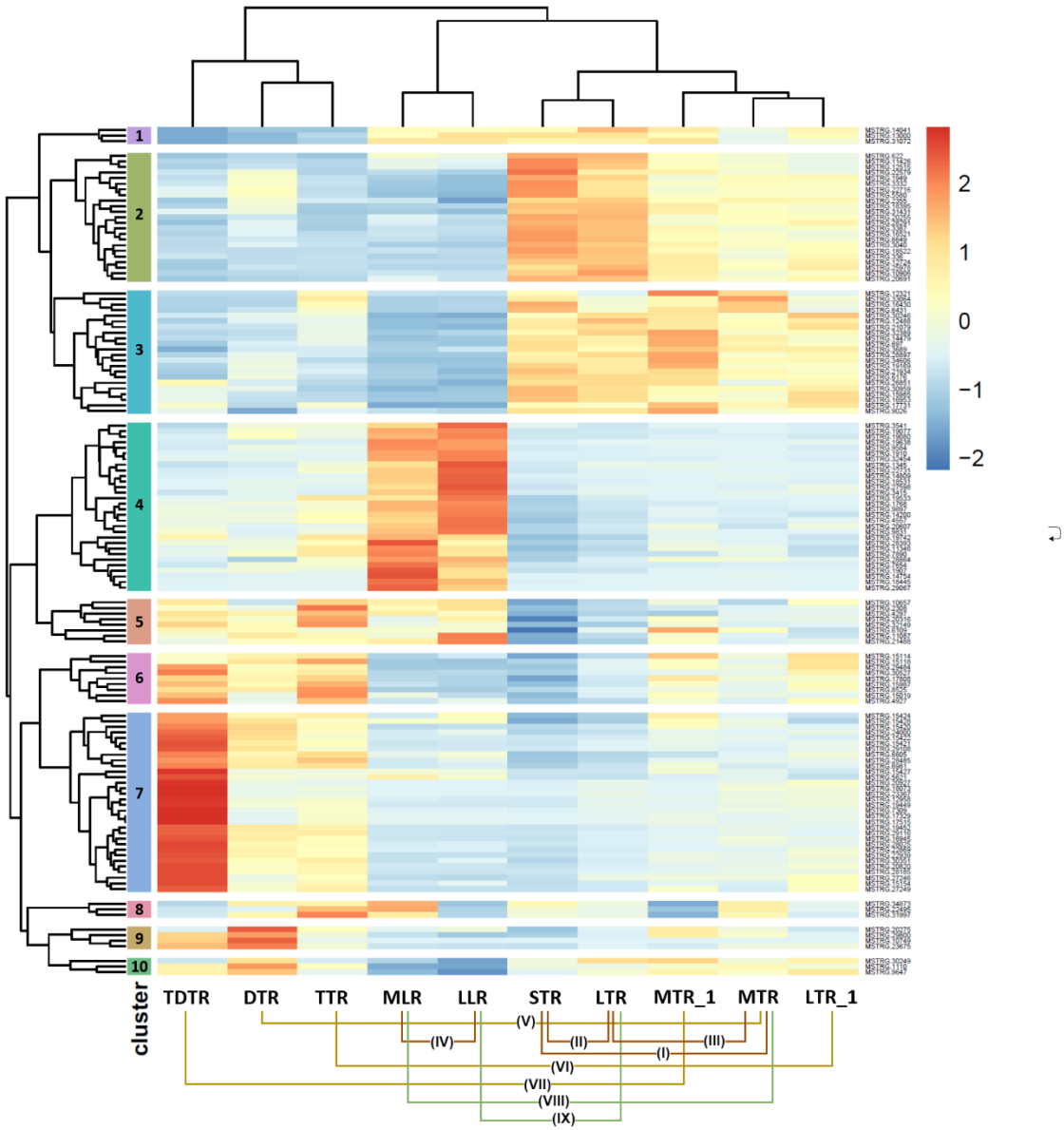

Figure 14. Heatmap illustrating relationships among selected genes expressed during root elongation within specific taproot and lateral root tip variants. Gene expression levels are indicated at the top of the heatmap, with red and blue representing upregulated and downregulated expression, respectively. The heatmap contains the top-expressed DEGs (minimum 1000 TPM in any sample, expression values: mean TPM from three biological replicates). Comparisons are displayed at the bottom of the heatmap, with changes during root elongation shown in brown: (I) short and medium taproot (STR and MTR), (II) short and long taproot (STR and LTR), (III) medium and long taproot (MTR and LTR), and (IV) lateral root

from medium root and lateral root from long root (MLR and LLR); changes in the meristem are marked in gold: (V) dying taproot and standard taproot (DTR and MTR), (VI) thick taproot and standard taproot (LTR_1), and (VII) thick and dying taproot and standard taproot (MTR_1); changes in different types of roots are shown in green: (VIII) medium lateral root and taproot (MLR and MTR), and (IX) long lateral root and taproot.

3.3.Anatomical analysis

The developing tree root system comprises a primary root from which lateral roots emerge. Using histological techniques and longitudinal sections, we examined the development and organization of thick taproots and the apical root apex of *Quercus robur* growing in a rhizotron system. The primary oak root has an open organization in its apex, which consists of four groups of initials: vascular cylinder initials, cortical initials, lateral root-cap initials, and columella initials. The central cylinder within the ground meristem differentiates continuously near the QC. No differences in tissue organization between standard and wider root thicknesses were observed. In the differentiation zone, all stages of histogenesis were observed in root cross sections, starting from the vascular cylinder, distinguished by the maturation of the first protophloem elements, to the first primary phloem and xylem strands. Subsequently, metaxylem matures, and the stele consists of numerous primary phloem and xylem strands. This type of root is polyarch, with 6-10 vascular strands. The cortex forms outside the stele. In this zone, the only difference observed between standard and wider root thicknesses was the varying number of cortical parenchyma cells (Figure 15).

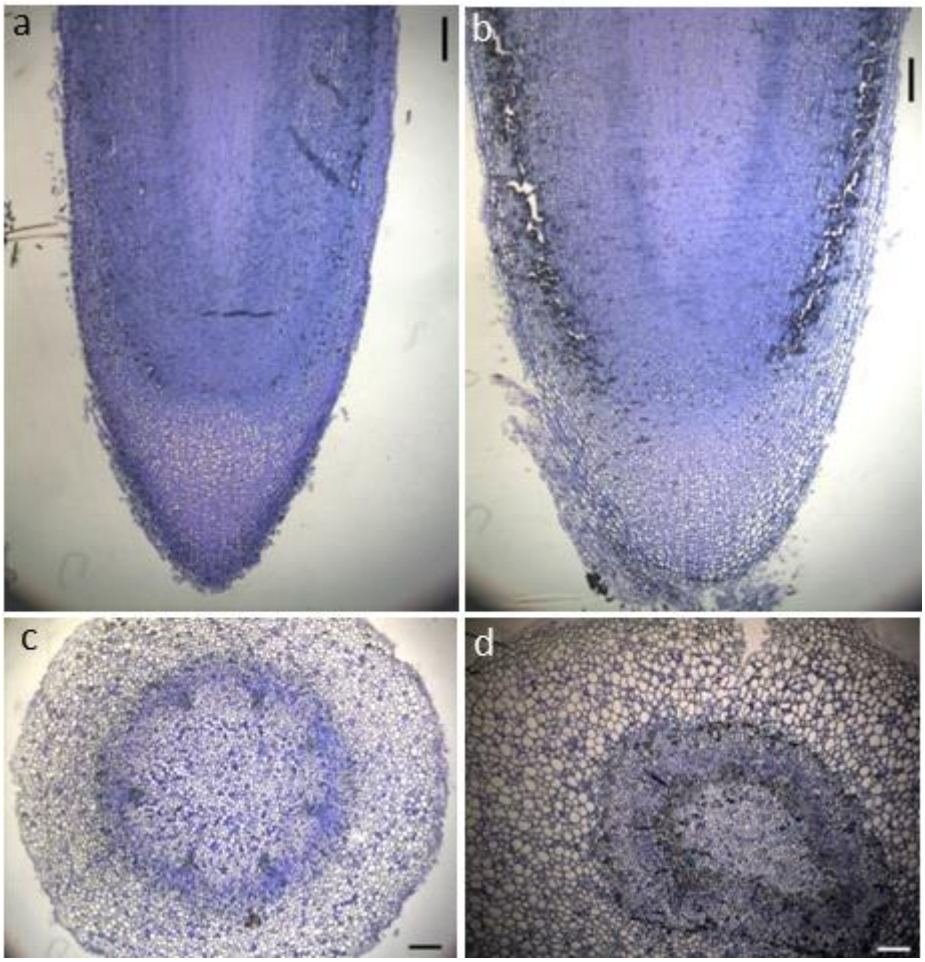

Figure 15. Comparative anatomy of longitudinal (a, b) and transverse (c, d) sections of standard (left column) and thick taproots (right column) viewed in light microscopy. Note the lower number of vascular strands within standard taproots (c) in comparison to thick taproots (d). Scale bars = 200μm.

4. Discussion

Root emergence and subsequent elongation are regulated by gene expression changes, and their thorough investigation has been undertaken during Arabidopsis root development (Benfey and Schiefelbein 1994). However, little is still known about the initial steps of root growth within trees, with divergence in structural and functional organization enabling rapid elongation through compacted soil and access to deep soil layers (Clowes 2000). As a result, initial stages of taproot elongation define their functional diversification from primary roots of annual plants. This is due to the activity of genes only during specific points of root development and during the development of different types of roots or the consequences of their morphology on growth patterns (Atkinson and Halfon 2014). Accordingly, our approach focused on understanding how molecular controls of taproot growth and the transcriptional characteristics of essential points

in their elongation enhance our knowledge of factors directly involved in perennial plant root development at both physiological and whole-genome levels.

In this study, we profiled gene expression to characterize global changes in transcripts that occurred during taproot and lateral root organogenesis. We also determined the expression pattern of morphological factors (root thicknesses) that regulate taproot growth and the transcriptional landscape of declining roots. Although the importance of tips and root diameter in primary or lateral root development has been investigated previously, to our knowledge, there has been no molecular basis for diverse growth patterns among standard and thick roots of trees (Waidmann et al. 2020). We found that the expression profile observed during taproot growth corresponded to specific checkpoints during elongation, as well as root thicknesses, and according to our knowledge, we demonstrated differential gene expression in *Quercus robur* roots for the first time. As expected, the RNA-Seq project generated a wealth of information that will help identify targets to understand the factors controlling growth and cessation of oak taproot.

4.1 Profiling of differentially expressed genes in roots

4.1.1 Identification of differences in gene expression in taproots and lateral roots

Our transcriptomic analysis showed that the gene expression examined here exhibited the highest differences when tips of short (STR) and medium (MTR) roots were contrasted. We also demonstrated that enhanced expression in long (LTR) roots promotes root elongation, as more genes had elevated expression levels and only fewer genes were downregulated in LTR.. This suggests that the decreasing change in expression when roots elongate during growth is concurrent with the profound observation of lateral root emergence within medium (MLR) or long (LLR) roots. Comparing lateral roots that emerged when taproots grew, we observed enhanced upregulation and a lower number of downregulated genes in LLR, suggesting that the point of emergence specifically impacts their growth and that specific expression in taproots may mediate the expression pattern of lateral roots. The low number of genes occurring simultaneously when roots become longer, i.e., MTR and LTR (only 140), suggests that different sets of genes may be involved at various points of root development. This gene expression pattern confirms a distinction between lateral roots growing earlier, soon after taproot emergence, and later lateral roots that display divergence in growth potential.

Studies in Arabidopsis have shown that MYB93, by responding to long-chain fatty acids, regulates lateral root development, which was inhibited without them, as observed in mutants

deficient in very long-chain fatty acids (Uemura et al. 2022). We also observed elevated levels of the *MYB93* gene during DEG analyses in medium and long lateral roots (MLR and LTR) (Supplementary Table 1). Linoleic acid is also a precursor of jasmonic acid (JA), which plays an important role in response to abiotic and biotic stresses, as demonstrated by the enrichment pathway - Plant-pathogen interaction in KEGG (Wang et al. 2020). Our GO analysis also showed increased roles of genes involved in response to biotic stimuli, indicating the activation of appropriate defense mechanisms (Figure 4). In addition to its role in plant defense, JA is involved in inhibiting the growth of the primary root and promoting the growth of lateral roots (LR), a natural process in root development (Huang et al. 2017). This is consistent with our observation of an increased MAPK (Mitogen-activated protein kinase) signaling pathway in KEGG. Studies in Arabidopsis have shown that auxin regulates lateral root development through MAPK-mediated biosynthesis of long-chain fatty acids. MAPK, in turn, is regulated by ERF13 (Ethylene response factor 13) (Lv et al. 2021). In our study, we showed increased expression levels of the gene encoding ERF113 in the taproot from which lateral roots are generated. This confirms a new molecular mechanism of lateral root formation in oak, through coupling between auxin and MAPK, which has not been widely reported in the literature so far. DEG analysis also confirmed increased expression levels of the *LRP1* gene in both medium and long taproots with standard morphology (MTR and LTR) and reduced expression levels in short roots (STR). Singh et al. (2020), on the other hand, showed that *LRP1* is expressed in all stages of LR development, besides the primary root, in contrast to our study. This may be due to a difference in the stage of root growth, as Arabidopsis roots grew for only 7 days, or represent a species-specific mechanism.

We also demonstrated a significant contribution of cysteine and methionine metabolism, amino sugar and nucleotide sugar metabolism, and diterpenoid biosynthesis in KEGG pathways in developing roots (Figure 5). Cysteine and methionine are sulfur amino acids that serve as substrates for protein biosynthesis and precursors of various metabolites, biomolecules, and defense compounds such as ethylene, S-adenosylmethionine, biotin, polyamines, phytochelatins, and glutathione (Romero et al. 2014). This was also confirmed by GO analysis, which shows increased pathways involved in the glutathione metabolic process and glutathione transferase activity (Figure 4), as well as the presence of increased GSTF gene expression in elongating roots with standard morphology (Figure 14). Moreover, the observed diterpenoid biosynthesis in the KEGG pathway may manifest brassinosteroid biosynthesis, which are a group of tetracyclic diterpenoids that promote lateral root development, which functionally

contrasts with increased zeatin biosynthesis (KEGG pathways, Figure 13) and negatively regulates lateral root development in GO analysis (Figure 12) due to demonstrated antagonism against auxin (Fukaki and Tasaka 2009; Peres et al. 2019). Thus, the inhibition of lateral root growth may favor taproot growth to extend the latter's depth (Bao et al. 2004). Our conclusion finds support in the enrichment response of gibberellin (GO pathways, Figure 5), as enhancing the expansion of endodermal cells may limit elongation of lateral roots.

Variation in gene expression also contributes to the diversity in root thicknesses, where thicker roots maintained a higher number of both up- and down-regulated genes (TTR). Interestingly, within TTR, which ceased growth, high variation in gene expression was not obviously linked to a high growth rate. Despite being thicker, these roots did not grow fast and reach the same length as roots of standard morphology. The thicker diameter and consequent tips likely reflect the growth potential of these roots, which may explain why containerized seedlings with TTR frequently restore taproot growth after planting (Zadworny et al. 2021). The relationship between diameter and future growth potential of roots with different meristems is supported by KEGG analysis, as these roots maintained enriched gene categories and pathways involved in Phenylpropanoid biosynthesis, Cyanoamino acid metabolism, Pentose and glucuronate interconversions, Metabolic pathways, Starch and sucrose metabolism, and Brassinosteroid biosynthesis (Figure 9). Consequently, it is not surprising that higher sucrose sink/supply into roots of wider diameter (Feldman 1976) make them more attractive to pathogens and could improve resistance associated with specific expression of phenylpropanoid biosynthesis, including cutin, suberin, lignin, and flavonoids, which enhances protection against pathogens as confirmed by enrichment of Phenylpropanoid biosynthesis (Figure 9). Moreover, increased Pentose and glucuronate interconversions, Metabolic pathways, Starch and sucrose metabolism, and Brassinosteroid biosynthesis indicate increased production of various root-building components, which seems reasonable in thick roots.

Flavonoids, in turn, are compounds with significant functions in defense against pathogens, signaling in symbiosis, and regulation of auxin transport (Hassan and Mathesius 2012). They have been shown to be transported by transporters of the ABC (ATP binding cassette) (Zhao and Dixon 2009), which were numerous in the dying roots (Supplementary Table 4). Our results also suggest that many pathogen response genes are more strongly expressed in dying roots and thick, dying roots simultaneously (Figure 14). It is plausible that the death of roots may contribute to greater pathogen attack.

4.1.2 Transcription factors - related genes involved in oak root development

Factors underlying plant development processes include transcription factors (TF), which specifically or implicitly activate or hamper the expression of specific genes (Drisch and Stahl 2015; Kościelniak et al. 2021). Considering the importance of TF function in plant organ development, we hypothesized which TFs activate to promote root development and which decreased activities are associated with hampered root growth. In our study, we observed an aboundance of genes coding TFs that may be directly engaged in root elongation at the intermediate points (MTR), whereas their content was lower in LTR and STR. Our data showed that only three of the DEGs had elevated expression in STR, which may contribute to lateral root formation as *bHLH120* (*Transcription factor bHLH120*) and *TCP15* (*Transcription factor TCP15*), key factors in their primordium initiation within the pericycle (Ding et al. 2009; Zhang et al. 2021), enhance lateral root production in MTRs. The observed enhanced expression of TCP15 should promote root elongation by increasing cell division and cytokinin and auxin responses (Li 2015). In addition, we showed that further elongation may be mediated by AtMYB111, which had enhanced presence in LTR, affecting GA signals integrated with IAA as suggested by Tan et al. (2019). Compared to STR, concomitant with root elongation, enhanced expression of *MYB2* (*Transcription factor MYB1*) and *WER* (*Transcription factor WER*) occurred not only in LTR but also in MTR, which together with CPC and MYB, presented in the latter, led to the formation of a three-component complex regulating root cell differentiation (Chen et al. 2022). Our results also indicated increased expression of TF *KUA1* (*Transcription factor KUA1*), which influences hypocotyl elongation through auxin accumulation in a phytochrome-interacting factor (PIF) proteins-dependent manner (Kwon et al. 2013), in LTR. Its enhanced expression may promote cell expansion, similar to its function in leaves and root development, along with enhanced expression of WRKY75 (Devaiah et al. 2007; Lu et al. 2014), which concurrently supports lateral root growth (Kwon et al. 2013). The increased expression of TF *ERF03* (*Ethylene-responsive transcription factor ERF003*) in LTR, acting as an integrator of hormonal pathways controlling the transcription of diverse jasmonate /ethylene-responsive defense genes, may maintain the high resistance potential of LTR.A higher presence of *MYB2* and *WER* in LTR may also promote lateral root development and induce root hair formation within them, as demonstrated by Chen et al. (2022). Within lateral roots, a significantly lower expression of DEGs was noticed, especially in lateral roots growing on MTR, confirming their increasing activity during LTR elongation. The presence of novel auxin-induced negative regulators of lateral root development and growth, such as AtMYB93

(Gibbs et al. 2014), may generally explain why lateral roots within MTR have lower growth potential (Pages 1995).

In summary, we observed increased expression mainly of the TF-encoding genes *MYB123* (*Transcription factor MYB123*), *TCP8* (*Transcription factor TCP8*), and AMS (*Transcription factor ABORTED MICROSPORES*) within MLR. BpMYB123 has been shown to regulate the expression of *BpLEA14* what enhances the drought resistance in *Betula platyphylla*. We also observed increased expression of *TCP8* compared to *LTR*, which directly promotes the expression of *ICS1* (Wang et al. 2015), a biosynthesis gene for the phytohormone salicylic acid (SA) enhancing protection against biotrophic pathogens (Pieterse et al. 2012), indicating the existence of resistance response since an initial stage of lateral root growth. Interestingly, for the first time, we showed the presence of a gene coding for TF *AMS* (*ABORTED MICROSPORES*) that in Arabidopsis regulates pollen wall formation (Xu et al. 2014), suggesting the existence of a uniform elongation mechanism across plants. Within LLR, a higher expression level of *WRK5*1 (*WRKY transcription factor 51*), promoting lateral root emergence and growth by inhibition of ethylene biosynthesis in wheat (*Triticum aestivum* L.) has been shown (Hu et al. 2018). Overexpression of the same gene (*TaWRKY51*) resulted in more crown and lateral roots in rice, and increased expression of *NAC56* (*NAC transcription factor 56*) and *RAX3* (*Transcription factor RAX3*), promoting lateral root growth and controlling shoot branching in *Arabidopsis thaliana* (Guo et al. 2015; Xu et al. 2022), suggesting that their expression can be an important regulator of lateral root branching occurring at the meristem of taproots.

4.1.3 Identification of transcription factor-related genes involved in oak roots with different morphologies

Declining root tips (DTR) exhibited a high number of TFs with reduced expression compared to root tips with standard morphology (TR). Declining primarily enhanced the expression of genes from the *ERF family* (*Ethylene-responsive transcription factors* - *ERF86*, *ERF87*, and *ERF115*). ERF115 is a transcription factor that plays a specific role in controlling cell division of the root quiescent center (QC) and stem cell replenishment in Arabidopsis, through an overlapping network. Its activity is regulated by two antagonistic mechanisms: proteolysis by the APC/C(CCS52A2) ubiquitin ligase, which restrains ERF115, and brassinosteroid-dependent ERF115 expression, which drives QC proliferation. The balance between these two mechanisms delimits ERF115 activity and is called upon when surrounding stem cells are damaged, providing a mechanism for regulating the cell cycle and maintaining the stem cell

niche longevity (Heyman et al. 2013). Other studies have shown that stem cell regeneration is improved by enhancing *ERF115* expression which is positively mediated by auxin accumulation (Heyman et al. 2013). Activation of ARF5/MONOPTEROS, an auxin-responsive transcription factor involved in wound-induced auxin (Canher et al. 2020), indicates that ERF115 functions as a positive regulator of stem cell regeneration, which promotes resistance and enhances prospective regeneration. Moreover, increased expression of *ERF115* resulted in enhanced auxin activity to promote xylem maturation and lateral root development, which, together with BZR1-mediated brassinosteroid signaling, confirms its role in root formation (Canher et al. 2022).

Apart from involvement in developmental issues, many studies have suggested that response to biotic stress is associated with transcription factors engaged in the modulation of the plant defense framework. In rice roots, it has been shown that the expression of *RSOsPR10* (*root-specific pathogenesis-related protein*) is negatively conditioned by jasmonate/ethylene and salicylic acid via the activator OsERF87 and the repressor OsWRKY76, respectively (Yamamoto et al. 2018). WRKY transcription factor, moreover, exhibits higher expression of *LrWRKY12* in response to SA and methyl jasmonate (MeJA) treatments, conferring more resistance to *B. cinerea* than in wild-type plants. These results show that WRKY12 has been crucial for plant disease resistance (Cui et al. 2018). These findings suggest that enhanced expression of *OsERF87/WRKY* family transcription factors observed in our study may contribute to the defense response within DTR.

Transcription factors contribute to growth patterns and elongation restriction in taproots with thick morphology (TTR). Higher expression of *AIL5* (*AP2-like ethylene-responsive transcription factor AIL5*), *MYB59* (*Transcription factor MYB59*), and *bHLH154* (*Transcription factor bHLH154*) are associated with stem cell maintenance and cell division in stem cell daughters within roots. This occurs through the translocation of auxin maxima into patterned cell division and cell differentiation zones (Scheres and Krizek 2018), which, along with MYB59, regulate root length and cause roots to become shorter by extending the metaphase of mitotic cells in root tips (Mu et al. 2009). Therefore, these references suggest that enhanced expression of *AtMYB59* could regulate the cell cycle and greatly reduce taproot elongation associated with its thickening (Mu et al. 2009). Moreover, we observed bHLH154, which acts as a positive regulator of cell elongation and plant growth by mediating brassinosteroid regulation of cell elongation (Zhang et al. 2009). This may interact to promote the potential of TTR through the coordination of root meristem activity maintenance, allowing

for further elongation. Furthermore, when TTR undergoes decline, i.e., TDTR, the pattern of gene expression is similar to dying standard taproots (DTR) with enhanced expression of the *ERF* family. In addition to *MYC2* (*Transcription factor MYC2*), which directly represses *PLETHORA* expression during jasmonate-mediated modulation of the root stem cell niche in Arabidopsis (Chen et al. 2011), we observed an elevated level of *NAC42* (*Transcription factor JUNGBRUNNEN 1*). NAC42 enhances H_2O_2 concentration, making plants less susceptible to pathogens (Wu et al. 2012); however, its dual role and interaction with auxin inhibit root growth (meristem length and the number of cells in the elongation zone) (Ivanchenko et al. 2013), suggests that hampering of root growth within TTR may be linked to changes in auxin metabolism activating H_2O_2.

4.1.4 Identification of transcription factors - related genes involved in oak root with different type

Elevated transcript levels of *ABI4* (*Ethylene-responsive transcription factor ABI4*), *BH096* (*Transcription factor bHLH96*), and *PRE6* (*Transcription factor PRE6*) are involved in MLR and LLR. These levels are mostly mediated by ABI4, which acts as a key positive regulator in the phytohormone abscisic acid (ABA) (Chandrasekaran et al., 2020) and negatively regulates lateral root emergence and growth (Fukaki and Tasaka 2009; Signora et al. 2001).

Within LLR, growth occurs concomitantly with enhanced accumulation of TFs *NFYB4* (*Nuclear transcription factor Y subunit B-4*), *MOF1* (*Myb family transcription factor MOF1*), *TCP2* (*Transcription factor TCP2*), and *ORG2* (*Transcription factor ORG2*), among which the first is upregulated in both leaves and roots (Wan et al. 2021). Although their roles in lateral root growth are not yet known, considering the large number of transcripts, it seems that they are necessary for lateral root initiation and growth within LTR but not MTR. This indicates strict coordination of transcription factors among relatively short but distinct points during taproot elongation.

4.2 Identification of genes involved in plant hormones

Plant hormones are chemical compounds produced by plants that affect their growth and development. In the context of oak root development and morphology, plant hormones' participation in regulating processes such as meristem development, tissue differentiation, organ development, and response to biotic and abiotic stresses seems particularly important.

Our RNA-Seq analyses identified hormone-related genes whose expression changes during the development of taproot tips and lateral roots of oak trees that grew in rhizotron systems. Genes related to biosynthesis, conjugation, transport, signal transduction, and response (Supplementary table 2, 4, and 6) were selected for analysis. In the analyzed transcriptomes, the identified genes are associated with the biosynthesis and action of ABA, BR, IAA, CK, ET, and JA.

4.2.1 Identification of plant hormone-related genes involved in oak root development

Several plant hormone-related genes were involved in hormonally mediated taproot elongation. We identified enhanced expression of analyzed DEGs primarily within short (STR) and medium (MTR) root tips, including transduction pathway genes and hormone response genes (especially ET and IAA). As roots become longer (LTR), they exhibit lower DEG expression compared to MTR tips (Table 1 and Supplementary table 2), strongly suggesting that DEG activity mainly participates in hormone regulation necessary for MTR formation and growth. This observation may also imply that MTR serves as the growing point where coordination of root growth predominates over other functions. Subsequently, when taproots reach a greater length (LTR), the activity of hormone-related genes in these organs increases (Table 1 and Supplementary table 2), indicating that many of them control lateral root growth and promote elongation through ERF115 interaction with jasmonate and cytokinin signaling machinery or auxin-ethylene crosstalk (Heyman et al. 2013; Lakehal et al. 2020).

Indeed, it has been identified that RESPONSE FACTOR 1 (ERF1) and PHYTOCHROME INTERACTING FACTOR 4 (PIF4), which belong to the ERF family, play crucial roles in regulating root growth by affecting auxin-mediated growth. They directly control the expression of *TAA1* and *YUC* genes, inhibiting root elongation through ethylene-induced root growth inhibition (Franklin et al. 2011; Mao et al. 2016; Sun et al. 2012). Despite clustering within the same ERF family, *ERF15* expression patterns lead to taproot elongation rather than inhibition. Consequently, conclusions from previous studies on crosstalk regulating taproot elongation in annual plants do not entirely match those observed in oaks. We indicated that regulation of auxin metabolism in oak roots occurs not at the level of hormone biosynthesis, but rather at the level of conjugate synthesis and degradation (*GH3* and *ILL5* and *ILR1* genes), transport (*PIN*, *PIL*s, *LAX3*, and *ABCB* genes), and signal transduction and response pathways associated with, for example, restricting root and hypocotyl elongation inhibitors or enhancing the hydrolysis of IAA-Leu and IAA-Phe acting as IAA (Rampey et al. 2004).

Medium root tips (MTR) exhibited higher expression of the gene encoding the *IAA response factor ARF4*, *AUX/IAA* genes (*7*, *11*, *14*, and *27*), *SAUR*, and *WOX4*, which are directly involved in coordinating primary and lateral root length (ARF), controlling cell division, and differentiating vascular cambium (WOX) by regulating auxin or gibberellin concentration, as demonstrated in various plants including wild and mutant *Medicago truncatula* or Populus (Etchells et al. 2013; Kucukoglu et al. 2017). ARF proteins are also involved in auxin/indole-3-acetic acid (Aux/IAA) modules mediating lateral root (LR) founder cell initiation, specification, and formation in Arabidopsis (Goh et al. 2012). Possibly, the identified genes perform similar functions during oak root development.

The presence of both ET and IAA-related genes among the identified DEGs may also indicate the interaction of ET and IAA hormones in regulating oak root development. Additionally, modulation of IAA transporter levels in oaks may lead to local gradients of IAA concentration in specific oak root tissues, resulting in localized responses related to organ growth. Changes at the level of genes encoding proteins involved in phytohormone biosynthesis, affecting GA (*G3OX* and *G20X2*), ABA (*NCED1*), and most notably JA (*LOX* and *OPR* family genes), could explain the weakening of lateral root growth at MTR. Furthermore, elevated expression of GA biosynthesis genes in MTR, which may indicate higher levels of this phytohormone in growing roots, suggests increased cell sensitivity to GA. This increase is likely due to the elevated transcript encoding the GA receptor (*GID1B*), which plays a crucial role in non-proteolytic GA signaling during stem elongation in *A. thaliana* (Hauvermale et al. 2014). As a result, the expression of response genes to this phytohormone (*GASA1* and *GASA9*) is altered in oak, although GASA9 has no known function. In the case of *GASA1* in *A. thaliana*, mRNAs were predominantly detected in flower buds and immature siliques (Herzog et al. 1995), making it difficult to determine their potential function in oak roots. However, enhanced expression of *MYC2*-JA response genes may further confirm that MTR is the point of regulation for lateral root formation, corresponding to their role in controlling adventitious and lateral root development, as indicated by Browse (2009) for a review. JA may act as a complex network also inhibiting cell division in the meristematic cells of Arabidopsis primary root in a MYC2-dependent manner, consequently affecting primary root elongation (Chen et al. 2011). Therefore, *MYC2* may be a key gene mediating primary root response to restrict growth, long before encountering barriers such as rhizotron walls. Conversely, the expression of *CYTOKININ DEHYDROGENASE* (*CKX*) within MTR, promoting root system enlargement in Arabidopsis and tobacco, may enable oaks to develop not only an extensive taproot system but

also regulate apical dominance of primary roots, causing lateral roots to emerge and grow at a greater distance from the root tip (Aloni et al. 2006). A similar response may be mediated by enhanced expression of AKH1, which promotes root growth in Arabidopsis. The identified genes may have comparable functions during oak root development. The expression of another hormone response gene, *SCL3*, a positive regulator of GA signaling that mediates middle cortex (MC) formation in the root endodermis of Arabidopsis (Cui et al. 2007; Heo et al. 2011; Levesque et al. 2006), indicates that GA is necessary for tissue maturation when taproots are <15.5 cm long.

4.2.2 Identification of plant hormone-related genes involved in oak roots with different morphology

Changes in gene expression determining phytohormone biosynthesis influence dying root formation through the reduction of hormones other than ABA and ET. We also demonstrated that the formation of TTR is associated with reduced activity of GA, CK, IAA, and JA biosynthesis genes, and an increase in the expression of the ABA biosynthesis gene (*NCED1*) without any modification in the expression of ET biosynthesis genes. Data showing that overexpressing any member of the *YUC* family (required for auxin production) in Arabidopsis resulted in the inhibition of primary root growth (Cao et al. 2019; Qin and Huang 2018) indicate that reduced IAA levels lead to alterations in root morphology. Reduced IAA gene expression is also directly linked to meristem cell enlargement within TTR, confirming previous findings from the *yuc3, yuc5, yuc7, yuc8,* and *yuc9* quintuple mutant (Chen et al. 2014). Furthermore, altered expression of *AHK5* His-kinase, a negative regulator in the ethylene-ABA related inhibition of root elongation through ETR1 (an ethylene receptor) (Iwama et al. 2007), suggests that this signaling pathway is essential for the continuous elongation of taproots. This, combined with CK biosynthesis and ABA-dependent restriction of ethylene production at low water potential enables taproot elongation through soil to access water in deep layers (Chen et al. 2006).

Typically, exogenously applied ABA inhibits shoot and root growth in well-watered plants. However, at low water potentials, the accumulation of endogenous ABA restricts ethylene production in response to compacted soil and maintains continuous root elongation. This can be associated with the fact that in TRs of DTR and TDTR roots, there is lower expression compared to TRs of the gene encoding histidine kinase 5 (*AHK5*). Research in *A. thaliana* suggests that TDTR roots exhibit significant changes in phytohormone biosynthesis expression, as the activity of BR, ABA, and CK biosynthesis genes increases, GA and IAA decrease, and

JA expression varies, indicating its specific regulation depending on root morphology. In summary, the expression of three genes encoding the JA-inactivating enzyme, *JOX2*, was specifically higher in TDTR compared to TR, but not in DTR, enhancing resistance or activating the defense response of primary root types through jasmonate-induced oxygenases (JOXs), which play a role in JA reaction during growth and defense (Caarls et al. 2017). Similarly, altered expression of genes related to degradation/inactivation of ABA (4 genes), BR (5 genes), CK (2 genes), and GA (2 genes) in TDTR suggests a situation where, as hormone biosynthesis is altered in the roots, the activity of genes encoding enzymes that degrade the hormone in question is also altered, forming a feedback loop that regulates hormone homeostasis in the tissue.

Within root tips of TDTR, expression of ET response-related DEGs, mainly from the ERF family such as *WIN1*, *ERN1*, *LEP*, *ERF9*, *8*, *3*, *13*, etc., has been identified, among which WIN1 in *Arabidopsis thaliana* functions as an ethylene response factor-type transcription factor, promoting wax deposition in overexpressing plants (Broun et al. 2004). The slight decrease of *ARF17* and *ARF18* within TDTR suggests that IAA likely mediates root growth by impacting auxin signaling, similar to *OsARF10*, *OsARF16*, and *OsARF17* in rice (Huang et al. 2016), indicating that increased expression of *ARF17* and *ARF18*/higher auxin concentration inhibits root growth and elongation.

4.2.3 Identification of plant hormone-related genes involved in oak taproot and lateral roots growth

Considering the interaction between genes and hormones that differentiate growth and functionality among taproots, characterized by apical dominance, and lateral roots, we found that both MLR and LLR exhibited lower expression of BR biosynthesis genes (*BRH1*) and higher expression of the BR response repressor (*BKI1*) and genes encoding BR catabolism-related enzymes compared to TR. This pattern of BR biosynthesis gene expression suggests that during the initial stages of taproot growth in species such as oaks, which are characterized by large reserves accumulated in acorns, priority is given to deep soil exploration by rapidly growing taproots at the expense of lateral root growth. The observed higher expression of BR biosynthesis genes in root tips of TR, together with genes encoding CK, may further underline the apical dominance of taproot tips, resulting in their elongation to accelerate water uptake, as shown for lateral roots by (Bao et al. 2004; Fàbregas et al. 2018; Kościelniak et al. 2021; Vukašinović et al. 2021). On the other hand, enhanced expression of the *CKX* gene, encoding the cytokinin-degrading enzyme cytokinin oxidase, in lateral roots suggests functional root type

diversification of CK biosynthesis. This diversification, on one hand, allows lateral root development by removing the cytokinin signal (Del Bianco et al. 2013; Kuroha et al. 2009), and on the other hand, enables CK-related apical dominance of the taproot.

5. Conclusion

In this study, oak taproots of different morphologies were collected at various points during their elongation in relation to lateral root emergence. The direct consequences of post-emergence growth time on the distribution of gene expression provide insight into how gene patterning related to root elongation is connected to the mechanism of taproot organogenesis and the regulation of lateral root development. To enhance deep soil exploration, taproot tips increase the expression of genes involved in BR biosynthesis (*BRH1*) and cytokinin-degrading enzyme encoding *CKX* gene expression in taproots. This increased expression, coupled with the successive expression of hormone precursors of brassinosteroid and cytokinin, enables hormone-related apical dominance of taproots. Furthermore, the patterning of lateral roots involves the interaction of auxin, ERF13, and MAPK, suggesting that this regulation is a common process. The tradeoff in growth between taproot elongation and lateral root emergence may be linked to the genes coding for transcription factors such as *bHLH12*, *TCP15*, and *WRKY75*, which exhibit greater expression of *LRP*, especially in MTR. This is essential for allocating reserves to promote deep rooting during the initial stage of growth, when resources contained in the acorn are abundant, and enabling lateral root emergence when sustained taproot growth is maintained. This supports our assumption that taproot regulators play a significant role in shaping the growth of oak root systems.

Root morphology appears to significantly affect gene expression within elongating taproots, with a particular impact on organizing taproot growth inhibition. This includes the activation of signaling pathways that promote root thickening rather than root elongation. This would indicate that the control of root growth suppression must involve the engagement of enhanced gene expression coding for transcription factors *AIL5*, *MYB59*, and *bHLH154*, which are associated with stem cell maintenance and cell division in stem cell daughters within roots. Through the translocation of auxin maxima into patterned cell division and cell differentiation zones, these transcription factors regulate root length and cause roots to become shorter. Enhanced expression of these transcription factors could regulate the cell cycle and greatly reduce taproot elongation associated with its thickening. Our research, conducted using a rhizotron system that resembles the natural growth conditions of oak seedlings, improves our understanding of the molecular processes driving root system development not only within

model species but also in long-lived trees. This knowledge carries strong practical implications for enhancing forest management operations related to seedling regeneration.

Author contributions

PK drafted the manuscript. PK and PG conducted the analyses. MZ conceived the project and sought funding for it. All authors contributed to the article editing, and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Ahn, Y.O., B.-i. Shimizu, K. Sakata, D. Gantulga, Z. Zhou, D.R. Bevan and A. Esen. 2009. Scopolin-hydrolyzing β-glucosidases in roots of *Arabidopsis*. Plant and Cell Physiology 51:132-143.

Aloni, R., E. Aloni, M. Langhans and C.I. Ullrich. 2006. Role of cytokinin and auxin in shaping root architecture: regulating vascular differentiation, lateral root initiation, root apical dominance and root gravitropism. Annals of Botany 97:883-93.

Atkinson, T.J. and M.S. Halfon. 2014. Regulation of gene expression in the genomic context. Computational and Structural Biotechnology Journal 9:e201401001.

Baesso, B., D. Chiatante, M. Terzaghi, D. Zenga, K. Nieminen, A.P. Mahonen, R. Siligato, Y. Helariutta, G.S. Scippa and A. Montagnoli. 2018. Transcription factors PRE3 and WOX11 are involved in the formation of new lateral roots from secondary growth taproot in *A.thaliana*. Plant Biology 20:426-432.

Bagniewska-Zadworna, A., J. Byczyk, D.M. Eissenstat, J. Oleksyn and M. Zadworny. 2012. Avoiding transport bottlenecks in an expanding root system: xylem vessel development in fibrous and pioneer roots under field conditions. American Journal of Botany 99:1417-26.

Bao, F., J. Shen, S.R. Brady, G.K. Muday, T. Asami and Z. Yang. 2004. Brassinosteroids interact with auxin to promote lateral root development in *Arabidopsis*. Plant Physiology 134:1624-31.

Bardou, P., J. Mariette, F. Escudié, C. Djemiel and C. Klopp. 2014. jvenn: an interactive Venn diagram viewer. BMC Bioinformatics 15:293.

Benfey, P.N. and J.W. Schiefelbein. 1994. Getting to the root of plant development: the genetics of *Arabidopsis* root formation. Trend in Genetics 10:84-8.

Benková, E. and J. Hejatko. 2009. Hormone interactions at the root apical meristem. Plant Molecular Biology 69:383-396.

Blilou, I., J. Xu, M. Wildwater, V. Willemsen, I. Paponov, J. Friml, R. Heidstra, M. Aida, K. Palme and B. Scheres. 2005. The PIN auxin efflux facilitator network controls growth and patterning in *Arabidopsis* roots. Nature 433:39-44.

Bonawitz, N.D., M. Chatenay-Lapointe, C.M. Wearn and G.S. Shadel. 2008. Expression of the rDNA-encoded mitochondrial protein Tar1p is stringently controlled and responds differentially to mitochondrial respiratory demand and dysfunction. Current genetics 54:83-94.

Broun, P., P. Poindexter, E. Osborne, C.-Z. Jiang and J.L. Riechmann. 2004. WIN1, a transcriptional activator of epidermal wax accumulation in *Arabidopsis*. Proceedings of the National Academy of Sciences 101:4706-4711.

Browse, J. 2009. Jasmonate passes muster: a receptor and targets for the defense hormone. Annual Review of Plant Biology 60:183-205.

Caarls, L., J. Elberse, M. Awwanah, N.R. Ludwig, M. de Vries, T. Zeilmaker, S.C.M. Van Wees, R.C. Schuurink and G. Van den Ackerveken. 2017. *Arabidopsis* JASMONATE-INDUCED OXYGENASES down-regulate plant immunity by hydroxylation and inactivation of the hormone jasmonic acid. Proc Natl Acad Sci U S A 114:6388-6393.

Canher, B., J. Heyman, M. Savina, A. Devendran, T. Eekhout, I. Vercauteren, E. Prinsen, R. Matosevich, J. Xu, V. Mironova and L. De Veylder. 2020. Rocks in the auxin stream: Wound-induced auxin accumulation and *ERF115* expression synergistically drive stem cell regeneration. Proc Natl Acad Sci U S A 117:16667-16677.

Canher, B., F. Lanssens, A. Zhang, A. Bisht, S. Mazumdar, J. Heyman, S. Wolf, C.W. Melnyk and L. De Veylder. 2022. The regeneration factors ERF114 and ERF115 regulate auxin-mediated lateral root development in response to mechanical cues. Molecular Plant 15:1543-1557.

Cao, X., H. Yang, C. Shang, S. Ma, L. Liu and J. Cheng. 2019. The roles of auxin biosynthesis YUCCA gene family in plants. International Journal of Molecular Sciences 20:6343

Carlsbecker, A., J.Y. Lee, C.J. Roberts, J. Dettmer, S. Lehesranta, J. Zhou, O. Lindgren, M.A. Moreno-Risueno, A. Vatén, S. Thitamadee, A. Campilho, J. Sebastian, J.L. Bowman, Y. Helariutta and P.N. Benfey. 2010. Cell signalling by microRNA165/6 directs gene dose-dependent root cell fate. Nature 465:316-21.

Casson, S.A. and K. Lindsey. 2003. Genes and signalling in root development. New Phytologist 158:11-38.

Chaiwanon, J., W. Wang, J.Y. Zhu, E. Oh and Z.Y. Wang. 2016. Information integration and communication in plant growth regulation. Cell 164:1257-1268.

Chen, C.-W., Y.-W. Yang, H.-S. Lur, Y.-G. Tsai and M.-C. Chang. 2006. A novel function of abscisic acid in the regulation of rice (*Oryza sativa* L.) root growth and development. Plant and Cell Physiology 47:1-13.

Chen, Q., X. Dai, H. De-Paoli, Y. Cheng, Y. Takebayashi, H. Kasahara, Y. Kamiya and Y. Zhao. 2014. Auxin overproduction in shoots cannot rescue auxin deficiencies in *Arabidopsis* roots. Plant Cell Physiology 55:1072-9.

Chen, Q., J. Sun, Q. Zhai, W. Zhou, L. Qi, L. Xu, B. Wang, R. Chen, H. Jiang, J. Qi, X. Li, K. Palme and C. Li. 2011. The basic helix-loop-helix transcription factor MYC2 directly represses PLETHORA expression during jasmonate-mediated modulation of the root stem cell niche in *Arabidopsis*. Plant Cell 23:3335-52.

Chen, Z., Z. Wu, W. Dong, S. Liu, L. Tian, J. Li and H. Du. 2022. MYB transcription factors becoming mainstream in plant roots. International Journal of Molecular Sciences 23:9262.

Clowes, F.A.L. 2000. Pattern in root meristem development in angiosperms. New Phytologist 146:83-94.

Cui, H., M.P. Levesque, T. Vernoux, J.W. Jung, A.J. Paquette, K.L. Gallagher, J.Y. Wang, I. Blilou, B. Scheres and P.N. Benfey. 2007. An evolutionarily conserved mechanism delimiting SHR movement defines a single layer of endodermis in plants. Science 316:421-5.

Cui, Q., X. Yan, X. Gao, D.M. Zhang, H.B. He and G.X. Jia. 2018. Analysis of WRKY transcription factors and characterization of two *Botrytis cinerea*-responsive LrWRKY genes from *Lilium regale*. Plant Physiology and Biochemistry 127:525-536.

Del Bianco, M., L. Giustini and S. Sabatini. 2013. Spatiotemporal changes in the role of cytokinin during root development. New Phytologist 199:324-338.

Devaiah, B.N., A.S. Karthikeyan and K.G. Raghothama. 2007. WRKY75 transcription factor is a modulator of phosphate acquisition and root development in *Arabidopsis*. Plant Physiology 143:1789-801.

Ding, W., Z. Yu, Y. Tong, W. Huang, H. Chen and P. Wu. 2009. A transcription factor with a bHLH domain regulates root hair development in rice. Cell Research 19:1309-11.

do Amaral, M., A.C.O. Freitas, A.S. Santos, E.C. dos Santos, M.M. Ferreira, A. da Silva Gesteira, K.P. Gramacho, J.S. Marinho-Prado and C.P. Pirovani. 2022. TcTI, a Kunitz-type trypsin inhibitor from cocoa associated with defense against pathogens. Scientific Reports 12:698.

Drisch, R.C. and Y. Stahl. 2015. Function and regulation of transcription factors involved in root apical meristem and stem cell maintenance. Frontiers in Plant Science 6:505.

Etchells, J.P., C.M. Provost, L. Mishra and S.R. Turner. 2013. WOX4 and WOX14 act downstream of the PXY receptor kinase to regulate plant vascular proliferation independently of any role in vascular organisation. Development 140:2224-34.

Fàbregas, N., F. Lozano-Elena, D. Blasco-Escámez, T. Tohge, C. Martínez-Andújar, A. Albacete, S. Osorio, M. Bustamante, J.L. Riechmann, T. Nomura, T. Yokota, A. Conesa, F.P. Alfocea, A.R. Fernie and A.I. Caño-Delgado. 2018. Overexpression of the vascular brassinosteroid receptor BRL3 confers drought resistance without penalizing plant growth. Nature Communications 9:4680.

Feldman, L.J. 1976. The *de Novo* origin of the quiescent center regenerating root apices of *Zea mays*. Planta 128:207-212.

Fowler, T.J., C. Bernhardt and M.L. Tierney. 1999. Characterization and expression of four proline-rich cell wall protein genes in *Arabidopsis* encoding two distinct subsets of multiple domain proteins. Plant Physiology 121:1081-92.

Franklin, K.A., S.H. Lee, D. Patel, S.V. Kumar, A.K. Spartz, C. Gu, S. Ye, P. Yu, G. Breen, J.D. Cohen, P.A. Wigge and W.M. Gray. 2011. Phytochrome-interacting factor 4 (PIF4) regulates auxin biosynthesis at high temperature. Proc Natl Acad Sci U S A 108:20231-5.

Freschet, G.T., C. Roumet, L.H. Comas, M. Weemstra, A.G. Bengough, B. Rewald, R.D. Bardgett, G.B. De Deyn, D. Johnson, J. Klimešová, M. Lukac, M.L. McCormack, I.C. Meier, L. Pagès, H. Poorter, I. Prieto, N. Wurzburger, M. Zadworny, A. Bagniewska-Zadworna, E.B. Blancaflor, I. Brunner, A. Gessler, S.E. Hobbie, C.M. Iversen, L. Mommer, C. Picon-Cochard, J.A. Postma, L. Rose, P. Ryser, M. Scherer-Lorenzen, N.A. Soudzilovskaia, T. Sun, O.J. Valverde-Barrantes, A. Weigelt, L.M. York and A. Stokes. 2021a. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. New Phytologist 232:1123-1158.

Fukaki, H. and M. Tasaka. 2009. Hormone interactions during lateral root formation. Plant Molecular Biology 69:437-449.

Gibbs, D.J., U. Voß, S.A. Harding, J. Fannon, L.A. Moody, E. Yamada, K. Swarup, C. Nibau, G.W. Bassel, A. Choudhary, J. Lavenus, S.J. Bradshaw, D.J. Stekel, M.J. Bennett and J.C. Coates. 2014. AtMYB93 is a novel negative regulator of lateral root development in *Arabidopsis*. New Phytologist 203:1194-1207.

Goh, T., H. Kasahara, T. Mimura, Y. Kamiya and H. Fukaki. 2012. Multiple AUX/IAA-ARF modules regulate lateral root formation: the role of *Arabidopsis* SHY2/IAA3-mediated auxin signalling. Philosophical Transactions of the Royal Society B: Biological Sciences 367:1461-8.

González-García, M.P., J. Vilarrasa-Blasi, M. Zhiponova, F. Divol, S. Mora-García, E. Russinova and A.I. Caño-Delgado. 2011. Brassinosteroids control meristem size by promoting cell cycle progression in *Arabidopsis* roots. Development 138:849-59.

Gou, J., S.H. Strauss, C.J. Tsai, K. Fang, Y. Chen, X. Jiang and V.B. Busov. 2010. Gibberellins regulate lateral root formation in *Populus* through interactions with auxin and other hormones. Plant Cell 22:623-39.

Gullner, G., T. Komives, L. Király and P. Schröder. 2018. Glutathione s-transferase enzymes in plant-pathogen interactions. Frontiers in Plant Science 9:1836.

Guo, D., J. Zhang, X. Wang, X. Han, B. Wei, J. Wang, B. Li, H. Yu, Q. Huang, H. Gu, L.J. Qu and G. Qin. 2015. The WRKY Transcription factor WRKY71/EXB1 controls shoot branching by transcriptionally regulating *RAX* genes in *Arabidopsis*. Plant Cell 27:3112-27.

Hacham, Y., N. Holland, C. Butterfield, S. Ubeda-Tomas, M.J. Bennett, J. Chory and S. Savaldi-Goldstein. 2011. Brassinosteroid perception in the epidermis controls root meristem size. Development 138:839-48.

Hashimoto, T. 2015. Microtubules in plants. Arabidopsis Book. 13:e0179.

Hassan, S. and U. Mathesius. 2012. The role of flavonoids in root–rhizosphere signalling: opportunities and challenges for improving plant–microbe interactions. Journal of Experimental Botany 63:3429-3444.

Haswell, E.S. and P.E. Verslues. 2015. The ongoing search for the molecular basis of plant osmosensing. The Journal of General Physiology 145:389-94.

Hauvermale, A.L., T. Ariizumi and C.M. Steber. 2014. The roles of the GA receptors GID1a, GID1b, and GID1c in sly1-independent GA signaling. Plant Signaling & Behavior 9:e28030.

Heo, J.O., K.S. Chang, I.A. Kim, M.H. Lee, S.A. Lee, S.K. Song, M.M. Lee and J. Lim. 2011. Funneling of gibberellin signaling by the GRAS transcription regulator scarecrow-like 3 in the *Arabidopsis* root. Proc Natl Acad Sci U S A 108:2166-71.

Herzog, M., A.M. Dorne and F. Grellet. 1995. GASA, a gibberellin-regulated gene family from *Arabidopsis thaliana* related to the tomato *GAST1* gene. Plant Molecular Biology 27:743-52.

Heyman, J., T. Cools, F. Vandenbussche, K.S. Heyndrickx, J. Van Leene, I. Vercauteren, S. Vanderauwera, K. Vandepoele, G. De Jaeger, D. Van Der Straeten and L. De Veylder. 2013. ERF115 controls root quiescent center cell division and stem cell replenishment. Science 342:860-3.

Hu, X. and L. Xu. 2016. Transcription factors WOX11/12 directly activate *WOX5/7* to promote root primordia initiation and organogenesis. Plant Physiology 172:2363-2373.

Hu, Z., R. Wang, M. Zheng, X. Liu, F. Meng, H. Wu, Y. Yao, M. Xin, H. Peng, Z. Ni and Q. Sun. 2018. TaWRKY51 promotes lateral root formation through negative regulation of ethylene biosynthesis in wheat (*Triticum aestivum* L.). The Plant Journal 96:372-388.

Huang, H., B. Liu, L. Liu and S. Song. 2017. Jasmonate action in plant growth and development. Journal of Experimental Botany 68:1349-1359.

Huang, J., Z. Li and D. Zhao. 2016. Deregulation of the OsmiR160 Target gene *OsARF18* causes growth and developmental defects with an alteration of auxin signaling in rice. Scientific Reports 6:29938.

Hussain, A., N. Asif, A.R. Pirzada, A. Noureen, J. Shaukat, A. Burhan, M. Zaynab, E. Ali, K. Imran, A. Ameen, M.A. Mahmood, A. Nazar and M.S. Mukhtar. 2022. Genome wide study of cysteine rich receptor like proteins in *Gossypium* sp. Scientific Reports 12:4885.

Ivanchenko, M.G., D. den Os, G.B. Monshausen, J.G. Dubrovsky, A. Bednárová and N. Krishnan. 2013. Auxin increases the hydrogen peroxide (H2O2) concentration in tomato (*Solanum lycopersicum*) root tips while inhibiting root growth. Annals of Botany 112:1107-16.

Iwama, A., T. Yamashino, Y. Tanaka, H. Sakakibara, T. Kakimoto, S. Sato, T. Kato, S. Tabata, A. Nagatani and T. Mizuno. 2007. AHK5 histidine kinase regulates root elongation through an ETR1-dependent abscisic acid and ethylene signaling pathway in *Arabidopsis thaliana*. Plant Cell Physiology 48:375-80.

Jin, K., J. Shen, R.W. Ashton, I.C. Dodd, M.A.J. Parry and W.R. Whalley. 2013. How do roots elongate in a structured soil? Journal of Experimental Botany 64:4761-4777.

Kavi Kishor, P.B., P. Hima Kumari, M.S. Sunita and N. Sreenivasulu. 2015. Role of proline in cell wall synthesis and plant development and its implications in plant ontogeny. Frontiers in Plant Science 6:544.

Kościelniak, P., P. Glazińska, J. Kęsy and M. Zadworny. 2021. Formation and development of taproots in deciduous tree species. Frontiers in Plant Science 12:772567

Kościelniak, P., P. Glazińska and M. Zadworny. 2022. OakRootRNADB—a consolidated RNA-seq database for coding and noncoding RNA in roots of pedunculate oak (*Quercus robur*). Database: The Journal of Biological Databases and Curation, baac097

Kucukoglu, M., J. Nilsson, B. Zheng, S. Chaabouni and O. Nilsson. 2017. *WUSCHEL-RELATED HOMEOBOX4* (*WOX4*)-like genes regulate cambial cell division activity and secondary growth in *Populus* trees. New Phytologist 215:642-657.

Kuroha, T., H. Tokunaga, M. Kojima, N. Ueda, T. Ishida, S. Nagawa, H. Fukuda, K. Sugimoto and H. Sakakibara. 2009. Functional analyses of *LONELY GUY* cytokinin-activating enzymes reveal the importance of the direct activation pathway in *Arabidopsis*. Plant Cell 21:3152-69.

Kwon, Y., J.H. Kim, H.N. Nguyen, Y. Jikumaru, Y. Kamiya, S.W. Hong and H. Lee. 2013. A novel *Arabidopsis* MYB-like transcription factor, MYBH, regulates hypocotyl elongation by enhancing auxin accumulation. Journal of Experimental Botany 64:3911-22.

Lakehal, A., A. Dob, Z. Rahneshan, O. Novák, S. Escamez, S. Alallaq, M. Strnad, H. Tuominen and C. Bellini. 2020. *ETHYLENE RESPONSE FACTOR 115* integrates jasmonate and cytokinin signaling machineries to repress adventitious rooting in *Arabidopsis*. New Phytologist 228:1611-1626.

Langmead, B. and S.L. Salzberg. 2012. Fast gapped-read alignment with Bowtie 2. Nature Methods 9:357-359.

Lascombe, M.B., B. Bakan, N. Buhot, D. Marion, J.P. Blein, V. Larue, C. Lamb and T. Prangé. 2008. The structure of "defective in induced resistance" protein of *Arabidopsis thaliana*, DIR1, reveals a new type of lipid transfer protein. Protein Science 17:1522-30.

Léon-Kloosterziel, K.M., B.W. Verhagen, J.J. Keurentjes, J.A. VanPelt, M. Rep, L.C. VanLoon and C.M. Pieterse. 2005. Colonization of the *Arabidopsis* rhizosphere by fluorescent

Pseudomonas spp. activates a root-specific, ethylene-responsive *PR-5* gene in the vascular bundle. Plant Molecular Biology 57:731-48.

Levesque, M.P., T. Vernoux, W. Busch, H. Cui, J.Y. Wang, I. Blilou, H. Hassan, K. Nakajima, N. Matsumoto, J.U. Lohmann, B. Scheres and P.N. Benfey. 2006. Whole-genome analysis of the SHORT-ROOT developmental pathway in *Arabidopsis*. PLoS Biology 4:e143.

Li, J., B.-Z. Pan, L. Niu, M.-S. Chen, M. Tang and Z.-F. Xu. 2018. Gibberellin inhibits floral initiation in the perennial woody plant J*atropha curcas*. Journal of Plant Growth Regulation 37:999-1006.

Li, S. 2015. The *Arabidopsis thaliana* TCP transcription factors: A broadening horizon beyond development. Plant Signaling & Behavior 10:e1044192.

Liu, L.H., U. Ludewig, B. Gassert, W.B. Frommer and N. von Wirén. 2003. Urea transport by nitrogen-regulated tonoplast intrinsic proteins in *Arabidopsis*. Plant Physiology 133:1220-8.

Love, M.I., W. Huber and S. Anders. 2014. Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. Genome Biology 15:550.

Lu, D., T. Wang, S. Persson, B. Mueller-Roeber and J.H. Schippers. 2014. Transcriptional control of ROS homeostasis by KUODA1 regulates cell expansion during leaf development. Nature Communications 5:3767.

Lv, B., K. Wei, K. Hu, T. Tian, F. Zhang, Z. Yu, D. Zhang, Y. Su, Y. Sang, X. Zhang and Z. Ding. 2021. MPK14-mediated auxin signaling controls lateral root development via ERF13-regulated very-long-chain fatty acid biosynthesis. Molecular Plant 14:285-297.

Malamy, J.E. 2005. Intrinsic and environmental response pathways that regulate root system architecture. Plant, Cell & Environment 28:67-77.

Maldonado, A.M., P. Doerner, R.A. Dixon, C.J. Lamb and R.K. Cameron. 2002. A putative lipid transfer protein involved in systemic resistance signalling in *Arabidopsis*. Nature 419:399-403.

Mao, J.L., Z.Q. Miao, Z. Wang, L.H. Yu, X.T. Cai and C.B. Xiang. 2016. *Arabidopsis* ERF1 mediates cross-talk between ethylene and auxin biosynthesis during primary root elongation by regulating *ASA1* expression. PLoS Genetics 12:e1005760.

Mitsis, T., A. Efthimiadou, F. Bacopoulou, D. Vlachakis, G.P. Chrousos and E. Eliopoulos. 2020. Transcription factors and evolution: An integral part of gene expression (Review). World Academy of Sciences Journal 2:3-8.

Mu, R.-L., Y.-R. Cao, Y.-F. Liu, G. Lei, H.-F. Zou, Y. Liao, H.-W. Wang, W.-K. Zhang, B. Ma, J.-Z. Du, M. Yuan, J.-S. Zhang and S.-Y. Chen. 2009. An R2R3-type transcription factor gene *AtMYB59* regulates root growth and cell cycle progression in *Arabidopsis*. Cell Research 19:1291-1304.

Müller, C.J., A.E. Valdés, G. Wang, P. Ramachandran, L. Beste, D. Uddenberg and A. Carlsbecker. 2016. PHABULOSA mediates an auxin signaling loop to regulate vascular patterning in *Arabidopsis*. Plant Physiology 170:956-70.

Nishiyama, R., Y. Watanabe, Y. Fujita, D.T. Le, M. Kojima, T. Werner, R. Vankova, K. Yamaguchi-Shinozaki, K. Shinozaki, T. Kakimoto, H. Sakakibara, T. Schmülling and L.-S.P. Tran. 2011. Analysis of cytokinin mutants and regulation of cytokinin metabolic genes reveals important regulatory roles of cytokinins in drought, salt and abscisic acid responses, and abscisic acid biosynthesis. The Plant Cell 23:2169-2183.

Osakabe, Y., K. Osakabe, K. Shinozaki and L.S. Tran. 2014. Response of plants to water stress. Frontiers in Plant Science 5:86.

Pages, L. 1995. Growth patterns of the lateral roots of young oak (*Quercus robur*) tree seedlings Relationship with apical diameter. New Phytologist 130:503-509.

Peres, A., J.S. Soares, R.G. Tavares, G. Righetto, M.A.T. Zullo, N.B. Mandava and M. Menossi. 2019. Brassinosteroids, the sixth class of phytohormones: A molecular view from the discovery to hormonal interactions in plant development and stress adaptation. International Journal of Molecular Sciences 20:331

Petricka, J.J., C.M. Winter and P.N. Benfey. 2012. Control of *Arabidopsis* root development. Annual Review of Plant Biology 63:563-90.

Pierret, A., J.L. Maeght, C. Clement, J.P. Montoroi, C. Hartmann and S. Gonkhamdee. 2016. Understanding deep roots and their functions in ecosystems: an advocacy for more unconventional research. Annals of Botany 118:621-635.

Pieterse, C.M., D. Van der Does, C. Zamioudis, A. Leon-Reyes and S.C. Van Wees. 2012. Hormonal modulation of plant immunity. Annual Review of Cell and Developmental Biology 28:489-521.

Qin, H. and R. Huang. 2018. Auxin controlled by ethylene steers root development. International Journal of Molecular Sciences 19:3656

Rampey, R.A., S. LeClere, M. Kowalczyk, K. Ljung, G. Sandberg and B. Bartel. 2004. A family of auxin-conjugate hydrolases that contributes to free indole-3-acetic acid levels during *Arabidopsis* germination. Plant Physiology 135:978-88.

Romero, L.C., M.Á. Aroca, A.M. Laureano-Marín, I. Moreno, I. García and C. Gotor. 2014. Cysteine and cysteine-related signaling pathways in *Arabidopsis thaliana*. Molecular Plant 7:264-276.

Sarkar, A.K., M. Luijten, S. Miyashima, M. Lenhard, T. Hashimoto, K. Nakajima, B. Scheres, R. Heidstra and T. Laux. 2007. Conserved factors regulate signalling in *Arabidopsis thaliana* shoot and root stem cell organizers. Nature 446:811-814.

Scheres, B. and B.A. Krizek. 2018. Coordination of growth in root and shoot apices by AIL/PLT transcription factors. Current Opinion in Plant Biology 41:95-101.

Scheres, B., H. van den Toorn and R. Heidstra. 2004. Root genomics: towards digital in situ hybridization. Genome Biology 5:227.

Shi, Y., X. Zhang, Z.Y. Xu, L. Li, C. Zhang, M. Schläppi and Z.Q. Xu. 2011. Influence of EARLI1-like genes on flowering time and lignin synthesis of *Arabidopsis thaliana*. Plant Biol (Stuttg) 13:731-9.

Shibasaka, M., T. Horie and M. Katsuhara. 2021. Mechanisms activating latent functions of PIP aquaporin water channels via the interaction between PIP1 and PIP2 proteins. Plant and Cell Physiology 62:92-99.

Signora, L., I. De Smet, C.H. Foyer and H. Zhang. 2001. ABA plays a central role in mediating the regulatory effects of nitrate on root branching in *Arabidopsis*. The Plant Journal 28:655-62.

Singh, S., S. Yadav, A. Singh, M. Mahima, A. Singh, V. Gautam and A.K. Sarkar. 2020. Auxin signaling modulates *LATERAL ROOT PRIMORDIUM1* (*LRP1*) expression during lateral root development in *Arabidopsis*. The Plant Journal 101:87-100.

Slovak, R., T. Ogura, S.B. Satbhai, D. Ristova and W. Busch. 2016. Genetic control of root growth: from genes to networks. Annals of Botany 117:9-24.

Smith, S. and I. De Smet. 2012. Root system architecture: insights from *Arabidopsis* and cereal crops. Philosophical Transactions of the Royal Society B: Biological Sciences 367:1441-52.

Sun, J., L. Qi, Y. Li, J. Chu and C. Li. 2012. PIF4-mediated activation of *YUCCA8* expression integrates temperature into the auxin pathway in regulating *Arabidopsis* hypocotyl growth. PLoS Genetics 8:e1002594.

Svolacchia, N., E. Salvi and S. Sabatini. 2020. *Arabidopsis* primary root growth: let it grow, can't hold it back anymore! Current Opinion in Plant Biology 57:133-141.

Tan, H., C. Man, Y. Xie, J. Yan, J. Chu and J. Huang. 2019. A crucial role of GA-regulated flavonol biosynthesis in root growth of *Arabidopsis*. Molecular Plant 12:521-537.

Uemura, Y., S. Kimura, T. Ohta, T. Suzuki, K. Mase, H. Kato, S. Sakaoka, Y. Komine, K. Hotta, M. Shimizu, A. Morikami and H. Tsukagoshi. 2022. A very long chain fatty acid responsive transcription factor, MYB93, regulates lateral root development in *Arabidopsis* bioRxiv: 2022.05.24.493307.

Vaghela, B., R. Vashi, K. Rajput and R. Joshi. 2022. Plant chitinases and their role in plant defense: A comprehensive review. Enzyme and Microbial Technology 159:110055.

Vieten, A., S. Vanneste, J. Wisniewska, E. Benková, R. Benjamins, T. Beeckman, C. Luschnig and J. Friml. 2005. Functional redundancy of PIN proteins is accompanied by auxindependent cross-regulation of PIN expression. Development 132:4521-4531.

Vukašinović, N., Y. Wang, I. Vanhoutte, M. Fendrych, B. Guo, M. Kvasnica, P. Jiroutová, J. Oklestkova, M. Strnad and E. Russinova. 2021. Local brassinosteroid biosynthesis enables optimal root growth. Nature Plants 7:619-632.

Waidmann, S., M. Ruiz Rosquete, M. Schöller, E. Sarkel, H. Lindner, T. LaRue, I. Petřík, K. Dünser, S. Martopawiro, R. Sasidharan, O. Novak, K. Wabnik, J.R. Dinneny and J. Kleine-Vehn. 2019. Cytokinin functions as an asymmetric and anti-gravitropic signal in lateral roots. Nature Communications 10:3540.

Waidmann, S., E. Sarkel and J. Kleine-Vehn. 2020. Same same, but different: growth responses of primary and lateral roots. Journal of Experimental Botany 71:2397-2411.

Wan, Q., L. Luo, X. Zhang, Y. Lv, S. Zhu, L. Kong, Y. Wan, F. Liu and K. Zhang. 2021. Genome-wide identification and abiotic stress response pattern analysis of NF-Y gene family in peanut (*Arachis Hypogaea* L.). Tropical Plant Biology 14:329-344.

Wang, J., L. Song, X. Gong, J. Xu and M. Li. 2020. Functions of jasmonic acid in plant regulation and response to abiotic stress. International Journal of Molecular Sciences 21:8568

Wang, X., J. Gao, Z. Zhu, X. Dong, X. Wang, G. Ren, X. Zhou and B. Kuai. 2015. TCP transcription factors are critical for the coordinated regulation of isochorismate synthase 1 expression in *Arabidopsis thaliana*. The Plant Juornal 82:151-62.

Wang, Y., Y. Shi, K. Li, D. Yang, N. Liu, L. Zhang, L. Zhao, X. Zhang, Y. Liu, L. Gao, T. Xia and P. Wang. 2021. Roles of the 2-sxoglutarate-dependent dioxygenase superfamily in the flavonoid pathway: A review of the functional diversity of F3H, FNS I, FLS, and LDOX/ANS. Molecules 26:6745.

Watson, C.F., L. Zheng and D. DellaPenna. 1994. Reduction of tomato polygalacturonase beta subunit expression affects pectin solubilization and degradation during fruit ripening. Plant Cell 6:1623-34.

Weijers, D., A. Schlereth, J.S. Ehrismann, G. Schwank, M. Kientz and G. Jürgens. 2006. Auxin triggers transient local signaling for cell specification in *Arabidopsis* embryogenesis. Developmental Cell 10:265-270.

Wendrich, J.R., B.K. Möller, S. Li, S. Saiga, R. Sozzani, P.N. Benfey, B. De Rybel and D. Weijers. 2017. Framework for gradual progression of cell ontogeny in the *Arabidopsis* root meristem. Proceedings of the National Academy of Sciences 114:E8922-E8929.

Whitford, R., A. Fernandez, R. De Groodt, E. Ortega and P. Hilson. 2008. Plant CLE peptides from two distinct functional classes synergistically induce division of vascular cells. Proceedings of the National Academy of Sciences 105:18625-18630.

Wu, A., A.D. Allu, P. Garapati, H. Siddiqui, H. Dortay, M.I. Zanor, M.A. Asensi-Fabado, S. Munné-Bosch, C. Antonio, T. Tohge, A.R. Fernie, K. Kaufmann, G.P. Xue, B. Mueller-Roeber and S. Balazadeh. 2012. *JUNGBRUNNEN1*, a reactive oxygen species-responsive NAC transcription factor, regulates longevity in *Arabidopsis*. The Plant Cell 24:482-506.

Xu, D., X. Huang, Z.Q. Xu and M. Schläppi. 2011. The HyPRP gene *EARLI1* has an auxiliary role for germinability and early seedling development under low temperature and salt stress conditions in *Arabidopsis thaliana*. Planta 234:565-77.

Xu, J., Z. Ding, G. Vizcay-Barrena, J. Shi, W. Liang, Z. Yuan, D. Werck-Reichhart, L. Schreiber, Z.A. Wilson and D. Zhang. 2014. *ABORTED MICROSPORES* acts as a master regulator of pollen wall formation in *Arabidopsis*. The Plant Cell 26:1544-1556.

Xu, P., W. Ma, J. Hu and W. Cai. 2022. The nitrate-inducible NAC transcription factor *NAC056* controls nitrate assimilation and promotes lateral root growth in *Arabidopsis thaliana*. PLoS Genetics 18:e1010090.

Xuan, W., L.R. Band, R.P. Kumpf, D. Van Damme, B. Parizot, G. De Rop, D. Opdenacker, B.K. Moller, N. Skorzinski, M.F. Njo, B. De Rybel, D. Audenaert, M.K. Nowack, S. Vanneste and T. Beeckman. 2016. Cyclic programmed cell death stimulates hormone signaling and root development in *Arabidopsis*. Science 351:384-387.

Yahong, L., Y. Tsuji, N. Nishikubo, S. Kajita and N. Morohoshi. 2001. Analysis of transgenic poplar in which the expression of peroxidase gene is suppressed. *In* Progress in Biotechnology Eds. N. Morohoshi and A. Komamine. Elsevier, pp 195-204.

Yamamoto, T., Y. Yoshida, K. Nakajima, M. Tominaga, A. Gyohda, H. Suzuki, T. Okamoto, T. Nishimura, N. Yokotani, E. Minami, Y. Nishizawa, K. Miyamoto, H. Yamane, K. Okada and T. Koshiba. 2018. Expression of *RSOsPR10* in rice roots is antagonistically regulated by jasmonate/ethylene and salicylic acid via the activator OsERF87 and the repressor OsWRKY76, respectively. Plant Direct 2:e00049.

Zadworny, M., J. Mucha, A.M. Jagodziński, P. Kościelniak, P. Łakomy, M. Modrzejewski, K. Ufnalski, R. Żytkowiak, L.H. Comas and J. Rodríguez-Calcerrada. 2021. Seedling regeneration techniques affect root systems and the response of *Quercus robur* seedlings to water shortages. Forest Ecology and Management 479:11.

Zhang, L.-Y., M.-Y. Bai, J. Wu, J.-Y. Zhu, H. Wang, Z. Zhang, W. Wang, Y. Sun, J. Zhao, X. Sun, H. Yang, Y. Xu, S.-H. Kim, S. Fujioka, W.-H. Lin, K. Chong, T. Lu and Z.-Y. Wang. 2009. Antagonistic HLH/bHLH transcription factors mediate brassinosteroid regulation of cell elongation and plant development in rice and *Arabidopsis*. The Plant Cell 21:3767-3780.

Zhang, Y., N. Mitsuda, T. Yoshizumi, Y. Horii, Y. Oshima, M. Ohme-Takagi, M. Matsui and T. Kakimoto. 2021. Two types of bHLH transcription factor determine the competence of the pericycle for lateral root initiation. Nature Plants 7:633-643.

Zhao, J. and R.A. Dixon. 2009. MATE transporters facilitate vacuolar uptake of epicatechin 3'-O-glucoside for proanthocyanidin biosynthesis in *Medicago truncatula* and *Arabidopsis*. The Plant Cell 21:2323-40.

Supplementary table 1. Genes encoding transcription factors identified in STR vs. MTR, STR vs. LTR, MTR vs. LTR and MLR vs. LLR comparisons.

STR vs. MTR

No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	MTR Genes Results	STR Genes Results
1	MPH1	Myb family transcription factor MPH1	MSTRG.21849.1	MSTRG.21849	-7,10	53,67	0,33
2	MPH1	Myb family transcription factor MPH1	MSTRG.21849.2	MSTRG.21849	-7,10	53,67	0,33
3	WRK51	Probable WRKY transcription factor 51	MSTRG.16082.1	MSTRG.16082	-6,76	80,00	0,67
4	WRK51	Probable WRKY transcription factor 51	MSTRG.16082.2	MSTRG.16082	-6,76	80,00	0,67
5	WRK51	Probable WRKY transcription factor 51	MSTRG.16082.3	MSTRG.16082	-6,76	80,00	0,67
6	NAC42	Transcription factor JUNGBRUNNEN 1	MSTRG.32214.1	MSTRG.32214	-6,41	17,00	0,00
7	NAC42	Transcription factor JUNGBRUNNEN 1	MSTRG.32214.2	MSTRG.32214	-6,41	17,00	0,00
8	WRK75	Probable WRKY transcription factor 75	MSTRG.29989.1	MSTRG.29989	-5,87	11,67	0,00
9	MYB93	Transcription factor MYB93	MSTRG.3372.1	MSTRG.3372	-5,58	19,00	0,33
10	HSFB1	Heat stress transcription factor B-1	MSTRG.12950.1	MSTRG.12950	-5,44	172,33	3,67
11	BH154	Transcription factor bHLH154	MSTRG.22604.1	MSTRG.22604	-5,29	28,00	0,67
12	BH123	Transcription factor bHLH123	MSTRG.22604.2	MSTRG.22604	-5,29	28,00	0,67
13	BH123	Transcription factor bHLH123	MSTRG.22604.3	MSTRG.22604	-5,29	28,00	0,67
14	BH123	Transcription factor bHLH123	MSTRG.22604.4	MSTRG.22604	-5,29	28,00	0,67
15	WRK18	WRKY transcription factor 18	MSTRG.12932.1	MSTRG.12932	-4,96	68,00	2,00
16	WRK18	WRKY transcription factor 18	MSTRG.12932.2	MSTRG.12932	-4,96	68,00	2,00
17	WRK40	Probable WRKY transcription factor 40	MSTRG.12932.3	MSTRG.12932	-4,96	68,00	2,00
18	WRK71	WRKY transcription factor 71	MSTRG.30798.1	MSTRG.30798	-4,84	91,33	3,00
19	WRK71	WRKY transcription factor 71	MSTRG.30798.2	MSTRG.30798	-4,84	91,33	3,00
20	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25340.1	MSTRG.25340	-4,69	187,33	6,67
21	VRN1	B3 domain-containing transcription factor VRN1	MSTRG.24276.1	MSTRG.24276	-4,46	8,67	0,33
22	MY108	Transcription factor MYB108	MSTRG.15027.1	MSTRG.15027	-4,37	156,00	7,00
23	BH051	Transcription factor bHLH51	MSTRG.21715.1	MSTRG.21715	-4,17	46,67	2,33
24	WRK74	Probable WRKY transcription factor 74	MSTRG.21830.1	MSTRG.21830	-4,16	52,67	2,67
25	WRK74	Probable WRKY transcription factor 74	MSTRG.21830.2	MSTRG.21830	-4,16	52,67	2,67
26	MYB72	Transcription factor MYB72	MSTRG.26206.1	MSTRG.26206	-4,03	88,33	5,00

27	WRK43	Probable WRKY transcription factor 43	MSTRG.11159.1	MSTRG.11159	-4,00	39,67	2,33
28	BH041	Putative transcription factor bHLH041	MSTRG.5733.1	MSTRG.5733	-3,72	19,33	1,33
29	BH041	Putative transcription factor bHLH041	MSTRG.5733.2	MSTRG.5733	-3,72	19,33	1,33
30	WRK53	Probable WRKY transcription factor 53	MSTRG.11257.1	MSTRG.11257	-3,69	223,67	16,00
31	HSFB3	Heat stress transcription factor B-3	MSTRG.17389.1	MSTRG.17389	-3,61	154,33	11,67
32	WRK70	WRKY DNA-binding transcription factor 70	MSTRG.18748.1	MSTRG.18748	-3,56	153,67	12,00
33	WRK28	WRKY transcription factor 28	MSTRG.13343.1	MSTRG.13343	-3,45	120,67	10,33
34	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.35144.1	MSTRG.35144	-3,44	15,67	1,33
35	MYB15	Transcription factor MYB15	MSTRG.2089.1	MSTRG.2089	-3,36	104,00	9,33
36	MY102	Transcription factor MYB102	MSTRG.14278.1	MSTRG.14278	-3,35	50,00	4,33
37	WRK41	Probable WRKY transcription factor 41	MSTRG.4799.1	MSTRG.4799	-3,19	188,00	19,33
38	WRK75	Probable WRKY transcription factor 75	MSTRG.9226.1	MSTRG.9226	-3,07	422,00	46,67
39	ERF92	Ethylene-responsive transcription factor 1B	MSTRG.15418.1	MSTRG.15418	-2,87	134,33	17,33
40	WRKY6	WRKY transcription factor 6	MSTRG.20348.1	MSTRG.20348	-2,85	58,67	7,67
41	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.34676.1	MSTRG.34676	-2,80	94,00	12,33
42	ODO1	MYB-like transcription factor ODO1	MSTRG.24008.1	MSTRG.24008	-2,77	22,33	3,00
43	MY102	Transcription factor MYB102	MSTRG.13316.1	MSTRG.13316	-2,74	108,67	15,00
44	MYB2	Transcription factor MYB2	MSTRG.15699.1	MSTRG.15699	-2,69	33,00	4,67
45	MYB2	Transcription factor MYB2	MSTRG.15699.2	MSTRG.15699	-2,69	33,00	4,67
46	MYB2	Transcription factor MYB2	MSTRG.15699.3	MSTRG.15699	-2,69	33,00	4,67
47	DIV	Transcription factor DIVARICATA	MSTRG.22698.1	MSTRG.22698	-2,67	88,67	12,67
48	DIV	Transcription factor DIVARICATA	MSTRG.22698.2	MSTRG.22698	-2,67	88,67	12,67
49	TCP20	Transcription factor TCP20	MSTRG.9215.1	MSTRG.9215	-2,56	310,33	48,00
50	TCP20	Transcription factor TCP20	MSTRG.9215.2	MSTRG.9215	-2,56	310,33	48,00
51	TCP20	Transcription factor TCP20	MSTRG.9215.3	MSTRG.9215	-2,56	310,33	48,00
52	TCP20	Transcription factor TCP20	MSTRG.9215.4	MSTRG.9215	-2,56	310,33	48,00
53	TCP20	Transcription factor TCP20	MSTRG.9215.5	MSTRG.9215	-2,56	310,33	48,00
54	TCP20	Transcription factor TCP20	MSTRG.9215.6	MSTRG.9215	-2,56	310,33	48,00
55	WER	Transcription factor WER	MSTRG.9637.1	MSTRG.9637	-2,54	163,00	25,33
56	MYBS3	Transcription factor MYBS3	MSTRG.5695.1	MSTRG.5695	-2,53	21,33	3,33

57	MYB62	Transcription factor MYB62	MSTRG.26416.1	MSTRG.26416	-2,44	82,67	14,33
58	WRK70	Probable WRKY transcription factor 70	MSTRG.22918.1	MSTRG.22918	-2,41	145,67	25,67
59	CPC	Transcription factor CPC	MSTRG.14145.1	MSTRG.14145	-2,39	65,00	11,33
60	KUA1	Transcription factor KUA1	MSTRG.2485.1	MSTRG.2485	-2,34	34,67	6,33
61	MYB1	Transcription factor MYB1	MSTRG.29645.1	MSTRG.29645	-2,29	190,67	35,67
62	MYB1	Transcription factor MYB1	MSTRG.29645.2	MSTRG.29645	-2,29	190,67	35,67
63	MYB2	Transcription factor MYB1	MSTRG.29645.3	MSTRG.29645	-2,29	190,67	35,67
64	PHL6	Myb family transcription factor PHL6	MSTRG.27626.1	MSTRG.27626	-2,28	89,67	16,67
65	PHL6	Myb family transcription factor PHL6	MSTRG.27626.2	MSTRG.27626	-2,28	89,67	16,67
66	PHL6	Myb family transcription factor PHL6	MSTRG.27626.3	MSTRG.27626	-2,28	89,67	16,67
67	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.4032.1	MSTRG.4032	-2,28	452,00	83,67
68	GAT22	Putative GATA transcription factor 22	MSTRG.2559.1	MSTRG.2559	-2,28	98,00	18,33
69	NGA1	B3 domain-containing transcription factor NGA1	MSTRG.7200.1	MSTRG.7200	-2,26	311,33	60,00
70	NGA1	B3 domain-containing transcription factor NGA1	MSTRG.7200.2	MSTRG.7200	-2,26	311,33	60,00
71	NGA1	B3 domain-containing transcription factor NGA1	MSTRG.7200.3	MSTRG.7200	-2,26	311,33	60,00
72	HFA4B	Heat stress transcription factor A-4b	MSTRG.14253.1	MSTRG.14253	-2,25	79,00	15,33
73	SRM1	Transcription factor SRM1	MSTRG.26383.1	MSTRG.26383	-2,24	53,33	10,33
74	BZIP2	bZIP transcription factor 2	MSTRG.16355.1	MSTRG.16355	-2,23	167,00	32,00
75	WK72A	WRKY transcription factor 72A	MSTRG.25671.1	MSTRG.25671	-2,16	227,00	47,33
76	WK72A	WRKY transcription factor 72A	MSTRG.25671.2	MSTRG.25671	-2,16	227,00	47,33
77	TCP2	Transcription factor TCP2	MSTRG.21778.1	MSTRG.21778	-2,13	55,00	11,67
78	TCP2	Transcription factor TCP2	MSTRG.21778.2	MSTRG.21778	-2,13	55,00	11,67
79	TCP2	Transcription factor TCP2	MSTRG.21778.3	MSTRG.21778	-2,13	55,00	11,67
80	TCP2	Transcription factor TCP2	MSTRG.21778.4	MSTRG.21778	-2,13	55,00	11,67
81	TCP2	Transcription factor TCP2	MSTRG.21778.5	MSTRG.21778	-2,13	55,00	11,67
82	TCP2	Transcription factor TCP2	MSTRG.21778.6	MSTRG.21778	-2,13	55,00	11,67
83	TGA10	bZIP transcription factor TGA10	MSTRG.18034.1	MSTRG.18034	-2,09	234,67	50,00
84	BH025	Transcription factor bHLH25	MSTRG.28211.1	MSTRG.28211	-2,05	283,00	63,00
85	BH137	Transcription factor bHLH137	MSTRG.25369.1	MSTRG.25369	-2,03	120,00	26,33
86	BH137	Transcription factor bHLH137	MSTRG.25369.2	MSTRG.25369	-2,03	120,00	26,33

87	ETC1	MYB-like transcription factor ETC1	MSTRG.20476.1	MSTRG.20476	-2,01	45,33	10,33
88	ETC1	MYB-like transcription factor ETC1	MSTRG.20476.2	MSTRG.20476	-2,01	45,33	10,33
89	BH096	Transcription factor bHLH96	MSTRG.11440.1	MSTRG.11440	-1,95	50,67	11,67
90	SPT	Transcription factor SPATULA	MSTRG.2742.1	MSTRG.2742	-1,92	49,67	11,67
91	SPT	Transcription factor SPATULA	MSTRG.2742.2	MSTRG.2742	-1,92	49,67	11,67
92	WRK47	Probable WRKY transcription factor 47	MSTRG.31313.1	MSTRG.31313	-1,91	600,67	145,67
93	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.24071.1	MSTRG.24071	-1,90	415,33	101,67
94	BH153	Transcription factor bHLH153	MSTRG.31849.1	MSTRG.31849	-1,88	1275,00	314,67
95	BH153	Transcription factor bHLH153	MSTRG.31849.2	MSTRG.31849	-1,88	1275,00	314,67
96	SRM1	Transcription factor SRM1	MSTRG.628.1	MSTRG.628	-1,87	114,67	29,00
97	NFYA1	Nuclear transcription factor Y subunit A-1	MSTRG.4176.1	MSTRG.4176	-1,86	130,33	33,00
98	BH030	Transcription factor bHLH30	MSTRG.13027.1	MSTRG.13027	-1,84	379,00	97,67
99	PTL	Trihelix transcription factor PTL	MSTRG.19364.1	MSTRG.19364	-1,81	63,33	16,67
100	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.1	MSTRG.3750	-1,78	423,00	113,67
101	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.2	MSTRG.3750	-1,78	423,00	113,67
102	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.3	MSTRG.3750	-1,78	423,00	113,67
103	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.4	MSTRG.3750	-1,78	423,00	113,67
104	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.5	MSTRG.3750	-1,78	423,00	113,67
105	WRK29	Probable WRKY transcription factor 29	MSTRG.32007.1	MSTRG.32007	-1,77	54,33	14,67
106	WRK29	Probable WRKY transcription factor 29	MSTRG.32007.2	MSTRG.32007	-1,77	54,33	14,67
107	WRK29	Probable WRKY transcription factor 29	MSTRG.32007.3	MSTRG.32007	-1,77	54,33	14,67
108	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.1	MSTRG.30184	-1,75	313,33	86,00
109	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.2	MSTRG.30184	-1,75	313,33	86,00
110	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.3	MSTRG.30184	-1,75	313,33	86,00
111	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.4	MSTRG.30184	-1,75	313,33	86,00
112	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.5	MSTRG.30184	-1,75	313,33	86,00
113	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.6	MSTRG.30184	-1,75	313,33	86,00
114	ERF5	Ethylene-responsive transcription factor 5	MSTRG.30184.7	MSTRG.30184	-1,75	313,33	86,00
115	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.8	MSTRG.30184	-1,75	313,33	86,00
116	WRKY6	WRKY transcription factor 6	MSTRG.15365.1	MSTRG.15365	-1,75	84,33	23,00

117	EF106	Ethylene-responsive transcription factor ERF106	MSTRG.24337.1	MSTRG.24337	-1,75	150,67	41,00
118	EF106	Ethylene-responsive transcription factor ERF106	MSTRG.24337.2	MSTRG.24337	-1,75	150,67	41,00
119	WRK33	Probable WRKY transcription factor 33	MSTRG.18819.1	MSTRG.18819	-1,74	287,67	80,00
120	SRM1	Transcription factor SRM1	MSTRG.10932.1	MSTRG.10932	-1,71	89,67	25,00
121	ASIL2	Trihelix transcription factor ASIL2	MSTRG.3056.1	MSTRG.3056	-1,69	438,33	123,67
122	MY123	Transcription factor MYB123	MSTRG.3778.1	MSTRG.3778	-1,68	285,67	79,33
123	RAP23	Ethylene-responsive transcription factor RAP2-3	MSTRG.15090.1	MSTRG.15090	-1,66	2790,33	802,67
124	TCP3	Transcription factor TCP3	MSTRG.21481.1	MSTRG.21481	-1,64	106,67	31,00
125	TCP3	Transcription factor TCP3	MSTRG.21481.2	MSTRG.21481	-1,64	106,67	31,00
126	TCP3	Transcription factor TCP3	MSTRG.21481.3	MSTRG.21481	-1,64	106,67	31,00
127	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.32025.1	MSTRG.32025	-1,63	704,00	212,00
128	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.32025.2	MSTRG.32025	-1,63	704,00	212,00
129	KUA1	Transcription factor KUA1	MSTRG.9806.1	MSTRG.9806	-1,62	839,00	245,67
130	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.4030.1	MSTRG.4030	-1,62	194,00	57,00
131	ILR3	Transcription factor ILR3	MSTRG.14109.1	MSTRG.14109	-1,60	543,33	163,33
132	ILR3	Transcription factor ILR3	MSTRG.14109.2	MSTRG.14109	-1,60	543,33	163,33
133	ILR3	Transcription factor ILR3	MSTRG.14109.3	MSTRG.14109	-1,60	543,33	163,33
134	ILR3	Transcription factor ILR3	MSTRG.14109.4	MSTRG.14109	-1,60	543,33	163,33
135	WRK48	Probable WRKY transcription factor 48	MSTRG.7237.1	MSTRG.7237	-1,60	477,00	146,33
136	TGA7	Transcription factor TGA7	MSTRG.31376.1	MSTRG.31376	-1,60	552,00	166,00
137	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.23899.1	MSTRG.23899	-1,59	26,67	8,00
138	TGA1	Transcription factor TGA1	MSTRG.16154.1	MSTRG.16154	-1,55	1197,00	376,00
139	TGA1	Transcription factor TGA1	MSTRG.16154.2	MSTRG.16154	-1,55	1197,00	376,00
140	MUTE	Transcription factor MUTE	MSTRG.14638.1	MSTRG.14638	-1,54	44,67	14,00
141	ERF80	Ethylene-responsive transcription factor 9	MSTRG.12010.1	MSTRG.12010	-1,51	637,33	205,33
142	MYC2	Transcription factor MYC2	MSTRG.15281.1	MSTRG.15281	-1,51	150,00	46,00
143	TCP15	Transcription factor TCP15	MSTRG.23976.1	MSTRG.23976	1,51	56,67	144,33
144	ERF22	Ethylene-responsive transcription factor ERF022	MSTRG.23479.1	MSTRG.23479	2,17	16,33	68,33
145	BH120	Transcription factor bHLH120	MSTRG.31546.1	MSTRG.31546	2,30	5,33	23,33

STR vs. LTR

No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	LTR Genes Results	STR Genes Results
146	NAC42	Transcription factor JUNGBRUNNEN 1	MSTRG.32214.1	MSTRG.32214	-6,22	14,33	0,00
147	NAC42	Transcription factor JUNGBRUNNEN 1	MSTRG.32214.2	MSTRG.32214	-6,22	14,33	0,00
148	MPH1	Myb family transcription factor MPH1	MSTRG.21849.1	MSTRG.21849	-5,95	23,67	0,33
149	MPH1	Myb family transcription factor MPH1	MSTRG.21849.2	MSTRG.21849	-5,95	23,67	0,33
150	WRK51	Probable WRKY transcription factor 51	MSTRG.16082.1	MSTRG.16082	-5,70	36,67	0,67
151	WRK51	Probable WRKY transcription factor 51	MSTRG.16082.2	MSTRG.16082	-5,70	36,67	0,67
152	WRK51	Probable WRKY transcription factor 51	MSTRG.16082.3	MSTRG.16082	-5,70	36,67	0,67
153	MY108	Transcription factor MYB108	MSTRG.15027.1	MSTRG.15027	-3,47	82,00	7,00
154	WRK74	Probable WRKY transcription factor 74	MSTRG.21830.1	MSTRG.21830	-3,39	30,67	2,67
155	WRK74	Probable WRKY transcription factor 74	MSTRG.21830.2	MSTRG.21830	-3,39	30,67	2,67
156	WRK70	WRKY DNA-binding transcription factor 70	MSTRG.18748.1	MSTRG.18748	-3,36	132,00	12,00
157	WRK28	WRKY transcription factor 28	MSTRG.13343.1	MSTRG.13343	-3,29	106,67	10,33
158	MYB72	Transcription factor MYB72	MSTRG.26206.1	MSTRG.26206	-3,25	51,33	5,00
159	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25340.1	MSTRG.25340	-3,23	66,33	6,67
160	WRK71	WRKY transcription factor 71	MSTRG.30798.1	MSTRG.30798	-3,07	26,33	3,00
161	WRK71	WRKY transcription factor 71	MSTRG.30798.2	MSTRG.30798	-3,07	26,33	3,00
162	HSFB1	Heat stress transcription factor B-1	MSTRG.12950.1	MSTRG.12950	-2,81	27,33	3,67
163	MY102	Transcription factor MYB102	MSTRG.14278.1	MSTRG.14278	-2,73	31,33	4,33
164	WRKY6	WRKY transcription factor 6	MSTRG.20348.1	MSTRG.20348	-2,55	47,00	7,67
165	MYB2	Transcription factor MYB2	MSTRG.15699.1	MSTRG.15699	-2,41	26,33	4,67
166	MYB2	Transcription factor MYB2	MSTRG.15699.2	MSTRG.15699	-2,41	26,33	4,67
167	MYB2	Transcription factor MYB2	MSTRG.15699.3	MSTRG.15699	-2,41	26,33	4,67
168	HSFB3	Heat stress transcription factor B-3	MSTRG.17389.1	MSTRG.17389	-2,40	65,33	11,67
169	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.34676.1	MSTRG.34676	-2,22	60,33	12,33
170	WRK75	Probable WRKY transcription factor 75	MSTRG.9226.1	MSTRG.9226	-2,19	221,67	46,67
171	MYB62	Transcription factor MYB62	MSTRG.26416.1	MSTRG.26416	-2,07	62,67	14,33
172	MY102	Transcription factor MYB102	MSTRG.13316.1	MSTRG.13316	-1,87	58,00	15,00
173	WRK53	Probable WRKY transcription factor 53	MSTRG.11257.1	MSTRG.11257	-1,81	58,33	16,00

174	WRK55	WRKY transcription factor 55	MSTRG.22916.1	MSTRG.22916	-1,78	69,67	19,67
175	GAT22	Putative GATA transcription factor 22	MSTRG.2559.1	MSTRG.2559	-1,73	64,00	18,33
176	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.4032.1	MSTRG.4032	-1,69	286,33	83,67
177	WRK29	Probable WRKY transcription factor 29	MSTRG.32007.1	MSTRG.32007	-1,65	48,00	14,67
178	WRK29	Probable WRKY transcription factor 29	MSTRG.32007.2	MSTRG.32007	-1,65	48,00	14,67
179	WRK29	Probable WRKY transcription factor 29	MSTRG.32007.3	MSTRG.32007	-1,65	48,00	14,67
180	VRN1	B3 domain-containing transcription factor VRN1	MSTRG.24274.1	MSTRG.24274	-1,61	44,00	13,67
181	SRM1	Transcription factor SRM1	MSTRG.628.1	MSTRG.628	-1,55	88,67	29,00
182	WER	Transcription factor WER	MSTRG.9637.1	MSTRG.9637	-1,52	78,33	25,33
183	PHL6	Myb family transcription factor PHL6	MSTRG.27626.1	MSTRG.27626	-1,52	50,33	16,67
184	PHL6	Myb family transcription factor PHL6	MSTRG.27626.2	MSTRG.27626	-1,52	50,33	16,67
185	PHL6	Myb family transcription factor PHL6	MSTRG.27626.3	MSTRG.27626	-1,52	50,33	16,67
186	WER	Transcription factor WER	MSTRG.20889.1	MSTRG.20889	2,03	8,33	32,00
187	ERF22	Ethylene-responsive transcription factor ERF022	MSTRG.23479.1	MSTRG.23479	3,72	5,33	68,33
188	MYB2	Transcription factor MYB1	MSTRG.5586.1	MSTRG.5586	4,35	7,00	140,00

MTR vs. LTR

No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	LTR Genes Results	MTR Genes Results
189	WRK55	WRKY transcription factor 55	MSTRG.22916.1	MSTRG.22916	-2,11	69,67	18,00
190	HFA4B	Heat stress transcription factor A-4b	MSTRG.14253.1	MSTRG.14253	1,52	25,67	79,00
191	KUA1	Transcription factor KUA1	MSTRG.9806.1	MSTRG.9806	1,53	270,67	839,00
192	CPC	Transcription factor CPC	MSTRG.14145.1	MSTRG.14145	1,53	21,00	65,00
193	EBIII	MYB-like transcription factor 4	MSTRG.21876.1	MSTRG.21876	1,58	27,00	85,67
194	MY111	Transcription factor MYB111	MSTRG.21876.2	MSTRG.21876	1,58	27,00	85,67
195	BH014	Transcription factor bHLH14	MSTRG.21857.1	MSTRG.21857	1,70	117,67	411,33
196	ETC1	MYB-like transcription factor ETC1	MSTRG.20476.1	MSTRG.20476	1,71	13,00	45,33
197	ETC1	MYB-like transcription factor ETC1	MSTRG.20476.2	MSTRG.20476	1,71	13,00	45,33
198	WRK53	Probable WRKY transcription factor 53	MSTRG.11257.1	MSTRG.11257	1,84	58,33	223,67
199	MYB2	Transcription factor MYB1	MSTRG.5581.1	MSTRG.5581	1,89	233,00	922,67
200	MYB2	Transcription factor MYB1	MSTRG.5581.2	MSTRG.5581	1,89	233,00	922,67
201	MYB2	Transcription factor MYB1	MSTRG.5581.3	MSTRG.5581	1,89	233,00	922,67
202	MYB2	Transcription factor MYB1	MSTRG.5581.4	MSTRG.5581	1,89	233,00	922,67
203	MYB2	Transcription factor MYB1	MSTRG.5581.5	MSTRG.5581	1,89	233,00	922,67
204	MYB15	Transcription factor MYB15	MSTRG.2089.1	MSTRG.2089	1,99	24,33	104,00
205	WRK41	Probable WRKY transcription factor 41	MSTRG.4799.1	MSTRG.4799	2,01	43,67	188,00
206	BH051	Transcription factor bHLH51	MSTRG.21715.1	MSTRG.21715	2,03	10,67	46,67
207	ERF99	Ethylene-responsive transcription factor 13	MSTRG.10673.1	MSTRG.10673	2,41	14,00	79,67
208	ERF99	Ethylene-responsive transcription factor 13	MSTRG.10673.2	MSTRG.10673	2,41	14,00	79,67
209	HSFB1	Heat stress transcription factor B-1	MSTRG.12950.1	MSTRG.12950	2,59	27,33	172,33
210	WRK43	Probable WRKY transcription factor 43	MSTRG.11159.1	MSTRG.11159	2,74	5,67	39,67
211	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.1	MSTRG.5571	3,20	1,33	13,00
212	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.2	MSTRG.5571	3,20	1,33	13,00
213	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.3	MSTRG.5571	3,20	1,33	13,00
214	WRK12	Probable WRKY transcription factor 12	MSTRG.10638.1	MSTRG.10638	3,24	1,33	13,67
215	MYB1	Transcription factor MYB1	MSTRG.29645.1	MSTRG.29645	3,42	16,33	190,67
216	MYB1	Transcription factor MYB1	MSTRG.29645.2	MSTRG.29645	3,42	16,33	190,67

217	MYB2	Transcription factor MYB1	MSTRG.29645.3	MSTRG.29645	3,42	16,33	190,67
218	MYB93	Transcription factor MYB93	MSTRG.3372.1	MSTRG.3372	3,74	1,33	19,00
219	MYB2	Transcription factor MYB1	MSTRG.5586.1	MSTRG.5586	4,58	7,00	177,67

MLR vs. LLR

No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	MLR Genes Results	LLR Genes Results
220	EF100	Ethylene-responsive transcription factor 1A	MSTRG.30183.1	MSTRG.30183	-6,21	30,67	0,33
221	WRK51	Probable WRKY transcription factor 51	MSTRG.33801.1	MSTRG.33801	-6,18	15,67	0,00
222	MY123	Transcription factor MYB123	MSTRG.3781.1	MSTRG.3781	-5,25	16,00	0,33
223	NAC56	NAC transcription factor 56	MSTRG.28986.1	MSTRG.28986	-2,29	29,67	5,00
224	RAX3	Transcription factor RAX3	MSTRG.2669.1	MSTRG.2669	-1,52	76,67	23,33
225	MY123	Transcription factor MYB123	MSTRG.3778.1	MSTRG.3778	1,62	252,33	659,67
226	TCP8	Transcription factor TCP8	MSTRG.21111.1	MSTRG.21111	1,66	56,00	148,67
227	AMS	Transcription factor ABORTED MICROSPORES	MSTRG.35221.1	MSTRG.35221	2,09	10,67	38,67

Supplementary Table 2. DEGs related to hormones identified in STR vs. MTR, STR vs. LTR, MTR vs. LTR and MLR vs. LLR comparisons.

STR vs. MTR

Hormone	No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	MTR Genes Results	STR Genes Results	Function
IAA	1	IAMT1	Indole-3-acetate O-methyltransferase 1	MSTRG.20288.1	MSTRG.20288	-5,8187	96	2	Conjugate synthesis
	2	GH31	Probable indole-3-acetic acid-amido synthetase GH3.1	MSTRG.16511.1	MSTRG.16511	-2,6558	131	33	Conjugate synthesis
	3	GH31	Probable indole-3-acetic acid-amido synthetase GH3.1	MSTRG.28521.1	MSTRG.28521	-1,6456	619	144	Conjugate synthesis
	4	ILL5	IAA-amino acid hydrolase ILR1-like 5	MSTRG.21216.1	MSTRG.21216	-5,204	32	1	Conjugate degradation
	5	ILL1	IAA-amino acid hydrolase ILR1-like 1	MSTRG.9014.1	MSTRG.9014	-2,6648	45	5	Conjugate degradation
	6	LAX3	Auxin transporter-like protein 3	MSTRG.24617.1	MSTRG.24617	1,5637	816	2029	Transport
	7	AB8B	Putative ABC transporter B family member 8	MSTRG.5121.1	MSTRG.5121	-2,0039	286	73	Transport
	8	AB15B	ABC transporter B family member 15	MSTRG.4010.1	MSTRG.4010	-1,743	668	173	Transport
	9	AB11B	ABC transporter B family member 11	MSTRG.22987.1	MSTRG.22987	-1,5843	725	169	Transport
	10	IAA7	Auxin-responsive protein IAA7	MSTRG.15336.1	MSTRG.15336	-5,2247	380	7	Signal transduction-related
	11	SAU71	Auxin-responsive protein SAUR71	MSTRG.9206.1	MSTRG.9206	-3,2177	814	87	Signal transduction-related
	12	SAU32	Auxin-responsive protein SAUR32	MSTRG.25422.1	MSTRG.25422	-3,1421	40	3	Signal transduction-related
	13	SAU76	Auxin-responsive protein SAUR76	MSTRG.32895.1	MSTRG.32895	-2,6188	16	4	Signal transduction-related
	14	SAU71	Auxin-responsive protein SAUR71	MSTRG.25418.1	MSTRG.25418	-2,5796	34	6	Signal transduction-related
	15	IAA14	Auxin-responsive protein IAA14	MSTRG.6453.1	MSTRG.6453	-2,4332	330	65	Signal transduction-related

	16	IAA11	Auxin-responsive protein IAA11	MSTRG.35314.1	MSTRG.35314	-2,1882	63	12	Signal transduction-related
	17	ARFD	Auxin response factor 4	MSTRG.1418.1	MSTRG.1418	-1,8851	52	11	Signal transduction-related
	18	SAU32	Auxin-responsive protein SAUR32	MSTRG.21851.1	MSTRG.21851	-1,6844	117	33	Signal transduction-related
	19	IAA27	Auxin-responsive protein IAA27	MSTRG.5225.1	MSTRG.5225	-1,5517	1099	365	Signal transduction-related
	20	ARFD	Auxin response factor 4	MSTRG.1419.1	MSTRG.1419	-1,5271	241	88	Signal transduction-related
	21	SAU40	Auxin-responsive protein SAUR40	MSTRG.3770.1	MSTRG.3770	2,4915	8	58	Signal transduction-related
	22	WOX4	WUSCHEL-related homeobox 4	MSTRG.2733.1	MSTRG.2733	-4,0306	157	9	Signal transduction-related
CK	23	CKX6	Cytokinin dehydrogenase 6	MSTRG.14015.1	MSTRG.14015	-4,7305	59	3	Degradation/ Inactivation
	24	CKX7	Cytokinin dehydrogenase 7	MSTRG.3787.1	MSTRG.3787	-2,4724	41	5	Degradation/ Inactivation
	25	CKX3	Cytokinin dehydrogenase 3	MSTRG.13748.1	MSTRG.13748	-1,9699	42	12	Degradation/ Inactivation
	26	ORR26	Two-component response regulator ORR26	MSTRG.9399.1	MSTRG.9399	-1,5281	565	190	Signal transduction-related
ABA	27	ABAH2	Abscisic acid 8'-hydroxylase 2	MSTRG.1823.1	MSTRG.1823	-2,1271	132	26	Degradation/ Inactivation
	28	ABAH4	Abscisic acid 8'-hydroxylase 4	MSTRG.28704.1	MSTRG.28704	-1,7702	78	22	Degradation/ Inactivation
	29	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.4140.1	MSTRG.4140	-5,6307	11	0	Degradation/ Inactivation
	30	LEA29	Late embryogenesis abundant protein D-29	MSTRG.16902.1	MSTRG.16902	-3,3739	64	0	Degradation/ Inactivation
	31	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.1674.1	MSTRG.1674	-3,0308	89	12	Degradation/ Inactivation

	32	LEA65	Late embryogenesis abundant protein At5g17165	MSTRG.24262.1	MSTRG.24262	-2,3531	5263	1020	Degradation/ Inactivation
	33	LEA5	Late embryogenesis abundant protein Lea5	MSTRG.15019.1	MSTRG.15019	-2,1399	18703	3929	Degradation/ Inactivation
	34	AHK1	Histidine kinase 1	MSTRG.17005.1	MSTRG.17005	-3,565	655	40	Degradation/ Inactivation
ET	35	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25340.1	MSTRG.25340	-4,6931	244	4	Signal transduction-related
	36	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.35144.1	MSTRG.35144	-3,4356	12	0	Signal transduction-related
	37	ERF92	Ethylene-responsive transcription factor 1B	MSTRG.15418.1	MSTRG.15418	-2,8672	196	19	Signal transduction-related
	38	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.34676.1	MSTRG.34676	-2,7962	117	13	Signal transduction-related
	39	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.4032.1	MSTRG.4032	-2,2768	470	81	Signal transduction-related
	40	ERFC3	Ethylene-response factor C3	MSTRG.24682.1	MSTRG.24682	-1,7952	74	21	Signal transduction-related
	41	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.1	MSTRG.30184	-1,7463	355	91	Signal transduction-related
	42	EF106	Ethylene-responsive transcription factor ERF106	MSTRG.24337.1	MSTRG.24337	-1,746	150	58	Signal transduction-related
	43	RAP23	Ethylene-responsive transcription factor RAP2-3	MSTRG.15090.1	MSTRG.15090	-1,6574	2986	861	Signal transduction-related
	44	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.32025.1	MSTRG.32025	-1,6291	890	291	Signal transduction-related
	45	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.4030.1	MSTRG.4030	-1,6168	203	52	Signal transduction-related
	46	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.23899.1	MSTRG.23899	-1,5926	26	12	Signal transduction-related
	47	ERF80	Ethylene-responsive transcription factor 9	MSTRG.12010.1	MSTRG.12010	-1,5142	696	248	Signal transduction-related

	48	ERF22	Ethylene-responsive transcription factor ERF022	MSTRG.23479.1	MSTRG.23479	2,1681	22	96	Signal transduction-related
JA	49	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34851.1	MSTRG.34851	-4,2143	176	11	Biosynthesis
	50	LOX6	Lipoxygenase 6	MSTRG.9345.1	MSTRG.9345	-3,834	105	7	Biosynthesis
	51	OPR2	12-oxophytodienoate reductase 2	MSTRG.24084.1	MSTRG.24084	-3,7371	70	3	Biosynthesis
	52	OPR2	12-oxophytodienoate reductase 2	MSTRG.24102.1	MSTRG.24102	-1,7655	54	16	Biosynthesis
	53	JOX4	Jasmonate-induced oxygenase 4	MSTRG.6775.3	MSTRG.6775	-3,0311	985	75	Degradation/ Inactivation
	54	MYC2	Transcription factor MYC2	MSTRG.15281.1	MSTRG.15281	-1,5056	100	39	Signal transduction-related
GA	55	G3OX	Gibberellin 3-beta-dioxygenase 1	MSTRG.31144.1	MSTRG.31144	-2,8977	19	3	Biosynthesis
	56	G2OX2	Gibberellin 2-beta-dioxygenase 2	MSTRG.33954.1	MSTRG.33954	-2,3035	116	18	Biosynthesis
	57	GID1B	Gibberellin receptor GID1B	MSTRG.29907.1	MSTRG.29907	-1,9746	1464	379	Signal transduction-related
	58	GASA9	Gibberellin-regulated protein 9	MSTRG.771.1	MSTRG.771	-1,5613	195	56	Signal transduction-related
	59	GASA1	Gibberellin-regulated protein 1	MSTRG.20696.1	MSTRG.20696	1,9573	195	794	Signal transduction-related
BR	60	BRAT1	Brassinosteroid-related acyltransferase 1	MSTRG.3982.1	MSTRG.3982	-3,0087	33	4	Degradation/ Inactivation
	61	BRH1	Brassinosteroid-responsive RING protein 1	MSTRG.27142.1	MSTRG.27142	-2,8269	14	1	Signal transduction-related
	62	BAK1	BRASSINOSTEROID INSENSITIVE 1-associated receptor kinase 1	MSTRG.25201.1	MSTRG.25201	-1,8816	35	9	Signal transduction-related

STR vs. LTR

Hormone	No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	LTR Genes Results	STR Genes Results	Function
IAA	63	ILR1	IAA-amino acid hydrolase ILR1	MSTRG.19113.1	MSTRG.19113	-1,7443	99	27	Conjugate degradation
	64	ILL5	IAA-amino acid hydrolase ILR1-like 5	MSTRG.21216.1	MSTRG.21216	-4,4324	15	1	Conjugate degradation
	65	PILS1	Protein PIN-LIKES 1	MSTRG.17183.1	MSTRG.17183	2,1426	11	124	Transport
	66	IAA7	Auxin-responsive protein IAA7	MSTRG.15336.1	MSTRG.15336	-4,0378	407	7	Signal transduction-related
	67	SAU32	Auxin-responsive protein SAUR32	MSTRG.25422.1	MSTRG.25422	-2,6389	20	3	Signal transduction-related
	68	IAA14	Auxin-responsive protein IAA14	MSTRG.6453.1	MSTRG.6453	-2,5144	336	65	Signal transduction-related
	69	SAU71	Auxin-responsive protein SAUR71	MSTRG.9206.1	MSTRG.9206	-2,2825	234	87	Signal transduction-related
CK	70	CKX3	Cytokinin dehydrogenase 3	MSTRG.13748.1	MSTRG.13748	-2,0878	32	12	Degradation/ Inactivation
ABA	71	ABAH2	Abscisic acid 8'-hydroxylase 2	MSTRG.1823.1	MSTRG.1823	-2,5957	140	26	Degradation/ Inactivation
	72	LEA29	Late embryogenesis abundant protein D-29	MSTRG.16902.1	MSTRG.16902	-2,5169	17	0	Signal transduction-related
	73	AHK1	Histidine kinase 1	MSTRG.17005.1	MSTRG.17005	-2,284	175	40	Signal transduction-related
	74	LEA5	Late embryogenesis abundant protein Lea5	MSTRG.15019.1	MSTRG.15019	-1,8216	12104	3929	Signal transduction-related
ET	75	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25340.1	MSTRG.25340	-3,2263	40	4	Signal transduction-related
	76	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.34676.1	MSTRG.34676	-2,216	67	13	Signal transduction-related
	77	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.4032.1	MSTRG.4032	-1,687	248	81	Signal transduction-related
	78	ERF22	Ethylene-responsive transcription factor ERF022	MSTRG.23479.1	MSTRG.23479	3,7166	5	96	Signal transduction-related

JA	79	JOX4	Jasmonate-induced oxygenase 4	MSTRG.6775.3	MSTRG.6775	-1,655	208	75	Degradation/ Inactivation
GA	80	SCL3	Scarecrow-like protein 3	MSTRG.10290.1	MSTRG.10290	-2,7414	62	14	Signal transduction-related
BR	81	BRAT1	Brassinosteroid-related acyltransferase 1	MSTRG.3982.1	MSTRG.3982	-2,5594	20	4	Degradation/ Inactivation
	82	BAK1	BRASSINOSTEROID INSENSITIVE 1-associated receptor kinase 1	MSTRG.25201.1	MSTRG.25201	-1,8717	11	9	Signal transduction-related

MTR vs. LTR

Hormone	No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	LTR Genes Results	MTR Genes Results	Function
IAA	83	PIN6	Auxin efflux carrier component 6	MSTRG.4274.1	MSTRG.4274	1,5622	12	53	Transport
	84	PIN6	Auxin efflux carrier component 6	MSTRG.35377.1	MSTRG.35377	1,8803	7	28	Transport
	85	PILS1	Protein PIN-LIKES 1	MSTRG.17183.1	MSTRG.17183	2,0515	11	109	Transport
	86	AB11B	ABC transporter B family member 11	MSTRG.22987.1	MSTRG.22987	1,8529	136	725	Transport
	87	AB8B	Putative ABC transporter B family member 8	MSTRG.5121.1	MSTRG.5121	1,9268	75	286	Transport
	88	WOX4	WUSCHEL-related homeobox 4	MSTRG.2733.1	MSTRG.2733	2,508	11	157	Signal transduction-related
CK	89	CKX6	Cytokinin dehydrogenase 6	MSTRG.14015.1	MSTRG.14015	1,9964	9	59	Degradation/ Inactivation
ABA	90	ABAH4	Abscisic acid 8'-hydroxylase 4	MSTRG.187.1	MSTRG.187	4,6367	0	28	Degradation/ Inactivation
ET	91	ERF99	Ethylene-responsive transcription factor 13	MSTRG.10673.1	MSTRG.10673	2,4108	11	86	Signal transduction-related
JA	92	LOX6	Lipoxygenase 6	MSTRG.9345.1	MSTRG.9345	2,2798	17	105	Biosynthesis
	93	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34851.1	MSTRG.34851	7,3583	3	176	Biosynthesis
	94	JOX2	Jasmonate-induced oxygenase 2	MSTRG.22752.1	MSTRG.22752	1,9057	50	251	Degradation/

									Inactivation
GA	95	SCL3	Scarecrow-like protein 3	MSTRG.10290.1	MSTRG.10290	-3,9042	62	6	Signal transduction-related
	96	GASA1	Gibberellin-regulated protein 1	MSTRG.20696.1	MSTRG.20696	-2,5329	1200	195	Signal transduction-related
	97	GASAE	Gibberellin-regulated protein 14	MSTRG.20693.1	MSTRG.20693	-1,9979	1910	670	Signal transduction-related
	98	GASAE	Gibberellin-regulated protein 14	MSTRG.20694.1	MSTRG.20694	-1,5571	6561	2369	Signal transduction-related
	99	GASA9	Gibberellin-regulated protein 9	MSTRG.771.1	MSTRG.771	1,9977	35	195	Signal transduction-related

MLR vs. LLR

Hormone	No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	LLR Genes Results	MLR Genes Results	Function
IAA	100	ILL3	IAA-amino acid hydrolase ILR1-like 3	MSTRG.19114.1	MSTRG.19114	-2,6293	348	71	Conjugate degradation
	101	ILR1	IAA-amino acid hydrolase ILR1	MSTRG.19113.1	MSTRG.19113	-1,8232	605	195	Conjugate degradation
	102	AB8B	Putative ABC transporter B family member 8	MSTRG.5121.1	MSTRG.5121	-2,1107	833	161	Transport
	103	PILS3	Protein PIN-LIKES 3	MSTRG.3734.1	MSTRG.3734	-1,743	220	46	Transport
	104	AB2B	ABC transporter B family member 2	MSTRG.29974.1	MSTRG.29974	-1,8193	62	6	Transport
	105	AB19A	Auxin-binding protein ABP19a	MSTRG.27398.1	MSTRG.27398	-3,4849	41	6	Signal transduction-related
	106	SAU40	Auxin-responsive protein SAUR40	MSTRG.1959.1	MSTRG.1959	3,1403	2	59	Signal transduction-related
ABA	107	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	MSTRG.32782.1	MSTRG.32782	-4,0469	148	16	Biosynthesis
	108	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	MSTRG.13453.1	MSTRG.13453	-3,9891	1435	83	Biosynthesis
	109	LEA29	Late embryogenesis abundant protein D-29	MSTRG.23000.1	MSTRG.23000	-4,3364	35	2	Signal transduction-related

	110	LEA7	Late embryogenesis abundant protein 7	MSTRG.12711.1	MSTRG.12711	-3,1329	23	4	Signal transduction-related
	111	PYL4	Abscisic acid receptor PYL4	MSTRG.21759.1	MSTRG.21759	1,8898	195	917	Signal transduction-related
ET	112	EF100	Ethylene-responsive transcription factor 1A	MSTRG.30183.1	MSTRG.30183	-6,206	47	0	Signal transduction-related
JA	113	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34851.1	MSTRG.34851	-2,4672	154	40	Biosynthesis
	114	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.575.1	MSTRG.575	-2,2278	44	11	Biosynthesis
	115	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34848.1	MSTRG.34848	-2,2275	52	7	Biosynthesis
	116	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.572.1	MSTRG.572	-2,0661	44	3	Biosynthesis
	117	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34849.1	MSTRG.34849	-1,9803	149	21	Biosynthesis
	118	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.570.1	MSTRG.570	-1,9081	146	25	Biosynthesis
	119	OPR2	12-oxophytodienoate reductase 2	MSTRG.24084.1	MSTRG.24084	-1,6156	730	249	Biosynthesis
	120	OPR1	12-oxophytodienoate reductase 1	MSTRG.3282.1	MSTRG.3282	3,2337	2	18	Biosynthesis
	121	JMT2	Probable jasmonic acid carboxyl methyltransferase 2	MSTRG.34341.2	MSTRG.34341	-3,2013	379	27	Conjugate synthesis
GA	122	SCL3	Scarecrow-like protein 3	MSTRG.10290.1	MSTRG.10290	-7,4602	112	2	Signal transduction-related
	123	GASA9	Gibberellin-regulated protein 9	MSTRG.771.1	MSTRG.771	2,5234	8	47	Signal transduction-related
	124	GASA9	Gibberellin-regulated protein 9	MSTRG.771.2	MSTRG.771.	2,5234	8	47	Signal transduction-related

Supplementary table 3. Genes encoding transcription factors identified in MTR vs. DTR, MTR_1 vs. TDTR and LTR_1 vs. TTR comparisons.

MTR vs. DTR

No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	DTR Genes Results	MTR Genes Results
1	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25339.1	MSTRG.25339	-2,74	84,67	12,00
2	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25339.2	MSTRG.25339	-2,74	84,67	12,00
3	MYB1	Transcription factor MYB1	MSTRG.23221.1	MSTRG.23221	-2,40	62,67	12,00
4	WRK12	Probable WRKY transcription factor 12	MSTRG.10638.1	MSTRG.10638	-2,39	74,33	13,67
5	ERF86	Ethylene-responsive transcription factor ERF086	MSTRG.24331.1	MSTRG.24331	-2,12	77,67	18,00
6	ERF87	Ethylene-responsive transcription factor ERF087	MSTRG.9157.1	MSTRG.9157	-2,07	315,33	74,33
7	ODO1	MYB-like transcription factor ODO1	MSTRG.30090.1	MSTRG.30090	-2,04	214,00	50,00
8	WRKY6	WRKY transcription factor 6	MSTRG.20348.1	MSTRG.20348	-1,97	241,67	58,67
9	WRK71	WRKY transcription factor 71	MSTRG.30798.1	MSTRG.30798	-1,91	356,67	91,33
10	WRK71	WRKY transcription factor 71	MSTRG.30798.2	MSTRG.30798	-1,91	356,67	91,33
11	BH051	Transcription factor bHLH51	MSTRG.21715.1	MSTRG.21715	-1,85	174,67	46,67
12	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25340.1	MSTRG.25340	-1,81	690,00	187,33
13	DIV	Transcription factor DIVARICATA	MSTRG.22698.1	MSTRG.22698	-1,79	316,00	88,67
14	DIV	Transcription factor DIVARICATA	MSTRG.22698.2	MSTRG.22698	-1,79	316,00	88,67
15	RA212	Ethylene-responsive transcription factor RAP2-12	MSTRG.5191.1	MSTRG.5191	-1,67	36,67	11,33
16	RA212	Ethylene-responsive transcription factor RAP2-12	MSTRG.5191.2	MSTRG.5191	-1,67	36,67	11,33
17	RA212	Ethylene-responsive transcription factor RAP2-12	MSTRG.5191.3	MSTRG.5191	-1,67	36,67	11,33
18	RA212	Ethylene-responsive transcription factor RAP2-12	MSTRG.5191.4	MSTRG.5191	-1,67	36,67	11,33
19	RA212	Ethylene-responsive transcription factor RAP2-12	MSTRG.5191.5	MSTRG.5191	-1,67	36,67	11,33
20	MYB88	Transcription factor MYB88	MSTRG.33976.1	MSTRG.33976	-1,66	55,67	17,67
21	MYB88	Transcription factor MYB88	MSTRG.33976.2	MSTRG.33976	-1,66	55,67	17,67
22	MYBF	Putative Myb family transcription factor At1g14600	MSTRG.2353.1	MSTRG.2353	1,50	63,67	179,00
23	MYB4	Transcription factor MYB4	MSTRG.11924.1	MSTRG.11924	1,54	28,00	81,33
24	MYB4	Transcription factor MYB4	MSTRG.11924.2	MSTRG.11924	1,54	28,00	81,33
25	RAX3	Transcription factor RAX3	MSTRG.4329.1	MSTRG.4329	1,65	45,00	138,67

26	MYBF	Putative Myb family transcription factor At1g14600	MSTRG.18857.1	MSTRG.18857	1,66	133,67	414,67
27	PRE6	Transcription factor PRE6	MSTRG.23961.1	MSTRG.23961	1,69	347,67	1123,67
28	TCP15	Transcription factor TCP15	MSTRG.23976.1	MSTRG.23976	1,72	17,67	56,67
29	HFB4B	Heat stress transcription factor B-4b	MSTRG.1031.1	MSTRG.1031	1,85	209,00	751,67
30	MYB82	Transcription factor MYB82	MSTRG.6631.1	MSTRG.6631	1,88	35,00	127,67
31	VRN1	B3 domain-containing transcription factor VRN1	MSTRG.28822.1	MSTRG.28822	2,07	14,00	58,00
32	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.1	MSTRG.16006	2,50	48,00	266,67
33	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.2	MSTRG.16006	2,50	48,00	266,67
34	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.3	MSTRG.16006	2,50	48,00	266,67
35	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.4	MSTRG.16006	2,50	48,00	266,67
36	WRK70	Probable WRKY transcription factor 70	MSTRG.22918.1	MSTRG.22918	2,58	24,67	145,67
37	BH036	Transcription factor bHLH36	MSTRG.31547.1	MSTRG.31547	2,92	4,33	32,00
38	GATA9	GATA transcription factor 9	MSTRG.12389.1	MSTRG.12389	3,04	133,67	1117,00
39	BH025	Transcription factor bHLH25	MSTRG.16343.1	MSTRG.16343	3,09	14,67	127,00
40	MYB2	Transcription factor MYB1	MSTRG.5581.1	MSTRG.5581	3,12	109,00	922,67
41	MYB2	Transcription factor MYB1	MSTRG.5581.2	MSTRG.5581	3,12	109,00	922,67
42	MYB2	Transcription factor MYB1	MSTRG.5581.3	MSTRG.5581	3,12	109,00	922,67
43	MYB2	Transcription factor MYB1	MSTRG.5581.4	MSTRG.5581	3,12	109,00	922,67
44	MYB2	Transcription factor MYB1	MSTRG.5581.5	MSTRG.5581	3,12	109,00	922,67
45	GATA2	GATA transcription factor 2	MSTRG.26685.1	MSTRG.26685	3,20	8,00	75,33
46	GATA9	GATA transcription factor 9	MSTRG.31632.1	MSTRG.31632	3,43	49,67	543,00
47	PRE3	Transcription factor PRE3	MSTRG.25650.1	MSTRG.25650	3,82	34,67	479,67
48	TGA10	bZIP transcription factor TGA10	MSTRG.17405.1	MSTRG.17405	4,00	1,00	15,33
49	MYB1	Transcription factor MYB1	MSTRG.29645.1	MSTRG.29645	4,04	11,33	190,67
50	MYB1	Transcription factor MYB1	MSTRG.29645.2	MSTRG.29645	4,04	11,33	190,67
51	MYB2	Transcription factor MYB1	MSTRG.29645.3	MSTRG.29645	4,04	11,33	190,67
52	GATA4	GATA transcription factor 4	MSTRG.10803.1	MSTRG.10803	4,06	19,00	316,33
53	WRK49	Probable WRKY transcription factor 49	MSTRG.31956.1	MSTRG.31956	4,30	1,00	19,33
54	BH151	Transcription factor UPBEAT1	MSTRG.33941.1	MSTRG.33941	4,42	4,33	92,33
55	WRK70	WRKY DNA-binding transcription factor 70	MSTRG.18748.1	MSTRG.18748	5,04	4,67	153,67

56	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.1	MSTRG.544	5,51	0,67	29,67
57	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.2	MSTRG.544	5,51	0,67	29,67
58	MY123	Transcription factor MYB123	MSTRG.3781.1	MSTRG.3781	5,91	0,00	11,00
59	ERF99	Ethylene-responsive transcription factor 13	MSTRG.10673.1	MSTRG.10673	5,94	1,33	79,67
60	ERF99	Ethylene-responsive transcription factor 13	MSTRG.10673.2	MSTRG.10673	5,94	1,33	79,67
61	RSL1	Putative transcription factor bHLH086	MSTRG.29744.1	MSTRG.29744	6,33	1,67	133,00
62	RSL2	Transcription factor RSL2	MSTRG.30608.1	MSTRG.30608	6,58	0,00	17,33
63	BH146	Transcription factor bHLH146	MSTRG.27597.1	MSTRG.27597	7,37	0,00	30,00
64	MYB2	Transcription factor MYB1	MSTRG.5586.1	MSTRG.5586	7,49	1,00	177,67

MTR_1 vs. TDTR

No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	TDTR Genes Results	MTR Genes Results
65	ERF95	Ethylene-responsive transcription factor ERF095	MSTRG.15416.1	MSTRG.15416	-5,35	7,33	0,00
66	MYC2	Transcription factor MYC2	MSTRG.15289.1	MSTRG.15289	-5,30	64,67	1,67
67	NAC42	Transcription factor JUNGBRUNNEN 1	MSTRG.32214.1	MSTRG.32214	-4,95	333,67	11,00
68	NAC42	Transcription factor JUNGBRUNNEN 1	MSTRG.32214.2	MSTRG.32214	-4,95	333,67	11,00
69	WRK75	Probable WRKY transcription factor 75	MSTRG.1070.1	MSTRG.1070	-4,94	251,67	8,33
70	WRK75	Probable WRKY transcription factor 75	MSTRG.29989.1	MSTRG.29989	-4,81	383,67	14,00
71	ERF98	Ethylene-responsive transcription factor ERF098	MSTRG.15417.1	MSTRG.15417	-4,81	18,00	0,67
72	UNE10	Transcription factor UNE10	MSTRG.26111.1	MSTRG.26111	-4,55	4,33	0,00
73	BH162	Transcription factor bHLH162	MSTRG.15528.1	MSTRG.15528	-4,38	27,67	1,33
74	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25339.1	MSTRG.25339	-4,35	147,33	7,33
75	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25339.2	MSTRG.25339	-4,35	147,33	7,33
76	RAX3	Transcription factor RAX3	MSTRG.2669.1	MSTRG.2669	-4,21	24,67	1,33
77	MYC3	Transcription factor MYC3	MSTRG.15287.1	MSTRG.15287	-4,21	73,67	4,00
78	MYB93	Transcription factor MYB93	MSTRG.29975.1	MSTRG.29975	-3,50	117,33	10,67
79	ERF87	Ethylene-responsive transcription factor ERF087	MSTRG.9157.1	MSTRG.9157	-3,45	823,33	76,67
80	HSFB1	Heat stress transcription factor B-1	MSTRG.12950.1	MSTRG.12950	-3,44	1171,00	109,67

81	MYC2	Transcription factor MYC2	MSTRG.15294.2	MSTRG.15294	-3,32	75,33	7,67
82	ERF98	Ethylene-responsive transcription factor ERF098	MSTRG.24680.1	MSTRG.24680	-3,32	87,67	9,00
83	VRN1	B3 domain-containing transcription factor VRN1	MSTRG.24276.1	MSTRG.24276	-3,31	50,00	5,00
84	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25340.1	MSTRG.25340	-3,21	1128,00	125,33
85	MOF1	Myb family transcription factor MOF1	MSTRG.35373.1	MSTRG.35373	-3,15	144,33	16,33
86	MOF1	Myb family transcription factor MOF1	MSTRG.35373.2	MSTRG.35373	-3,15	144,33	16,33
87	MOF1	Myb family transcription factor MOF1	MSTRG.35373.3	MSTRG.35373	-3,15	144,33	16,33
88	MOF1	Myb family transcription factor MOF1	MSTRG.35373.4	MSTRG.35373	-3,15	144,33	16,33
89	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.34676.1	MSTRG.34676	-3,14	1259,33	145,33
90	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.32025.1	MSTRG.32025	-3,10	5816,00	688,67
91	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.32025.2	MSTRG.32025	-3,10	5816,00	688,67
92	MY108	Transcription factor MYB108	MSTRG.15027.1	MSTRG.15027	-3,08	1676,00	202,33
93	HSFB3	Heat stress transcription factor B-3	MSTRG.17389.1	MSTRG.17389	-3,03	1206,33	150,67
94	MYB88	Transcription factor MYB88	MSTRG.33976.1	MSTRG.33976	-2,95	75,67	10,00
95	MYB88	Transcription factor MYB88	MSTRG.33976.2	MSTRG.33976	-2,95	75,67	10,00
96	MPH1	Myb family transcription factor MPH1	MSTRG.21849.1	MSTRG.21849	-2,84	433,00	61,67
97	MPH1	Myb family transcription factor MPH1	MSTRG.21849.2	MSTRG.21849	-2,84	433,00	61,67
98	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.1	MSTRG.5571	-2,79	32,67	5,00
99	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.2	MSTRG.5571	-2,79	32,67	5,00
100	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.3	MSTRG.5571	-2,79	32,67	5,00
101	UNE10	Transcription factor UNE10	MSTRG.7720.1	MSTRG.7720	-2,74	145,67	22,33
102	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.35144.1	MSTRG.35144	-2,73	95,33	14,67
103	MYB62	Transcription factor MYB62	MSTRG.32122.1	MSTRG.32122	-2,72	70,00	10,67
104	UNE12	Transcription factor UNE12	MSTRG.24264.1	MSTRG.24264	-2,72	10,67	1,67
105	UNE10	Transcription factor UNE10	MSTRG.15488.1	MSTRG.15488	-2,69	266,33	42,00
106	UNE10	Transcription factor UNE10	MSTRG.15488.2	MSTRG.15488	-2,69	266,33	42,00
107	WRK29	Probable WRKY transcription factor 29	MSTRG.32007.1	MSTRG.32007	-2,69	337,00	53,33
108	WRK29	Probable WRKY transcription factor 29	MSTRG.32007.2	MSTRG.32007	-2,69	337,00	53,33
109	WRK29	Probable WRKY transcription factor 29	MSTRG.32007.3	MSTRG.32007	-2,69	337,00	53,33
110	MYB2	Transcription factor MYB2	MSTRG.15699.1	MSTRG.15699	-2,67	303,67	48,67

111	MYB2	Transcription factor MYB2	MSTRG.15699.2	MSTRG.15699	-2,67	303,67	48,67
112	MYB2	Transcription factor MYB2	MSTRG.15699.3	MSTRG.15699	-2,67	303,67	48,67
113	MB3R5	Transcription factor MYB3R-5	MSTRG.30355.1	MSTRG.30355	-2,61	142,33	23,67
114	MB3R5	Transcription factor MYB3R-5	MSTRG.30355.2	MSTRG.30355	-2,61	142,33	23,67
115	MYB2	Transcription factor MYB2	MSTRG.30419.1	MSTRG.30419	-2,60	164,00	27,67
116	PCL1	Transcription factor PCL1	MSTRG.11326.10	MSTRG.11326	-2,55	811,67	140,67
117	PCL1	Transcription factor PCL1	MSTRG.11326.3	MSTRG.11326	-2,55	811,67	140,67
118	MYB15	Transcription factor MYB15	MSTRG.2089.1	MSTRG.2089	-2,48	380,00	70,00
119	EF110	Ethylene-responsive transcription factor ERF110	MSTRG.18963.1	MSTRG.18963	-2,46	491,67	91,00
120	MY102	Transcription factor MYB102	MSTRG.13316.1	MSTRG.13316	-2,35	585,67	116,00
121	WRK71	WRKY transcription factor 71	MSTRG.30798.1	MSTRG.30798	-2,34	599,33	120,67
122	WRK71	WRKY transcription factor 71	MSTRG.30798.2	MSTRG.30798	-2,34	599,33	120,67
123	NAC42	Transcription factor JUNGBRUNNEN 1	MSTRG.1886.1	MSTRG.1886	-2,33	101,67	20,67
124	WRKY6	WRKY transcription factor 6	MSTRG.15365.1	MSTRG.15365	-2,33	484,33	98,33
125	WK72A	WRKY transcription factor 72A	MSTRG.25671.1	MSTRG.25671	-2,30	1147,67	237,33
126	WK72A	WRKY transcription factor 72A	MSTRG.25671.2	MSTRG.25671	-2,30	1147,67	237,33
127	ETC1	MYB-like transcription factor ETC1	MSTRG.20476.1	MSTRG.20476	-2,30	148,00	30,67
128	ETC1	MYB-like transcription factor ETC1	MSTRG.20476.2	MSTRG.20476	-2,30	148,00	30,67
129	WRK22	WRKY transcription factor 22	MSTRG.11161.1	MSTRG.11161	-2,25	529,33	113,67
130	WRK51	Probable WRKY transcription factor 51	MSTRG.16082.1	MSTRG.16082	-2,25	331,33	72,00
131	WRK51	Probable WRKY transcription factor 51	MSTRG.16082.2	MSTRG.16082	-2,25	331,33	72,00
132	WRK51	Probable WRKY transcription factor 51	MSTRG.16082.3	MSTRG.16082	-2,25	331,33	72,00
133	ERF80	Ethylene-responsive transcription factor 9	MSTRG.12010.1	MSTRG.12010	-2,24	2116,00	454,67
134	WRK74	Probable WRKY transcription factor 74	MSTRG.21830.1	MSTRG.21830	-2,22	225,33	50,00
135	WRK74	Probable WRKY transcription factor 74	MSTRG.21830.2	MSTRG.21830	-2,22	225,33	50,00
136	NFYB3	Nuclear transcription factor Y subunit B-3	MSTRG.20204.1	MSTRG.20204	-2,22	17,67	4,00
137	NFYB3	Nuclear transcription factor Y subunit B-3	MSTRG.20204.2	MSTRG.20204	-2,22	17,67	4,00
138	ERF92	Ethylene-responsive transcription factor 1B	MSTRG.15418.1	MSTRG.15418	-2,17	814,00	181,33
139	AP2L1	AP2-like ethylene-responsive transcription factor At1g16060	MSTRG.7763.1	MSTRG.7763	-2,17	16,00	3,67

140	AP2L1	AP2-like ethylene-responsive transcription factor At1g16060	MSTRG.7763.2	MSTRG.7763	-2,17	16,00	3,67
141	AP2L1	AP2-like ethylene-responsive transcription factor At1g16060	MSTRG.7763.3	MSTRG.7763	-2,17	16,00	3,67
142	WRK75	Probable WRKY transcription factor 75	MSTRG.9226.1	MSTRG.9226	-2,16	2909,33	664,00
143	MY102	Transcription factor MYB102	MSTRG.21375.1	MSTRG.21375	-2,15	18,67	4,33
144	BH087	Transcription factor bHLH87	MSTRG.33264.1	MSTRG.33264	-2,13	250,00	58,33
145	BH087	Transcription factor bHLH87	MSTRG.33264.2	MSTRG.33264	-2,13	250,00	58,33
146	HSFA3	Heat stress transcription factor A-3	MSTRG.19355.1	MSTRG.19355	-2,12	42,33	10,00
147	HSFA3	Heat stress transcription factor A-3	MSTRG.19355.2	MSTRG.19355	-2,12	42,33	10,00
148	HSFA3	Heat stress transcription factor A-3	MSTRG.19355.3	MSTRG.19355	-2,12	42,33	10,00
149	WRK56	Probable WRKY transcription factor 56	MSTRG.32004.1	MSTRG.32004	-2,11	32,33	7,67
150	CPC	Transcription factor CPC	MSTRG.14145.1	MSTRG.14145	-2,09	118,00	28,67
151	WRK50	Probable WRKY transcription factor 50	MSTRG.2512.1	MSTRG.2512	-2,06	12,33	3,00
152	WRK50	Probable WRKY transcription factor 50	MSTRG.2512.2	MSTRG.2512	-2,06	12,33	3,00
153	WRK43	Probable WRKY transcription factor 43	MSTRG.11159.1	MSTRG.11159	-2,06	98,67	24,00
154	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.1	MSTRG.18391	-1,97	15,33	4,00
155	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.2	MSTRG.18391	-1,97	15,33	4,00
156	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.3	MSTRG.18391	-1,97	15,33	4,00
157	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.4	MSTRG.18391	-1,97	15,33	4,00
158	KUA1	Transcription factor KUA1	MSTRG.9806.1	MSTRG.9806	-1,95	1906,67	503,00
159	SRM1	Transcription factor SRM1	MSTRG.628.1	MSTRG.628	-1,92	539,67	146,00
160	WRK65	Probable WRKY transcription factor 65	MSTRG.30669.1	MSTRG.30669	-1,88	285,67	79,00
161	WRK65	Probable WRKY transcription factor 65	MSTRG.30669.2	MSTRG.30669	-1,88	285,67	79,00
162	WRK40	Probable WRKY transcription factor 40	MSTRG.3880.1	MSTRG.3880	-1,85	50,33	14,00
163	WRK40	Probable WRKY transcription factor 40	MSTRG.3880.2	MSTRG.3880	-1,85	50,33	14,00
164	WRK48	Probable WRKY transcription factor 48	MSTRG.7237.1	MSTRG.7237	-1,84	1963,67	558,67
165	ERF86	Ethylene-responsive transcription factor ERF086	MSTRG.24331.1	MSTRG.24331	-1,84	42,00	12,00
166	MYB62	Transcription factor MYB62	MSTRG.26416.1	MSTRG.26416	-1,83	719,33	205,33
167	MYB72	Transcription factor MYB72	MSTRG.26206.1	MSTRG.26206	-1,81	433,33	125,33

168	STKLA	Probable transcription factor At1g11510	MSTRG.35026.1	MSTRG.35026	-1,80	131,67	38,00
169	RAP23	Ethylene-responsive transcription factor RAP2-3	MSTRG.31022.1	MSTRG.31022	-1,80	7115,33	2082,00
170	RAX3	Transcription factor RAX3	MSTRG.25191.1	MSTRG.25191	-1,78	201,00	60,00
171	AS1	Transcription factor AS1	MSTRG.19748.1	MSTRG.19748	-1,78	1887,33	557,67
172	AS1	Transcription factor AS1	MSTRG.19748.2	MSTRG.19748	-1,78	1887,33	557,67
173	MYC2	Transcription factor MYC2	MSTRG.15281.1	MSTRG.15281	-1,78	742,67	220,67
174	MYB2	Transcription factor MYB1	MSTRG.27411.1	MSTRG.27411	-1,77	859,67	258,00
175	MYB1	Transcription factor MYB1	MSTRG.27411.2	MSTRG.27411	-1,77	859,67	258,00
176	MYB2	Transcription factor MYB1	MSTRG.27411.3	MSTRG.27411	-1,77	859,67	258,00
177	MYB2	Transcription factor MYB1	MSTRG.27411.4	MSTRG.27411	-1,77	859,67	258,00
178	MYB2	Transcription factor MYB1	MSTRG.27411.5	MSTRG.27411	-1,77	859,67	258,00
179	WRK41	Probable WRKY transcription factor 41	MSTRG.23601.1	MSTRG.23601	-1,74	40,67	12,33
180	HFA4B	Heat stress transcription factor A-4b	MSTRG.14253.1	MSTRG.14253	-1,68	261,00	82,33
181	TGT3B	Trihelix transcription factor GT-3b	MSTRG.34585.1	MSTRG.34585	-1,66	227,33	73,33
182	WRKY6	WRKY transcription factor 6	MSTRG.13925.1	MSTRG.13925	-1,62	3564,00	1180,00
183	WER	Transcription factor WER	MSTRG.9637.1	MSTRG.9637	-1,59	345,67	116,67
184	WRK28	WRKY transcription factor 28	MSTRG.13343.1	MSTRG.13343	-1,56	754,33	261,67
185	WRK19	Probable WRKY transcription factor 19	MSTRG.8920.17	MSTRG.8920	-1,56	1247,67	434,33
186	WRK19	Probable WRKY transcription factor 19	MSTRG.8920.22	MSTRG.8920	-1,56	1247,67	434,33
187	DF1	Trihelix transcription factor DF1	MSTRG.17060.1	MSTRG.17060	-1,56	1872,33	650,67
188	SPT	Transcription factor SPATULA	MSTRG.2742.1	MSTRG.2742	-1,55	119,33	41,00
189	SPT	Transcription factor SPATULA	MSTRG.2742.2	MSTRG.2742	-1,55	119,33	41,00
190	WRK24	WRKY transcription factor WRKY24	MSTRG.1559.1	MSTRG.1559	-1,50	3569,33	1293,00
191	PHL5	Myb family transcription factor PHL5	MSTRG.18051.1	MSTRG.18051	1,50	8,00	23,00
192	GTL1	Trihelix transcription factor GTL1	MSTRG.4360.1	MSTRG.4360	1,52	1341,67	3930,00
193	GTL1	Trihelix transcription factor GTL1	MSTRG.4360.2	MSTRG.4360	1,52	1341,67	3930,00
194	TGT2	Trihelix transcription factor GT-2	MSTRG.4209.1	MSTRG.4209	1,53	252,67	747,00
195	WRKY3	Probable WRKY transcription factor 3	MSTRG.19670.1	MSTRG.19670	1,61	4,67	14,67
196	MYB61	Transcription factor MYB61	MSTRG.34723.1	MSTRG.34723	1,63	147,33	467,33
197	ERF91	Ethylene-responsive transcription factor ERF091	MSTRG.29553.1	MSTRG.29553	1,66	69,67	223,33

198	ERF91	Ethylene-responsive transcription factor ERF091	MSTRG.29553.2	MSTRG.29553	1,66	69,67	223,33
199	ERF91	Ethylene-responsive transcription factor ERF091	MSTRG.29553.3	MSTRG.29553	1,66	69,67	223,33
200	MYB26	Transcription factor MYB26	MSTRG.31161.1	MSTRG.31161	1,67	11,00	35,67
201	IBH1	Transcription factor IBH1	MSTRG.34050.1	MSTRG.34050	1,68	116,33	377,67
202	MYB83	Transcription factor MYB83	MSTRG.10201.1	MSTRG.10201	1,68	6,00	19,67
203	TCP4	Transcription factor TCP4	MSTRG.21042.1	MSTRG.21042	1,68	166,00	547,67
204	TCP4	Transcription factor TCP4	MSTRG.21042.2	MSTRG.21042	1,68	166,00	547,67
205	TCP4	Transcription factor TCP4	MSTRG.21042.3	MSTRG.21042	1,68	166,00	547,67
206	LEP	Ethylene-responsive transcription factor LEP	MSTRG.32055.1	MSTRG.32055	1,69	21,00	68,67
207	ASIL2	Trihelix transcription factor ASIL2	MSTRG.21724.1	MSTRG.21724	1,71	6,00	19,67
208	BH094	Transcription factor BHLH094	MSTRG.33538.1	MSTRG.33538	1,72	378,00	1267,33
209	NFYB5	Nuclear transcription factor Y subunit B-5	MSTRG.31092.1	MSTRG.31092	1,73	6,00	19,67
210	NFYB5	Nuclear transcription factor Y subunit B-5	MSTRG.31092.2	MSTRG.31092	1,73	6,00	19,67
211	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.4668.1	MSTRG.4668	1,75	8,00	27,67
212	WRK14	Probable WRKY transcription factor 14	MSTRG.13688.1	MSTRG.13688	1,79	125,33	443,00
213	ERF79	Ethylene-responsive transcription factor 8	MSTRG.23857.1	MSTRG.23857	1,80	86,33	303,00
214	ERF53	Ethylene-responsive transcription factor ERF053	MSTRG.21403.1	MSTRG.21403	1,81	23,00	81,00
215	BH123	Transcription factor bHLH123	MSTRG.20606.1	MSTRG.20606	1,85	18,00	66,67
216	BH123	Transcription factor bHLH123	MSTRG.20606.2	MSTRG.20606	1,85	18,00	66,67
217	BH123	Transcription factor bHLH123	MSTRG.20606.3	MSTRG.20606	1,85	18,00	66,67
218	BEE3	Transcription factor BEE 3	MSTRG.26415.1	MSTRG.26415	1,86	21,00	78,33
219	MYB60	Transcription factor MYB60	MSTRG.17736.1	MSTRG.17736	1,92	6,67	25,67
220	ERF82	Ethylene-responsive transcription factor 3	MSTRG.16185.1	MSTRG.16185	1,95	5,67	22,00
221	MYB93	Transcription factor MYB93	MSTRG.17206.1	MSTRG.17206	1,96	13,00	51,00
222	ERF82	Ethylene-responsive transcription factor 3	MSTRG.16184.1	MSTRG.16184	1,99	10,33	41,67
223	MYB2	Transcription factor MYB1	MSTRG.7371.1	MSTRG.7371	1,99	190,33	769,00
224	GAT15	GATA transcription factor 15	MSTRG.30746.1	MSTRG.30746	1,99	16,00	64,67
225	MAD27	MADS-box transcription factor 27	MSTRG.28242.1	MSTRG.28242	2,09	14,33	62,67
226	BH126	Transcription factor bHLH126	MSTRG.31545.1	MSTRG.31545	2,15	108,00	488,00
227	BH126	Transcription factor bHLH126	MSTRG.31545.2	MSTRG.31545	2,15	108,00	488,00

228	RAP27	Ethylene-responsive transcription factor RAP2-7	MSTRG.2100.1	MSTRG.2100	2,18	163,00	755,67
229	WRI1	Ethylene-responsive transcription factor WRI1	MSTRG.11114.1	MSTRG.11114	2,19	63,33	293,67
230	WRI1	Ethylene-responsive transcription factor WRI1	MSTRG.11114.2	MSTRG.11114	2,19	63,33	293,67
231	NFYC4	Nuclear transcription factor Y subunit C-4	MSTRG.32241.1	MSTRG.32241	2,23	2,33	11,00
232	MYB86	Transcription factor MYB86	MSTRG.25820.1	MSTRG.25820	2,25	62,33	302,33
233	MOF1	Myb family transcription factor MOF1	MSTRG.13059.1	MSTRG.13059	2,33	12,33	63,33
234	BH048	Transcription factor bHLH48	MSTRG.18013.1	MSTRG.18013	2,36	14,00	72,67
235	PHL5	Myb family transcription factor PHL5	MSTRG.18049.1	MSTRG.18049	2,38	7,00	36,33
236	PHL5	Myb family transcription factor PHL5	MSTRG.18049.2	MSTRG.18049	2,38	7,00	36,33
237	PHL5	Myb family transcription factor PHL5	MSTRG.18049.3	MSTRG.18049	2,38	7,00	36,33
238	PHL5	Myb family transcription factor PHL5	MSTRG.18049.4	MSTRG.18049	2,38	7,00	36,33
239	PRE6	Transcription factor PRE6	MSTRG.23961.1	MSTRG.23961	2,41	212,33	1141,00
240	BH110	Transcription factor bHLH110	MSTRG.3085.1	MSTRG.3085	2,49	69,67	402,00
241	WRK13	Probable WRKY transcription factor 13	MSTRG.18952.1	MSTRG.18952	2,55	88,33	521,67
242	CRF4	Ethylene-responsive transcription factor CRF4	MSTRG.23591.1	MSTRG.23591	2,55	40,33	241,67
243	MYB61	Transcription factor MYB61	MSTRG.29228.1	MSTRG.29228	2,67	485,67	3161,00
244	MY123	Transcription factor MYB123	MSTRG.3783.1	MSTRG.3783	2,67	44,33	287,67
245	MY123	Transcription factor MYB123	MSTRG.3783.2	MSTRG.3783	2,67	44,33	287,67
246	ODO1	MYB-like transcription factor ODO1	MSTRG.24008.1	MSTRG.24008	2,82	6,33	45,00
247	ERF34	Ethylene-responsive transcription factor ERF034	MSTRG.12338.1	MSTRG.12338	2,88	23,33	175,67
248	MY123	Transcription factor MYB123	MSTRG.3778.1	MSTRG.3778	2,93	27,00	211,00
249	ASIL2	Trihelix transcription factor ASIL2	MSTRG.4550.1	MSTRG.4550	2,93	4,00	30,67
250	TCP14	Transcription factor TCP14	MSTRG.21117.1	MSTRG.21117	2,94	39,33	304,33
251	ILR3	Transcription factor ILR3	MSTRG.32423.1	MSTRG.32423	3,06	4,33	36,33
252	ILR3	Transcription factor ILR3	MSTRG.32423.2	MSTRG.32423	3,06	4,33	36,33
253	FIT	Transcription factor FER-LIKE IRON DEFICIENCY-INDUCED TRANSCRIPTION FACTOR	MSTRG.895.1	MSTRG.895	3,22	49,33	468,33
254	MY123	Transcription factor MYB123	MSTRG.3782.1	MSTRG.3782	3,22	9,67	93,00
255	ERF38	Ethylene-responsive transcription factor ERF038	MSTRG.16468.1	MSTRG.16468	3,25	10,67	103,67
256	MYBF	Putative Myb family transcription factor At1g14600	MSTRG.18857.1	MSTRG.18857	3,27	60,33	592,33

257	HSFC1	Heat stress transcription factor C-1	MSTRG.6282.1	MSTRG.6282	3,28	4,67	46,33
258	MYB46	Transcription factor MYB46	MSTRG.15784.1	MSTRG.15784	3,37	1,67	17,33
259	MYB1	Transcription factor MYB1	MSTRG.23221.1	MSTRG.23221	3,39	0,67	7,33
260	BH036	Transcription factor bHLH36	MSTRG.31547.1	MSTRG.31547	3,45	4,00	44,00
261	ASR3	Trihelix transcription factor ASR3	MSTRG.9030.1	MSTRG.9030	3,51	0,67	8,00
262	PAR1	Transcription factor PAR1	MSTRG.21806.1	MSTRG.21806	3,52	36,00	419,67
263	TCP3	Transcription factor TCP3	MSTRG.12982.1	MSTRG.12982	3,54	8,67	102,33
264	LAF1	Transcription factor LAF1	MSTRG.23733.1	MSTRG.23733	3,64	15,00	189,67
265	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.1	MSTRG.467	3,71	41,67	552,67
266	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.2	MSTRG.467	3,71	41,67	552,67
267	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.3	MSTRG.467	3,71	41,67	552,67
268	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.4	MSTRG.467	3,71	41,67	552,67
269	MYB48	Transcription factor MYB48	MSTRG.346.1	MSTRG.346	3,78	1,00	13,33
270	VRN1	B3 domain-containing transcription factor VRN1	MSTRG.28822.1	MSTRG.28822	4,06	3,67	62,00
271	BH025	Transcription factor bHLH25	MSTRG.16343.1	MSTRG.16343	4,36	8,00	168,33
272	HFB4B	Heat stress transcription factor B-4b	MSTRG.1031.1	MSTRG.1031	4,49	50,33	1149,67
273	NFYB3	Nuclear transcription factor Y subunit B-3	MSTRG.5885.1	MSTRG.5885	4,51	0,00	4,33
274	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.33443.1	MSTRG.33443	4,57	0,00	4,33
275	MYBF	Putative Myb family transcription factor At1g14600	MSTRG.2353.1	MSTRG.2353	4,58	10,33	252,67
276	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.1	MSTRG.16006	4,63	21,67	545,33
277	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.2	MSTRG.16006	4,63	21,67	545,33
278	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.3	MSTRG.16006	4,63	21,67	545,33
279	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.4	MSTRG.16006	4,63	21,67	545,33
280	GATA4	GATA transcription factor 4	MSTRG.10803.1	MSTRG.10803	4,68	9,67	252,67
281	MYB82	Transcription factor MYB82	MSTRG.6631.1	MSTRG.6631	4,72	5,33	145,00
282	ORG2	Transcription factor ORG2	MSTRG.13172.1	MSTRG.13172	4,85	0,00	5,33
283	ORG2	Transcription factor ORG2	MSTRG.13172.2	MSTRG.13172	4,85	0,00	5,33
284	RAV1	AP2/ERF and B3 domain-containing transcription factor RAV1	MSTRG.1319.1	MSTRG.1319	4,90	3,00	90,67
285	TCP8	Transcription factor TCP8	MSTRG.19238.1	MSTRG.19238	4,92	0,67	20,67

286	VRN1	B3 domain-containing transcription factor VRN1	MSTRG.6712.1	MSTRG.6712	4,93	2,33	73,67
287	VRN1	B3 domain-containing transcription factor VRN1	MSTRG.6712.2	MSTRG.6712	4,93	2,33	73,67
288	VRN1	B3 domain-containing transcription factor VRN1	MSTRG.6712.3	MSTRG.6712	4,93	2,33	73,67
289	HYH	Transcription factor HY5-like	MSTRG.15354.1	MSTRG.15354	5,12	0,33	13,00
290	MYB2	Transcription factor MYB1	MSTRG.5581.1	MSTRG.5581	5,32	10,00	411,00
291	MYB2	Transcription factor MYB1	MSTRG.5581.2	MSTRG.5581	5,32	10,00	411,00
292	MYB2	Transcription factor MYB1	MSTRG.5581.3	MSTRG.5581	5,32	10,00	411,00
293	MYB2	Transcription factor MYB1	MSTRG.5581.4	MSTRG.5581	5,32	10,00	411,00
294	MYB2	Transcription factor MYB1	MSTRG.5581.5	MSTRG.5581	5,32	10,00	411,00
295	BH120	Transcription factor bHLH120	MSTRG.31546.1	MSTRG.31546	5,37	1,00	42,67
296	GATA9	GATA transcription factor 9	MSTRG.31632.1	MSTRG.31632	5,39	14,33	612,67
297	BH025	Transcription factor bHLH25	MSTRG.16345.1	MSTRG.16345	5,39	0,00	8,00
298	BH025	Transcription factor bHLH25	MSTRG.16345.2	MSTRG.16345	5,39	0,00	8,00
299	RA211	Ethylene-responsive transcription factor RAP2-11	MSTRG.22022.1	MSTRG.22022	5,50	0,00	8,67
300	MY113	Transcription factor MYB113	MSTRG.1431.1	MSTRG.1431	5,50	0,00	8,33
301	MYB75	Transcription factor MYB75	MSTRG.1431.2	MSTRG.1431	5,50	0,00	8,33
302	MYB86	Transcription factor MYB86	MSTRG.27862.1	MSTRG.27862	5,58	0,00	9,33
303	GATA2	GATA transcription factor 2	MSTRG.26685.1	MSTRG.26685	5,74	1,33	72,00
304	GATA9	GATA transcription factor 9	MSTRG.12389.1	MSTRG.12389	5,78	24,00	1332,67
305	SRM1	Transcription factor SRM1	MSTRG.26383.1	MSTRG.26383	5,80	1,67	96,00
306	ASR3	Trihelix transcription factor ASR3	MSTRG.13635.1	MSTRG.13635	6,00	0,00	12,33
307	MYB2	Transcription factor MYB1	MSTRG.5586.1	MSTRG.5586	6,02	0,67	44,00
308	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.1	MSTRG.544	6,07	1,33	89,67
309	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.2	MSTRG.544	6,07	1,33	89,67
310	TCP8	Transcription factor TCP8	MSTRG.21111.1	MSTRG.21111	6,07	17,00	1158,00
311	TCP15	Transcription factor TCP15	MSTRG.23976.1	MSTRG.23976	6,11	1,33	94,00
312	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.26257.1	MSTRG.26257	6,29	0,67	53,67
313	ERF99	Ethylene-responsive transcription factor 13	MSTRG.10673.1	MSTRG.10673	6,42	0,33	32,33
314	ERF99	Ethylene-responsive transcription factor 13	MSTRG.10673.2	MSTRG.10673	6,42	0,33	32,33
315	MYB2	Transcription factor MYB1	MSTRG.3779.1	MSTRG.3779	6,44	1,67	147,67

316	MYB2	Transcription factor MYB1	MSTRG.3779.2	MSTRG.3779	6,44	1,67	147,67
317	MYB2	Transcription factor MYB1	MSTRG.3779.3	MSTRG.3779	6,44	1,67	147,67
318	BH151	Transcription factor UPBEAT1	MSTRG.33941.1	MSTRG.33941	6,89	2,67	322,33
319	WIN1	Ethylene-responsive transcription factor WIN1	MSTRG.6626.1	MSTRG.6626	7,09	0,33	49,67
320	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.33457.1	MSTRG.33457	7,09	0,33	50,33
321	MYB2	Transcription factor MYB1	MSTRG.4945.1	MSTRG.4945	7,13	0,00	26,00
322	MYB1	Transcription factor MYB1	MSTRG.29645.1	MSTRG.29645	7,57	0,00	35,67
323	MYB1	Transcription factor MYB1	MSTRG.29645.2	MSTRG.29645	7,57	0,00	35,67
324	MYB2	Transcription factor MYB1	MSTRG.29645.3	MSTRG.29645	7,57	0,00	35,67
325	WRK49	Probable WRKY transcription factor 49	MSTRG.31956.1	MSTRG.31956	7,69	0,00	39,00
326	RSL2	Transcription factor RSL2	MSTRG.30608.1	MSTRG.30608	7,80	0,00	42,33
327	BH146	Transcription factor bHLH146	MSTRG.27597.1	MSTRG.27597	8,05	0,00	49,67
328	RSL1	Putative transcription factor bHLH086	MSTRG.29744.1	MSTRG.29744	9,53	0,00	138,00
329	PRE3	Transcription factor PRE3	MSTRG.25650.1	MSTRG.25650	11,39	0,00	500,67

LTR_1 vs. TTR

No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	TTR	LTR_1
330	AIL5	AP2-like ethylene-responsive transcription factor AIL5	MSTRG.4591.1	MSTRG.4591	-5,35	6,67	0,00
331	MYB59	Transcription factor MYB59	MSTRG.347.1	MSTRG.347	-4,45	7,00	0,33
332	BH154	Transcription factor bHLH154	MSTRG.22604.1	MSTRG.22604	-3,28	58,33	6,67
333	BH123	Transcription factor bHLH123	MSTRG.22604.2	MSTRG.22604	-3,28	58,33	6,67
334	BH123	Transcription factor bHLH123	MSTRG.22604.3	MSTRG.22604	-3,28	58,33	6,67
335	BH123	Transcription factor bHLH123	MSTRG.22604.4	MSTRG.22604	-3,28	58,33	6,67
336	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.1	MSTRG.18391	-3,19	27,00	3,33
337	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.2	MSTRG.18391	-3,19	27,00	3,33
338	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.3	MSTRG.18391	-3,19	27,00	3,33
339	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.4	MSTRG.18391	-3,19	27,00	3,33
340	MYB27	Transcription factor MYB27	MSTRG.25709.1	MSTRG.25709	-3,05	7,33	1,00
341	WRK19	Probable WRKY transcription factor 19	MSTRG.25239.1	MSTRG.25239	-3,01	24,00	3,33

342	BH051	Transcription factor bHLH51	MSTRG.21715.1	MSTRG.21715	-2,88	85,67	13,00
343	MYBS3	Transcription factor MYBS3	MSTRG.5695.1	MSTRG.5695	-2,86	41,00	6,33
344	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.1	MSTRG.5571	-2,81	12,67	2,00
345	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.2	MSTRG.5571	-2,81	12,67	2,00
346	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.3	MSTRG.5571	-2,81	12,67	2,00
347	MYB2	Transcription factor MYB2	MSTRG.15699.1	MSTRG.15699	-2,55	302,33	57,33
348	MYB2	Transcription factor MYB2	MSTRG.15699.2	MSTRG.15699	-2,55	302,33	57,33
349	MYB2	Transcription factor MYB2	MSTRG.15699.3	MSTRG.15699	-2,55	302,33	57,33
350	WRK75	Probable WRKY transcription factor 75	MSTRG.29989.1	MSTRG.29989	-2,54	57,67	11,00
351	WRK74	Probable WRKY transcription factor 74	MSTRG.21830.1	MSTRG.21830	-2,53	140,33	26,67
352	WRK74	Probable WRKY transcription factor 74	MSTRG.21830.2	MSTRG.21830	-2,53	140,33	26,67
353	WRK71	WRKY transcription factor 71	MSTRG.30798.1	MSTRG.30798	-2,51	264,67	51,00
354	WRK71	WRKY transcription factor 71	MSTRG.30798.2	MSTRG.30798	-2,51	264,67	51,00
355	NAC56	NAC transcription factor 56	MSTRG.28986.1	MSTRG.28986	-2,47	15,00	3,00
356	VRN1	B3 domain-containing transcription factor VRN1	MSTRG.24276.1	MSTRG.24276	-2,45	19,33	4,00
357	MPH1	Myb family transcription factor MPH1	MSTRG.21849.1	MSTRG.21849	-2,44	265,33	54,67
358	MPH1	Myb family transcription factor MPH1	MSTRG.21849.2	MSTRG.21849	-2,44	265,33	54,67
359	PTL	Trihelix transcription factor PTL	MSTRG.19364.1	MSTRG.19364	-2,40	83,33	17,33
360	BH117	Transcription factor bHLH117	MSTRG.4475.1	MSTRG.4475	-2,40	12,67	2,67
361	MYB62	Transcription factor MYB62	MSTRG.32122.1	MSTRG.32122	-2,40	40,00	8,33
362	KUA1	Transcription factor KUA1	MSTRG.2485.1	MSTRG.2485	-2,23	90,67	21,67
363	ERF10	Ethylene-responsive transcription factor ERF010	MSTRG.16619.1	MSTRG.16619	-2,14	126,00	32,00
364	BZIP2	bZIP transcription factor 2	MSTRG.16355.1	MSTRG.16355	-2,11	651,33	168,00
365	WRK28	WRKY transcription factor 28	MSTRG.13343.1	MSTRG.13343	-2,11	793,33	202,00
366	NFYB3	Nuclear transcription factor Y subunit B-3	MSTRG.5885.1	MSTRG.5885	-2,07	11,33	3,00
367	IPN2	Myb family transcription factor IPN2	MSTRG.11369.1	MSTRG.11369	-1,87	39,33	12,00
368	IPN2	Myb family transcription factor IPN2	MSTRG.11369.2	MSTRG.11369	-1,87	39,33	12,00
369	IPN2	Myb family transcription factor IPN2	MSTRG.11369.3	MSTRG.11369	-1,87	39,33	12,00
370	IPN2	Myb family transcription factor IPN2	MSTRG.11369.4	MSTRG.11369	-1,87	39,33	12,00
371	WRK47	Probable WRKY transcription factor 47	MSTRG.31313.1	MSTRG.31313	-1,87	1653,33	506,67

372	NFYA1	Nuclear transcription factor Y subunit A-1	MSTRG.4176.1	MSTRG.4176	-1,82	330,33	104,33
373	WRKY6	WRKY transcription factor 6	MSTRG.20348.1	MSTRG.20348	-1,80	244,00	77,67
374	WRKY6	WRKY transcription factor 6	MSTRG.15365.1	MSTRG.15365	-1,78	350,33	114,00
375	TCP3	Transcription factor TCP3	MSTRG.21481.1	MSTRG.21481	-1,77	117,67	38,33
376	TCP3	Transcription factor TCP3	MSTRG.21481.2	MSTRG.21481	-1,77	117,67	38,33
377	TCP3	Transcription factor TCP3	MSTRG.21481.3	MSTRG.21481	-1,77	117,67	38,33
378	WRK12	Probable WRKY transcription factor 12	MSTRG.10638.1	MSTRG.10638	-1,74	14,00	4,67
379	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.24071.1	MSTRG.24071	-1,73	1367,00	458,33
380	MY102	Transcription factor MYB102	MSTRG.14278.1	MSTRG.14278	-1,72	215,00	72,67
381	MYB17	Transcription factor MYB17	MSTRG.23734.1	MSTRG.23734	-1,72	48,00	16,33
382	UNE12	Transcription factor UNE12	MSTRG.24264.1	MSTRG.24264	-1,71	28,33	9,67
383	DIV	Transcription factor DIVARICATA	MSTRG.22698.1	MSTRG.22698	-1,71	129,33	44,00
384	DIV	Transcription factor DIVARICATA	MSTRG.22698.2	MSTRG.22698	-1,71	129,33	44,00
385	WRK50	Probable WRKY transcription factor 50	MSTRG.2512.1	MSTRG.2512	-1,71	48,67	16,67
386	WRK50	Probable WRKY transcription factor 50	MSTRG.2512.2	MSTRG.2512	-1,71	48,67	16,67
387	ERF11	Ethylene-responsive transcription factor ERF011	MSTRG.2732.1	MSTRG.2732	-1,70	305,33	105,67
388	BH112	Transcription factor bHLH112	MSTRG.14135.1	MSTRG.14135	-1,69	233,67	80,67
389	BH112	Transcription factor bHLH112	MSTRG.14135.2	MSTRG.14135	-1,69	233,67	80,67
390	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.35144.1	MSTRG.35144	-1,69	50,67	17,67
391	MYB59	Transcription factor MYB59	MSTRG.13004.1	MSTRG.13004	-1,67	955,33	333,33
392	MYB48	Transcription factor MYB48	MSTRG.13004.2	MSTRG.13004	-1,67	955,33	333,33
393	MYB48	Transcription factor MYB48	MSTRG.13004.3	MSTRG.13004	-1,67	955,33	333,33
394	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25340.1	MSTRG.25340	-1,65	546,67	193,33
395	BH111	Transcription factor bHLH111	MSTRG.9033.1	MSTRG.9033	-1,62	162,67	59,00
396	BH111	Transcription factor bHLH111	MSTRG.9033.2	MSTRG.9033	-1,62	162,67	59,00
397	BH111	Transcription factor bHLH111	MSTRG.9033.3	MSTRG.9033	-1,62	162,67	59,00
398	BH111	Transcription factor bHLH111	MSTRG.9033.4	MSTRG.9033	-1,62	162,67	59,00
399	BH111	Transcription factor bHLH111	MSTRG.9033.5	MSTRG.9033	-1,62	162,67	59,00
400	BH111	Transcription factor bHLH111	MSTRG.9033.6	MSTRG.9033	-1,62	162,67	59,00
401	BH111	Transcription factor bHLH111	MSTRG.9033.7	MSTRG.9033	-1,62	162,67	59,00

402	WRK40	Probable WRKY transcription factor 40	MSTRG.3880.1	MSTRG.3880	-1,60	84,00	31,00
403	WRK40	Probable WRKY transcription factor 40	MSTRG.3880.2	MSTRG.3880	-1,60	84,00	31,00
404	NAC42	Transcription factor JUNGBRUNNEN 1	MSTRG.1886.1	MSTRG.1886	-1,59	93,00	34,67
405	MYB88	Transcription factor MYB88	MSTRG.33976.1	MSTRG.33976	-1,59	52,33	19,67
406	MYB88	Transcription factor MYB88	MSTRG.33976.2	MSTRG.33976	-1,59	52,33	19,67
407	MYC2	Transcription factor MYC2	MSTRG.15281.1	MSTRG.15281	-1,57	527,67	199,00
408	HSFB3	Heat stress transcription factor B-3	MSTRG.17389.1	MSTRG.17389	-1,56	709,67	267,33
409	TCP9	Transcription factor TCP9	MSTRG.22039.1	MSTRG.22039	-1,56	317,33	120,00
410	ODO1	MYB-like transcription factor ODO1	MSTRG.30090.1	MSTRG.30090	-1,53	106,33	41,33
411	ILR3	Transcription factor ILR3	MSTRG.14109.1	MSTRG.14109	-1,50	808,00	318,33
412	ILR3	Transcription factor ILR3	MSTRG.14109.2	MSTRG.14109	-1,50	808,00	318,33
413	ILR3	Transcription factor ILR3	MSTRG.14109.3	MSTRG.14109	-1,50	808,00	318,33
414	ILR3	Transcription factor ILR3	MSTRG.14109.4	MSTRG.14109	-1,50	808,00	318,33
415	WRI1	Ethylene-responsive transcription factor WRI1	MSTRG.11114.1	MSTRG.11114	1,52	50,67	163,00
416	WRI1	Ethylene-responsive transcription factor WRI1	MSTRG.11114.2	MSTRG.11114	1,52	50,67	163,00
417	MYB1	Transcription factor MYB1	MSTRG.23325.1	MSTRG.23325	1,55	126,33	414,33
418	MYBF	Putative Myb family transcription factor At1g14600	MSTRG.2353.1	MSTRG.2353	1,62	64,00	220,33
419	GATA9	GATA transcription factor 9	MSTRG.31632.1	MSTRG.31632	1,64	158,00	549,00
420	RSL1	Putative transcription factor bHLH086	MSTRG.29744.1	MSTRG.29744	1,64	30,67	107,00
421	TCP3	Transcription factor TCP3	MSTRG.12982.1	MSTRG.12982	1,67	16,33	59,00
422	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.1	MSTRG.16006	1,67	69,33	249,00
423	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.2	MSTRG.16006	1,67	69,33	249,00
424	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.3	MSTRG.16006	1,67	69,33	249,00
425	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.4	MSTRG.16006	1,67	69,33	249,00
426	WIN1	Ethylene-responsive transcription factor WIN1	MSTRG.6626.1	MSTRG.6626	1,68	13,33	48,00
427	GATA4	GATA transcription factor 4	MSTRG.10803.1	MSTRG.10803	1,89	90,67	380,00
428	MYB2	Transcription factor MYB1	MSTRG.3779.1	MSTRG.3779	1,98	24,00	104,00
429	MYB2	Transcription factor MYB1	MSTRG.3779.2	MSTRG.3779	1,98	24,00	104,00
430	MYB2	Transcription factor MYB1	MSTRG.3779.3	MSTRG.3779	1,98	24,00	104,00
431	GATA9	GATA transcription factor 9	MSTRG.12389.1	MSTRG.12389	1,98	226,67	1004,67

432	BH162	Transcription factor bHLH162	MSTRG.15528.1	MSTRG.15528	2,00	6,00	27,33
433	TCP8	Transcription factor TCP8	MSTRG.19238.1	MSTRG.19238	2,15	4,33	21,67
434	ERF82	Ethylene-responsive transcription factor 3	MSTRG.16184.1	MSTRG.16184	2,20	6,00	30,33
435	WRK55	WRKY transcription factor 55	MSTRG.22916.1	MSTRG.22916	2,59	3,67	24,67
436	TCP8	Transcription factor TCP8	MSTRG.21111.1	MSTRG.21111	2,60	148,33	1014,33
437	TCP15	Transcription factor TCP15	MSTRG.23976.1	MSTRG.23976	2,63	6,33	43,67
438	PRE3	Transcription factor PRE3	MSTRG.25650.1	MSTRG.25650	3,30	65,00	717,33
439	BH151	Transcription factor UPBEAT1	MSTRG.33941.1	MSTRG.33941	3,46	13,00	160,00
440	BH036	Transcription factor bHLH36	MSTRG.31547.1	MSTRG.31547	3,76	3,33	51,67
441	EF100	Ethylene-responsive transcription factor 1A	MSTRG.30183.1	MSTRG.30183	3,96	0,67	12,00
442	MYB1	Transcription factor MYB1	MSTRG.23221.1	MSTRG.23221	4,32	0,33	8,00
443	BH146	Transcription factor bHLH146	MSTRG.27597.1	MSTRG.27597	4,50	0,67	17,33
444	BH092	Transcription factor bHLH92	MSTRG.18061.1	MSTRG.18061	4,58	0,00	5,00
445	BH120	Transcription factor bHLH120	MSTRG.31546.1	MSTRG.31546	4,86	0,33	11,67
446	ASIL2	Trihelix transcription factor ASIL2	MSTRG.4550.1	MSTRG.4550	5,09	0,00	7,00
447	ERF95	Ethylene-responsive transcription factor ERF095	MSTRG.15416.1	MSTRG.15416	5,83	0,00	12,00
448	WRKY3	Probable WRKY transcription factor 3	MSTRG.19670.1	MSTRG.19670	5,93	0,00	12,33
449	MYB2	Transcription factor MYB1	MSTRG.4945.1	MSTRG.4945	6,39	0,00	17,67
450	WRK51	Probable WRKY transcription factor 51	MSTRG.33801.1	MSTRG.33801	6,60	0,00	19,67

Supplementary Table 4. DEGs related to hormones identified in MTR vs. DTR, MTR_1 vs. TDTR and LTR_1 vs. TTR comparisons.

MTR vs. DTR

Hormone	No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	DTR Genes Results	MTR Genes Results	Function
IAA	1	YUC10	Probable indole-3-pyruvate monooxygenase YUCCA10	MSTRG.12291.1	MSTRG.12291	3,4147	19	319	Biosynthesis
	2	YUC10	Probable indole-3-pyruvate monooxygenase YUCCA10	MSTRG.3084.1	MSTRG.3084	3,5645	25	257	Biosynthesis
	3	GH36	Indole-3-acetic acid-amido synthetase GH3.6	MSTRG.21271.1	MSTRG.21271	3,3106	27	226	Conjugate synthesis, Conjugate degradation
	4	IAA7	Auxin-responsive protein IAA7	MSTRG.15336.1	MSTRG.15336	8,6118	0	380	Signal transduction-related
	5	ILL3	IAA-amino acid hydrolase ILR1-like 3	MSTRG.19114.1	MSTRG.19114	8,0652	0	66	Conjugate degradation
	6	PIN2	Auxin efflux carrier component 2	MSTRG.5845.1	MSTRG.5845	-4,3695	59	4	Transport
	7	AB9B	ABC transporter B family member 9	MSTRG.13237.1	MSTRG.13237	-2,0869	77	31	Transport
	8	AB21B	ABC transporter B family member 21	MSTRG.31324.1	MSTRG.31324	-2,071	452	89	Transport
	9	AB11B	ABC transporter B family member 11	MSTRG.22987.1	MSTRG.22987	-1,5633	2761	725	Transport
	10	PIN6	Auxin efflux carrier component 6	MSTRG.4274.1	MSTRG.4274	-1,5125	152	53	Transport
	11	PIN2	Auxin efflux carrier component 2	MSTRG.5844.1	MSTRG.5844	1,5673	300	1333	Transport
	12	LAX3	Auxin transporter-like protein 3	MSTRG.24617.1	MSTRG.24617	2,3596	176	816	Transport
	13	IAA27	Auxin-responsive protein IAA27	MSTRG.5231.1	MSTRG.5231	-2,982	1547	141	Signal transduction-related
	14	SAU76	Auxin-responsive protein SAUR76	MSTRG.32895.1	MSTRG.32895	-2,1002	79	16	Signal transduction-related

	15	WOX4	WUSCHEL-related homeobox 4	MSTRG.2733.1	MSTRG.2733	-1,6104	527	157	Signal transduction-related
	16	IAA14	Auxin-responsive protein IAA14	MSTRG.15323.1	MSTRG.15323	1,8477	844	2865	Signal transduction-related
	17	SAU23	Auxin-responsive protein SAUR23	MSTRG.29253.1	MSTRG.29253	2,1135	22	60	Signal transduction-related
	18	AX22B	Auxin-induced protein 22B	MSTRG.15337.1	MSTRG.15337	2,283	185	1253	Signal transduction-related
	19	ARFQ	Auxin response factor 17	MSTRG.34776.1	MSTRG.34776	6,8318	0	39	Signal transduction-related
CK	20	C7351	Cytokinin hydroxylase	MSTRG.23760.1	MSTRG.23760	-4,2933	9	2	Biosynthesis
	21	LOG7	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG7	MSTRG.19148.1	MSTRG.19148	3,2079	4	31	Biosynthesis
	22	CKX7	Cytokinin dehydrogenase 7	MSTRG.3787.1	MSTRG.3787	-2,5678	288	41	Degradation/ Inactivation
	23	APRR2	Two-component response regulator-like APRR2	MSTRG.9487.1	MSTRG.9487	-2,5575	359	61	Signal transduction-related
	24	ARR5	Two-component response regulator ARR5	MSTRG.25879.1	MSTRG.25879	2,0404	33	109	Signal transduction-related
	25	ARR4	Two-component response regulator ARR4	MSTRG.8997.1	MSTRG.8997	2,0492	74	226	Signal transduction-related
ABA	26	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.4140.1	MSTRG.4140	-2,8798	99	11	Signal transduction-related

	27	AHK5	Histidine kinase 5	MSTRG.3825.1	MSTRG.3825	1,5781	181	413	Signal transduction-related
ET	28	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25339.1	MSTRG.25339	-2,7409	117	12	Signal transduction-related
	29	ERF86	Ethylene-responsive transcription factor ERF086	MSTRG.24331.1	MSTRG.24331	-2,1153	69	11	Signal transduction-related
	30	ERF87	Ethylene-responsive transcription factor ERF087	MSTRG.9157.1	MSTRG.9157	-2,0658	235	89	Signal transduction-related
	31	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25340.1	MSTRG.25340	-1,8052	890	244	Signal transduction-related
	32	RA212	Ethylene-responsive transcription factor RAP2-12	MSTRG.5191.1	MSTRG.5191	-1,6715	36	9	Signal transduction-related
	33	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.1	MSTRG.16006	2,5004	49	147	Signal transduction-related
	34	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.1	MSTRG.544	5,5088	1	29	Signal transduction-related
	35	ERF99	Ethylene-responsive transcription factor 13	MSTRG.10673.1	MSTRG.10673	5,9368	2	86	Signal transduction-related
JA	36	OPR2	12-oxophytodienoate reductase 2	MSTRG.24084.1	MSTRG.24084	-1,8172	283	70	Biosynthesis
	37	AOS1	Allene oxide synthase 1, chloroplastic	MSTRG.2880.1	MSTRG.2880	2,4188	3	20	Biosynthesis
	38	AOS3	Allene oxide synthase 3	MSTRG.28842.1	MSTRG.28842	3,3186	2	21	Biosynthesis
	39	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34851.1	MSTRG.34851	7,0805	0	176	Biosynthesis
	40	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.424.1	MSTRG.424	8,3315	0	53	Biosynthesis

GA	41	KO1	Ent-kaurene oxidase, chloroplastic	MSTRG.32736.1	MSTRG.32736	2,5508	28	147	Biosynthesis
	42	G3OX	Gibberellin 3-beta-dioxygenase 1	MSTRG.22681.1	MSTRG.22681	6,2662	4	154	Biosynthesis
	43	GASA6	Gibberellin-regulated protein 6	MSTRG.25978.1	MSTRG.25978	1,5157	1808	5952	Signal transduction-related
	44	SCL3	Scarecrow-like protein 3	MSTRG.3816.1	MSTRG.3816	2,0102	61	256	Signal transduction-related
	45	GASAE	Gibberellin-regulated protein 14	MSTRG.20694.1	MSTRG.20694	2,5288	644	2369	Signal transduction-related
	46	GASAE	Gibberellin-regulated protein 14	MSTRG.20691.1	MSTRG.20691	3,1494	1038	6398	Signal transduction-related
	47	GASAE	Gibberellin-regulated protein 14	MSTRG.20693.1	MSTRG.20693	3,4667	112	670	Signal transduction-related
BR	48	DET2	Steroid 5-alpha-reductase DET2	MSTRG.11000.1	MSTRG.11000	1,7877	26	119	Biosynthesis
	49	C90D1	3-epi-6-deoxocathasterone 23-monooxygenase CYP90D1	MSTRG.12229.1	MSTRG.12229	1,8882	171	565	Biosynthesis
	50	C90A1	Cytochrome P450 90A1	MSTRG.22789.1	MSTRG.22789	2,2983	125	456	Biosynthesis
	51	C734A	Cytochrome P450 734A1	MSTRG.2960.1	MSTRG.2960	2,664	50	286	Degradation/ Inactivation

MTR_1 vs. TDTR

Hormone	No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	TDTR Genes Results	MTR_1 Genes Results	Function
IAA	52	YUC10	Probable indole-3-pyruvate monooxygenase YUCCA10	MSTRG.12291.1	MSTRG.12291	2,944	27	130	Biosynthesis

53	YUC8	Probable indole-3-pyruvate monooxygenase YUCCA8	MSTRG.34007.1	MSTRG.34007	3,3165	1	27	Biosynthesis
54	YUC10	Probable indole-3-pyruvate monooxygenase YUCCA10	MSTRG.3084.1	MSTRG.3084	3,9568	9	185	Biosynthesis
55	YUC11	Probable indole-3-pyruvate monooxygenase YUCCA11	MSTRG.7314.1	MSTRG.7314	5,5012	0	9	Biosynthesis
56	IAMT1	Indole-3-acetate O-methyltransferase 1	MSTRG.20288.1	MSTRG.20288	-4,9224	244	11	Conjugate synthesis
57	GH31	Probable indole-3-acetic acid-amido synthetase GH3.1	MSTRG.28521.1	MSTRG.28521	-2,1014	1890	466	Conjugate synthesis
58	GH317	Indole-3-acetic acid-amido synthetase GH3.17	MSTRG.9152.1	MSTRG.9152	2,2019	93	536	Conjugate synthesis
59	GH39	Putative indole-3-acetic acid-amido synthetase GH3.9	MSTRG.32140.1	MSTRG.32140	3,4931	1	17	Conjugate synthesis
60	GH36	Indole-3-acetic acid-amido synthetase GH3.6	MSTRG.21271.1	MSTRG.21271	7,8119	2	461	Conjugate synthesis
61	ILL1	IAA-amino acid hydrolase ILR1-like 1	MSTRG.9014.1	MSTRG.9014	-3,3588	301	24	Conjugate degradation
62	ILL4	IAA-amino acid hydrolase ILR1-like 4	MSTRG.12194.1	MSTRG.12194	-1,7311	1747	613	Conjugate degradation
63	ILL5	IAA-amino acid hydrolase ILR1-like 5	MSTRG.21216.1	MSTRG.21216	-1,5282	62	19	Conjugate degradation
64	ILR1	IAA-amino acid hydrolase ILR1	MSTRG.19111.1	MSTRG.19111	1,6363	298	967	Conjugate degradation
65	ILR1	IAA-amino acid hydrolase ILR1	MSTRG.19113.1	MSTRG.19113	2,1842	25	100	Conjugate degradation
66	PIN2	Auxin efflux carrier component 2	MSTRG.5845.1	MSTRG.5845	-2,6167	52	4	Transport
67	PILS6	Protein PIN-LIKES 6	MSTRG.13861.3	MSTRG.13861	-2,0211	84	21	Transport
68	AB21B	ABC transporter B family member 21	MSTRG.31324.1	MSTRG.31324	-2,0189	480	128	Transport
69	AB8B	Putative ABC transporter B family member 8	MSTRG.5121.1	MSTRG.5121	-1,9228	408	105	Transport
70	AB21B	ABC transporter B family member 21	MSTRG.30599.1	MSTRG.30599	-1,8747	276	60	Transport
71	PILS3	Protein PIN-LIKES 3	MSTRG.10795.1	MSTRG.10795	-1,7283	669	197	Transport

72	PILS3	Protein PIN-LIKES 3	MSTRG.3734.1	MSTRG.3734	-1,5155	644	220	Transport
73	AB2B	ABC transporter B family member 2	MSTRG.29974.1	MSTRG.29974	2,2215	13	26	Transport
74	AB19B	ABC transporter B family member 19	MSTRG.6163.1	MSTRG.6163	2,4388	962	5676	Transport
75	PILS1	Protein PIN-LIKES 1	MSTRG.17183.1	MSTRG.17183	3,0095	10	90	Transport
76	PIN2	Auxin efflux carrier component 2	MSTRG.1664.1	MSTRG.1664	4,6461	0	17	Transport
77	LAX3	Auxin transporter-like protein 3	MSTRG.24617.1	MSTRG.24617	6,3039	26	1759	Transport
78	PIN2	Auxin efflux carrier component 2	MSTRG.5844.1	MSTRG.5844	8,5237	7	1910	Transport
79	SAU50	Auxin-responsive protein SAUR50	MSTRG.17680.1	MSTRG.17680	-3,3517	21	2	Signal transduction-related
80	SAU76	Auxin-responsive protein SAUR76	MSTRG.32895.1	MSTRG.32895	-2,8869	92	20	Signal transduction-related
81	ARFQ	Auxin response factor 17	MSTRG.34776.1	MSTRG.34776	-2,4092	140	30	Signal transduction-related
82	SAU71	Auxin-responsive protein SAUR71	MSTRG.35277.1	MSTRG.35277	-2,1715	27	11	Signal transduction-related
83	SAU71	Auxin-responsive protein SAUR71	MSTRG.25418.1	MSTRG.25418	-2,0708	74	22	Signal transduction-related
84	SAU50	Auxin-responsive protein SAUR50	MSTRG.3446.1	MSTRG.3446	-1,6238	101	36	Signal transduction-related
85	SAU36	Auxin-responsive protein SAUR36	MSTRG.10889.1	MSTRG.10889	-1,5936	437	167	Signal transduction-related
86	SAU32	Auxin-responsive protein SAUR32	MSTRG.26612.1	MSTRG.26612	1,5385	24	89	Signal transduction-related

87	AIR12	Auxin-induced in root cultures protein 12	MSTRG.25174.1	MSTRG.25174	1,5827	1334	4798	Signal transduction-related
88	ARFR	Auxin response factor 18	MSTRG.1361.1	MSTRG.1361	1,7217	629	1983	Signal transduction-related
89	IAA30	Auxin-responsive protein IAA30	MSTRG.34246.1	MSTRG.34246	2,1633	12	30	Signal transduction-related
90	IAA16	Auxin-responsive protein IAA16	MSTRG.8527.1	MSTRG.8527	2,361	1044	4699	Signal transduction-related
91	LAX5	Auxin transporter-like protein 5	MSTRG.30011.1	MSTRG.30011	2,4594	189	1174	Signal transduction-related
92	IAA7	Auxin-responsive protein IAA7	MSTRG.15336.1	MSTRG.15336	2,6236	105	514	Signal transduction-related
93	AUX22	Auxin-induced protein AUX22	MSTRG.12702.1	MSTRG.12702	2,6479	17	79	Signal transduction-related
94	SAU32	Auxin-responsive protein SAUR32	MSTRG.25422.1	MSTRG.25422	2,7861	11	88	Signal transduction-related
95	SAU40	Auxin-responsive protein SAUR40	MSTRG.3770.1	MSTRG.3770	3,4221	0	18	Signal transduction-related
96	IAA14	Auxin-responsive protein IAA14	MSTRG.15323.1	MSTRG.15323	3,7142	413	5268	Signal transduction-related
97	SAU24	Auxin-responsive protein SAUR24	MSTRG.29214.1	MSTRG.29214	5,4068	0	8	Signal transduction-related

	98	SAU71	Auxin-responsive protein SAUR71	MSTRG.30867.1	MSTRG.30867	6,0646	1	181	Signal transduction-related
	99	ARG7	Indole-3-acetic acid-induced protein ARG7	MSTRG.29251.1	MSTRG.29251	6,1063	0	21	Signal transduction-related
	100	SAU71	Auxin-responsive protein SAUR71	MSTRG.33530.1	MSTRG.33530	10,125	0	184	Signal transduction-related
CK	101	C7351	Cytokinin hydroxylase	MSTRG.23760.1	MSTRG.23760	-7,8881	35	0	Biosynthesis
	102	C7351	Cytokinin hydroxylase	MSTRG.23763.1	MSTRG.23763	-7,6981	68	0	Biosynthesis
	103	LOG3	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG3	MSTRG.19557.1	MSTRG.19557	-1,8079	206	57	Biosynthesis
	104	LOG1	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG1	MSTRG.1370.1	MSTRG.1370	-1,6962	51	15	Biosynthesis
	105	LOG7	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG7	MSTRG.19148.1	MSTRG.19148	6,0682	2	60	Biosynthesis
	106	CKX3	Cytokinin dehydrogenase 3	MSTRG.5730.1	MSTRG.5730	-3,2892	78	7	Degradation/ Inactivation
	107	CKX3	Cytokinin dehydrogenase 3	MSTRG.13748.1	MSTRG.13748	3,3299	4	44	Degradation/ Inactivation
	108	ARR18	Two-component response regulator ARR18	MSTRG.11326.1	MSTRG.11326	-2,5537	710	112	Signal transduction-related
	109	AHK3	Histidine kinase 3	MSTRG.9310.1	MSTRG.9310	-1,62	4518	1389	Signal transduction-related
	110	ARR9	Two-component response regulator ARR9	MSTRG.30826.1	MSTRG.30826	1,822	95	310	Signal transduction-related
	111	ARR9	Two-component response regulator ARR9	MSTRG.32331.1	MSTRG.32331	2,4242	139	761	Signal transduction-related

	112	ARR5	Two-component response regulator ARR5	MSTRG.25879.1	MSTRG.25879	3,8372	12	149	Signal transduction-related
	113	ARR4	Two-component response regulator ARR4	MSTRG.8997.1	MSTRG.8997	5,0711	20	547	Signal transduction-related
ABA	114	ABA2	Zeaxanthin epoxidase, chloroplastic	MSTRG.33024.1	MSTRG.33024	-2,1224	18	7	Biosynthesis
	115	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1, chloroplastic	MSTRG.32782.1	MSTRG.32782	1,8525	11	40	Biosynthesis
	116	ABAH1	Abscisic acid 8'-hydroxylase CYP707A1	MSTRG.2767.1	MSTRG.2767	-2,7406	9	1	Degradation/ Inactivation
	117	ABAH2	Abscisic acid 8'-hydroxylase CYP707A2	MSTRG.29805.1	MSTRG.29805	-2,53	6916	1168	Degradation/ Inactivation
	118	ABAH2	Abscisic acid 8'-hydroxylase 2	MSTRG.1823.1	MSTRG.1823	-2,2093	299	62	Degradation/ Inactivation
	119	ABAH4	Abscisic acid 8'-hydroxylase 4	MSTRG.187.1	MSTRG.187	1,9534	6	22	Degradation/ Inactivation
	120	KING1	SNF1-related protein kinase regulatory subunit gamma-1	MSTRG.25480.1	MSTRG.25480	-4,2812	0	0	Signal transduction-related
	121	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.1674.1	MSTRG.1674	-2,5595	277	48	Signal transduction-related
	122	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.4140.1	MSTRG.4140	-2,5237	74	14	Signal transduction-related
	123	KINB2	SNF1-related protein kinase regulatory subunit beta-2	MSTRG.5882.1	MSTRG.5882	1,5785	233	713	Signal transduction-related
	124	AHK5	Histidine kinase 5	MSTRG.3825.1	MSTRG.3825	4,7347	29	652	Signal transduction-related
ET	125	ETO1	Ethylene-overproduction protein 1	MSTRG.2351.1	MSTRG.2351	1,5178	604	1735	Biosynthesis

126	ERF95	Ethylene-responsive transcription factor ERF095	MSTRG.15416.1	MSTRG.15416	-5,3503	10	0	Signal transduction-related
127	ERF98	Ethylene-responsive transcription factor ERF098	MSTRG.15417.1	MSTRG.15417	-4,8051	17	0	Signal transduction-related
128	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25339.1	MSTRG.25339	-4,3517	132	4	Signal transduction-related
129	ERF87	Ethylene-responsive transcription factor ERF087	MSTRG.9157.1	MSTRG.9157	-3,448	701	80	Signal transduction-related
130	ERF98	Ethylene-responsive transcription factor ERF098	MSTRG.24680.1	MSTRG.24680	-3,3211	73	5	Signal transduction-related
131	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25340.1	MSTRG.25340	-3,2109	1020	90	Signal transduction-related
132	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.34676.1	MSTRG.34676	-3,1448	1242	112	Signal transduction-related
133	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.32025.1	MSTRG.32025	-3,0995	5298	689	Signal transduction-related
134	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.35144.1	MSTRG.35144	-2,7261	110	18	Signal transduction-related
135	EF110	Ethylene-responsive transcription factor ERF110	MSTRG.18963.1	MSTRG.18963	-2,4561	434	91	Signal transduction-related
136	ERF80	Ethylene-responsive transcription factor 9	MSTRG.12010.1	MSTRG.12010	-2,2438	2001	423	Signal transduction-related

137	ERF92	Ethylene-responsive transcription factor 1B	MSTRG.15418.1	MSTRG.15418	-2,1748	730	211	Signal transduction-related
138	EIL3	ETHYLENE INSENSITIVE 3-like 3 protein	MSTRG.10741.1	MSTRG.10741	-2,1409	162	42	Signal transduction-related
139	ERF86	Ethylene-responsive transcription factor ERF086	MSTRG.24331.1	MSTRG.24331	-1,8384	41	10	Signal transduction-related
140	RAP23	Ethylene-responsive transcription factor RAP2-3	MSTRG.31022.1	MSTRG.31022	-1,7964	6773	2124	Signal transduction-related
141	ERF91	Ethylene-responsive transcription factor ERF091	MSTRG.29553.1	MSTRG.29553	1,6556	58	195	Signal transduction-related
142	LEP	Ethylene-responsive transcription factor LEP	MSTRG.32055.1	MSTRG.32055	1,6911	13	74	Signal transduction-related
143	ERF79	Ethylene-responsive transcription factor 8	MSTRG.23857.1	MSTRG.23857	1,8044	73	325	Signal transduction-related
144	ERF53	Ethylene-responsive transcription factor ERF053	MSTRG.21403.1	MSTRG.21403	1,8084	15	75	Signal transduction-related
145	ERF82	Ethylene-responsive transcription factor 3	MSTRG.16185.1	MSTRG.16185	1,9532	4	28	Signal transduction-related
146	ERF82	Ethylene-responsive transcription factor 3	MSTRG.16184.1	MSTRG.16184	1,9854	10	39	Signal transduction-related
147	RAP27	Ethylene-responsive transcription factor RAP2-7	MSTRG.2100.1	MSTRG.2100	2,1818	140	552	Signal transduction-related

148	WRI1	Ethylene-responsive transcription factor WRI1	MSTRG.11114.1	MSTRG.11114	2,1902	47	295	Signal transduction-related
149	ERFC3	Ethylene-response factor C3	MSTRG.23838.1	MSTRG.23838	2,5275	1	13	Signal transduction-related
150	CRF4	Ethylene-responsive transcription factor CRF4	MSTRG.23591.1	MSTRG.23591	2,5519	49	238	Signal transduction-related
151	ERF34	Ethylene-responsive transcription factor ERF034	MSTRG.12338.1	MSTRG.12338	2,884	20	165	Signal transduction-related
152	ERF38	Ethylene-responsive transcription factor ERF038	MSTRG.16468.1	MSTRG.16468	3,245	10	100	Signal transduction-related
153	CTR1	Serine/threonine-protein kinase CTR1	MSTRG.22607.1	MSTRG.22607	3,5532	50	479	Signal transduction-related
154	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.33443.1	MSTRG.33443	4,5743	0	8	Signal transduction-related
155	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.1	MSTRG.16006	4,63	25	515	Signal transduction-related
156	AHK5	Histidine kinase 5	MSTRG.3825.1	MSTRG.3825	4,7347	29	652	Signal transduction-related
157	RA211	Ethylene-responsive transcription factor RAP2-11	MSTRG.22022.1	MSTRG.22022	5,4994	0	7	Signal transduction-related
158	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.1	MSTRG.544	6,067	1	115	Signal transduction-related

	159	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.26257.1	MSTRG.26257	6,2949	0	55	Signal transduction-related
	160	ERF99	Ethylene-responsive transcription factor 13	MSTRG.10673.1	MSTRG.10673	6,4236	0	25	Signal transduction-related
	161	WIN1	Ethylene-responsive transcription factor WIN1	MSTRG.6626.1	MSTRG.6626	7,0921	0	56	Signal transduction-related
	162	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.33457.1	MSTRG.33457	7,0944	0	45	Signal transduction-related
JA	163	OPR2	12-oxophytodienoate reductase 2	MSTRG.24102.1	MSTRG.24102	-2,8617	1614	221	Biosynthesis
	164	AOS3	Allene oxide synthase 3	MSTRG.9496.1	MSTRG.9496	-2,8082	512	59	Biosynthesis
	165	AOS3	Allene oxide synthase 3	MSTRG.28845.1	MSTRG.28845	-2,4411	4031	791	Biosynthesis
	166	LOX6	Lipoxygenase 6, chloroplastic	MSTRG.9345.1	MSTRG.9345	-2,2273	61	15	Biosynthesis
	167	OPR2	12-oxophytodienoate reductase 2	MSTRG.24084.1	MSTRG.24084	-2,1945	1025	222	Biosynthesis
	168	LOX15	Probable linoleate 9S-lipoxygenase 5	MSTRG.8017.1	MSTRG.8017	-2,1189	8	1	Biosynthesis
	169	LOX15	Probable linoleate 9S-lipoxygenase 5	MSTRG.8013.1	MSTRG.8013	-1,8344	18567	5118	Biosynthesis
	170	LOX31	Linoleate 13S-lipoxygenase 3-1	MSTRG.11870.1	MSTRG.11870	-1,5654	560	174	Biosynthesis
	171	AOC	Allene oxide cyclase, chloroplastic	MSTRG.1321.1	MSTRG.1321	1,7685	1017	3609	Biosynthesis
	172	AOS3	Allene oxide synthase 3	MSTRG.28842.1	MSTRG.28842	1,8718	8	29	Biosynthesis
	173	AOC	Allene oxide cyclase	MSTRG.5424.1	MSTRG.5424	1,9154	1016	4232	Biosynthesis
	174	LOX5	Linoleate 9S-lipoxygenase 5	MSTRG.14580.1	MSTRG.14580	2,0251	203	838	Biosynthesis
	175	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.424.1	MSTRG.424	11,5427	0	522	Biosynthesis
	176	JOX2	Jasmonate-induced oxygenase 2	MSTRG.34582.1	MSTRG.34582	-8,4146	1887	2	Degradation/ Inactivation
	177	JOX2	Jasmonate-induced oxygenase 2	MSTRG.22752.1	MSTRG.22752	-2,9222	884	118	Degradation/ Inactivation
	178	JOX2	Jasmonate-induced oxygenase 2	MSTRG.28807.5	MSTRG.28807	-2,0148	1924	461	Degradation/ Inactivation

	179	MYC2	Transcription factor MYC2	MSTRG.15289.1	MSTRG.15289	-5,2984	54	2	Signal transduction-related
	180	MYC2	Transcription factor MYC2	MSTRG.15281.1	MSTRG.15281	-1,7786	712	219	Signal transduction-related
GA	181	KAO2	Ent-kaurenoic acid oxidase 2	MSTRG.9502.1	MSTRG.9502	1,9037	161	621	Biosynthesis
	182	GAOXL	Gibberellin 20-oxidase-like protein	MSTRG.20624.1	MSTRG.20624	2,0688	37	144	Biosynthesis
	183	GAOXL	Gibberellin 20-oxidase-like protein	MSTRG.20624.1	MSTRG.20624	2,0688	37	144	Biosynthesis
	184	GAOX4	Gibberellin 20 oxidase 4	MSTRG.26764.1	MSTRG.26764	4,3611	0	3	Biosynthesis
	185	GAOX2	Gibberellin 20 oxidase 2	MSTRG.23935.1	MSTRG.23935	4,3996	3	112	Biosynthesis
	186	KO1	Ent-kaurene oxidase, chloroplastic	MSTRG.32736.1	MSTRG.32736	4,9814	7	253	Biosynthesis
	187	KO1	Ent-kaurene oxidase, chloroplastic	MSTRG.32735.1	MSTRG.32735	6,1901	0	96	Biosynthesis
	188	G3OX	Gibberellin 3-beta-dioxygenase 1	MSTRG.22681.1	MSTRG.22681	9,3938	1	259	Biosynthesis
	189	G2OX2	Gibberellin 2-beta-dioxygenase 2	MSTRG.15029.1	MSTRG.15029	-6,0668	100	1	Degradation/ Inactivation
	190	G2OX2	Gibberellin 2-beta-dioxygenase 2	MSTRG.33954.1	MSTRG.33954	-1,5615	457	154	Degradation/ Inactivation
	191	GAMT2	Gibberellic acid methyltransferase 2	MSTRG.478.1	MSTRG.478	-2,9566	96	11	Signal transduction-related
	192	DELA1	DELLA protein 1	MSTRG.1730.1	MSTRG.1730	1,6474	915	3419	Signal transduction-related
	193	SCL3	Scarecrow-like protein 3	MSTRG.344.1	MSTRG.344	2,5091	2	11	Signal transduction-related
	194	SCL3	Scarecrow-like protein 3	MSTRG.1129.1	MSTRG.1129	2,5775	33	274	Signal transduction-related

	195	SCL3	Scarecrow-like protein 3	MSTRG.3816.1	MSTRG.3816	2,601	39	260	Signal transduction-related
	196	GASA4	Gibberellin-regulated protein 4	MSTRG.6190.1	MSTRG.6190	4,1384	231	4752	Signal transduction-related
	197	GASA6	Gibberellin-regulated protein 6	MSTRG.25979.1	MSTRG.25979	5,174	0	7	Signal transduction-related
	198	SCL3	Scarecrow-like protein 3	MSTRG.10290.1	MSTRG.10290	5,0955	0	6	Signal transduction-related
	199	GASA1	Gibberellin-regulated protein 1	MSTRG.20696.1	MSTRG.20696	7,9783	0	449	Signal transduction-related
	200	GASAE	Gibberellin-regulated protein 14	MSTRG.20691.1	MSTRG.20691	8,6831	27	15221	Signal transduction-related
	201	GASAE	Gibberellin-regulated protein 14	MSTRG.20694.1	MSTRG.20694	9,4438	6	4342	Signal transduction-related
	202	GASAE	Gibberellin-regulated protein 14	MSTRG.20693.1	MSTRG.20693	12,515	0	2144	Signal transduction-related
BR	203	BEN1	Protein BRI1-5 ENHANCED 1	MSTRG.22124.1	MSTRG.22124	1,7533	17	59	Biosynthesis
	204	C85A	Cytochrome P450 85A	MSTRG.335.1	MSTRG.335	1,8709	223	808	Biosynthesis
	205	C90A1	Cytochrome P450 90A1	MSTRG.22789.1	MSTRG.22789	2,4861	79	490	Biosynthesis
	206	C90D1	3-epi-6-deoxocathasterone 23-monooxygenase CYP90D1	MSTRG.12229.1	MSTRG.12229	2,6366	210	1306	Biosynthesis
	207	C90B1	Cytochrome P450 90B1	MSTRG.16916.1	MSTRG.16916	2,8888	2	90	Biosynthesis
	208	BRAT1	Brassinosteroid-related acyltransferase 1	MSTRG.3982.1	MSTRG.3982	-2,2735	100	18	Degradation/ Inactivation
	209	BRAT1	Brassinosteroid-related acyltransferase 1	MSTRG.8870.1	MSTRG.8870	-1,5578	47	14	Degradation/

									Inactivation
	210	C734A	Cytochrome P450 734A1	MSTRG.6502.1	MSTRG.6502	1,9176	22	129	Degradation/ Inactivation
	211	C734A	Cytochrome P450 734A1	MSTRG.2961.1	MSTRG.2961	2,7639	4	52	Degradation/ Inactivation
	212	C734A	Cytochrome P450 734A1	MSTRG.2960.1	MSTRG.2960	6,4716	6	525	Degradation/ Inactivation
	213	BRH1	Brassinosteroid-responsive RING protein 1	MSTRG.23290.1	MSTRG.23290	1,6974	20	80	Signal transduction-related
	214	SERK2	LRR receptor kinase SERK2	MSTRG.34589.2	MSTRG.34589	2,3053	46	245	Signal transduction-related
	215	BRH1	Brassinosteroid-responsive RING protein 1	MSTRG.15844.1	MSTRG.15844	2,31	5	20	Signal transduction-related
	216	BRH1	Brassinosteroid-responsive RING protein 1	MSTRG.11139.1	MSTRG.11139	2,9515	50	404	Signal transduction-related
	217	BRH1	Brassinosteroid-responsive RING protein 1	MSTRG.27142.1	MSTRG.27142	7,0643	0	19	Signal transduction-related

LTR_1 vs. TTR

Hormone	No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	TTR Genes Results	LTR_1 Genes Results	Function
IAA	218	YUC10	Probable indole-3-pyruvate monooxygenase YUCCA10	MSTRG.3084.1	MSTRG.3084	2,049	55	158	Biosynthesis
	219	YUC10	Probable indole-3-pyruvate monooxygenase YUCCA10	MSTRG.12290.1	MSTRG.12290	5,3061	0	12	Biosynthesis

220	IAMT1	Indole-3-acetate O-methyltransferase 1	MSTRG.20288.1	MSTRG.20288	-2,7107	66	27	Conjugate synthesis
221	GH36	Indole-3-acetic acid-amido synthetase GH3.6	MSTRG.21271.1	MSTRG.21271	2,544	53	202	Conjugate synthesis
222	ILL1	IAA-amino acid hydrolase ILR1-like 1	MSTRG.9014.1	MSTRG.9014	-2,3811	57	12	Conjugate degradation
223	PIN2	Auxin efflux carrier component 2	MSTRG.5845.1	MSTRG.5845	-3,468	61	13	Transport
224	PIN6	Auxin efflux carrier component 6	MSTRG.35377.1	MSTRG.35377	-2,6419	86	20	Transport
225	PIN6	Auxin efflux carrier component 6	MSTRG.4274.1	MSTRG.4274	-2,3808	101	30	Transport
226	PIN2	Auxin efflux carrier component 2	MSTRG.5844.1	MSTRG.5844	1,6487	548	1636	Transport
227	PILS2	Protein PIN-LIKES 2	MSTRG.2594.1	MSTRG.2594	1,7588	32	93	Transport
228	LAX3	Auxin transporter-like protein 3	MSTRG.24617.1	MSTRG.24617	2,824	155	911	Transport
229	PILS6	Protein PIN-LIKES 6	MSTRG.13861.3	MSTRG.13861	4,6679	3	33	Transport
230	SAU76	Auxin-responsive protein SAUR76	MSTRG.32895.1	MSTRG.32895	-3,0206	18	5	Signal transduction-related
231	WOX4	WUSCHEL-related homeobox 4	MSTRG.2733.1	MSTRG.2733	-2,9646	259	49	Signal transduction-related
232	ARG7	Indole-3-acetic acid-induced protein ARG7	MSTRG.29248.1	MSTRG.29248	-2,6888	23	7	Signal transduction-related
233	SAU71	Auxin-responsive protein SAUR71	MSTRG.9206.1	MSTRG.9206	-2,1963	2020	514	Signal transduction-related
234	IAA32	Auxin-responsive protein IAA32	MSTRG.4635.1	MSTRG.4635	-1,6796	32	8	Signal transduction-related
235	ARFD	Auxin response factor 4	MSTRG.1418.1	MSTRG.1418	-1,6756	58	18	Signal transduction-related

236	SAU71	Auxin-responsive protein SAUR71	MSTRG.25417.1	MSTRG.25417	-1,6559	14	5	Signal transduction-related
237	ARFP	Auxin response factor 16	MSTRG.34222.1	MSTRG.34222	-1,588	414	115	Signal transduction-related
238	IAA14	Auxin-responsive protein IAA14	MSTRG.15323.1	MSTRG.15323	1,7831	867	3299	Signal transduction-related
239	SAU76	Auxin-responsive protein SAUR76	MSTRG.25098.1	MSTRG.25098	2,0791	2	10	Signal transduction-related
240	SAU40	Auxin-responsive protein SAUR40	MSTRG.3770.1	MSTRG.3770	2,4434	1	22	Signal transduction-related
241	SAU71	Auxin-responsive protein SAUR71	MSTRG.33530.1	MSTRG.33530	2,7803	11	71	Signal transduction-related
242	SAU67	Auxin-responsive protein SAUR67	MSTRG.35217.1	MSTRG.35217	5,0213	0	7	Signal transduction-related
243	ARFQ	Auxin response factor 17	MSTRG.12405.1	MSTRG.12405	5,4623	0	0	Signal transduction-related
244	ARG7	Indole-3-acetic acid-induced protein ARG7	MSTRG.29251.1	MSTRG.29251	5,823	0	11	Signal transduction-related
245	ARFQ	Auxin response factor 17	MSTRG.34776.1	MSTRG.34776	6,4965	0	1	Signal transduction-related
246	IAA7	Auxin-responsive protein IAA7	MSTRG.15336.1	MSTRG.15336	9,9796	0	371	Signal transduction-related

CK	247	LOG1	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG1	MSTRG.1370.1	MSTRG.1370	-2,3174	37	10	Biosynthesis
	248	LOG3	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG3	MSTRG.19557.1	MSTRG.19557	-1,94	264	105	Biosynthesis
	249	C7351	Cytokinin hydroxylase	MSTRG.5409.1	MSTRG.5409	1,7047	56	130	Biosynthesis
	250	LOG7	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG7	MSTRG.19148.1	MSTRG.19148	2,8607	9	40	Biosynthesis
	251	CKX6	Cytokinin dehydrogenase 6	MSTRG.14015.1	MSTRG.14015	-2,0793	145	42	Degradation/ Inactivation
	252	ORR26	Two-component response regulator ORR26	MSTRG.9399.1	MSTRG.9399	-1,7809	951	282	Signal transduction-related
	253	ARR5	Two-component response regulator ARR5	MSTRG.25879.1	MSTRG.25879	1,78	44	128	Signal transduction-related
	254	ARR4	Two-component response regulator ARR4	MSTRG.8997.1	MSTRG.8997	1,9041	119	388	Signal transduction-related
ABA	255	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	MSTRG.13453.1	MSTRG.13453	-2,0922	1224	362	Biosynthesis
	256	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	MSTRG.32782.1	MSTRG.32782	1,6777	42	209	Biosynthesis
	257	LEA34	Late embryogenesis abundant protein D-34	MSTRG.6820.1	MSTRG.6820	-4,5268	9	1	Signal transduction-related
	258	Y3304	Late embryogenesis abundant protein At3g53040	MSTRG.19319.1	MSTRG.19319	-3,9887	91	2	Signal transduction-related
	259	LEA29	Late embryogenesis abundant protein D-29	MSTRG.23000.1	MSTRG.23000	-3,7652	9	0	Signal transduction-related
	260	LEA7	Late embryogenesis abundant protein 7	MSTRG.12711.1	MSTRG.12711	-2,3649	69	24	Signal transduction-related

	261	LEA5	Late embryogenesis abundant protein Lea5	MSTRG.15021.1	MSTRG.15021	-1,8538	24	9	Signal transduction-related
	262	LEA5	Late embryogenesis abundant protein Lea5	MSTRG.15019.1	MSTRG.15019	-1,8538	40355	13920	Signal transduction-related
	263	AHK1	Histidine kinase 1	MSTRG.17005.1	MSTRG.17005	-1,6785	531	316	Signal transduction-related
	264	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.4806.1	MSTRG.4806	1,9077	14	76	Signal transduction-related
ET	265	ETR1	Ethylene receptor	MSTRG.995.1	MSTRG.995	-4,7001	6	0	Signal transduction-related
	266	ERF10	Ethylene-responsive transcription factor ERF010	MSTRG.16619.1	MSTRG.16619	-2,1375	110	42	Signal transduction-related
	267	ERF11	Ethylene-responsive transcription factor ERF011	MSTRG.2732.1	MSTRG.2732	-1,6954	327	82	Signal transduction-related
	268	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.35144.1	MSTRG.35144	-1,6871	53	15	Signal transduction-related
	269	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25340.1	MSTRG.25340	-1,6543	572	240	Signal transduction-related
	270	WRI1	Ethylene-responsive transcription factor WRI1	MSTRG.11114.1	MSTRG.11114	1,5215	62	142	Signal transduction-related
	271	ERF62	Ethylene-responsive transcription factor ERF062	MSTRG.16006.1	MSTRG.16006	1,6711	78	141	Signal transduction-related

	272	WIN1	Ethylene-responsive transcription factor WIN1	MSTRG.6626.1	MSTRG.6626	1,6802	14	36	Signal transduction-related
	273	ERF82	Ethylene-responsive transcription factor 3	MSTRG.16184.1	MSTRG.16184	2,1993	12	29	Signal transduction-related
	274	EF100	Ethylene-responsive transcription factor 1A	MSTRG.30183.1	MSTRG.30183	3,964	0	0	Signal transduction-related
	275	ERF95	Ethylene-responsive transcription factor ERF095	MSTRG.15416.1	MSTRG.15416	5,8344	0	1	Signal transduction-related
JA	276	LOX6	Lipoxygenase 6	MSTRG.9345.1	MSTRG.9345	-3,3652	184	34	Biosynthesis
	277	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34851.1	MSTRG.34851	-2,4601	27	0	Biosynthesis
	278	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.424.1	MSTRG.424	5,899	5	21	Biosynthesis
	279	JOX2	Jasmonate-induced oxygenase 2	MSTRG.34582.1	MSTRG.34582	2,3723	11	34	Degradation/ Inactivation
	280	MYC2	Transcription factor MYC2	MSTRG.15281.1	MSTRG.15281	-1,5729	531	154	Signal transduction-related
GA	281	GAOXL	Gibberellin 20-oxidase-like protein	MSTRG.20624.1	MSTRG.20624	2,1914	23	210	Biosynthesis
	282	G3OX	Gibberellin 3-beta-dioxygenase 1	MSTRG.22681.1	MSTRG.22681	2,4176	25	79	Biosynthesis
	283	KO1	Ent-kaurene oxidase	MSTRG.32736.1	MSTRG.32736	2,502	39	203	Biosynthesis
	284	KO1	Ent-kaurene oxidase	MSTRG.32735.1	MSTRG.32735	5,4355	1	71	Biosynthesis
	285	GAMT2	Gibberellic acid methyltransferase 2	MSTRG.478.1	MSTRG.478	-1,5805	22	8	Degradation/ Inactivation
	286	SNE	F-box protein SNE	MSTRG.34206.1	MSTRG.34206	-2,3407	34	3	Signal transduction-related
	287	GAI1	DELLA protein GAI1	MSTRG.20351.1	MSTRG.20351	-1,681	19	4	Signal transduction-related

	288	GASA6	Gibberellin-regulated protein 6	MSTRG.25978.1	MSTRG.25978	2,0619	2084	8594	Signal transduction-related
	289	GASAE	Gibberellin-regulated protein 14	MSTRG.20691.1	MSTRG.20691	3,0914	1173	7973	Signal transduction-related
	290	GASAE	Gibberellin-regulated protein 14	MSTRG.20694.1	MSTRG.20694	3,9141	217	1431	Signal transduction-related
	291	GASAE	Gibberellin-regulated protein 14	MSTRG.20693.1	MSTRG.20693	6,0968	15	229	Signal transduction-related
	292	GASA1	Gibberellin-regulated protein 1	MSTRG.20696.1	MSTRG.20696	7,1147	3	107	Signal transduction-related
	293	SCL3	Scarecrow-like protein 3	MSTRG.10290.1	MSTRG.10290	7,565	1	5	Signal transduction-related
BR	294	C90D1	3-epi-6-deoxocathasterone 23-monooxygenase CYP90D1	MSTRG.12229.1	MSTRG.12229	1,6218	190	507	Biosynthesis
	295	C734A	Cytochrome P450 734A1	MSTRG.2960.1	MSTRG.2960	2,2803	62	240	Degradation/ Inactivation
	296	BRH1	Brassinosteroid-responsive RING protein 1	MSTRG.27142.1	MSTRG.27142	-1,6068	14	4	Signal transduction-related

Supplementary table 5. Genes encoding transcription factors identified in MTR vs. MLR and LTR vs. LLR comparisons.

MTR vs. MLR

No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	MLR Genes Results	MTR Genes Results
1	NFYB4	Nuclear transcription factor Y subunit B-4	MSTRG.7981.1	MSTRG.7981	-8,43	122,33	0,33
2	NFYB4	Nuclear transcription factor Y subunit B-4	MSTRG.7602.1	MSTRG.7602	-8,37	59,67	0,00
3	MOF1	Myb family transcription factor MOF1	MSTRG.21728.1	MSTRG.21728	-8,21	53,33	0,00
4	ORG2	Transcription factor ORG2	MSTRG.13172.1	MSTRG.13172	-7,16	556,00	4,00
5	ORG2	Transcription factor ORG2	MSTRG.13172.2	MSTRG.13172	-7,16	556,00	4,00
6	ORG2	Transcription factor ORG2	MSTRG.20832.1	MSTRG.20832	-6,91	21,67	0,00
7	UNE10	Transcription factor UNE10	MSTRG.26111.1	MSTRG.26111	-5,66	17,67	0,33
8	BH120	Transcription factor bHLH120	MSTRG.31548.1	MSTRG.31548	-5,64	32,67	0,67
9	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.1	MSTRG.18391	-5,42	235,33	5,67
10	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.2	MSTRG.18391	-5,42	235,33	5,67
11	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.3	MSTRG.18391	-5,42	235,33	5,67
12	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.4	MSTRG.18391	-5,42	235,33	5,67
13	TCP2	Transcription factor TCP2	MSTRG.21778.1	MSTRG.21778	-5,38	2239,33	55,00
14	TCP2	Transcription factor TCP2	MSTRG.21778.2	MSTRG.21778	-5,38	2239,33	55,00
15	TCP2	Transcription factor TCP2	MSTRG.21778.3	MSTRG.21778	-5,38	2239,33	55,00
16	TCP2	Transcription factor TCP2	MSTRG.21778.4	MSTRG.21778	-5,38	2239,33	55,00
17	TCP2	Transcription factor TCP2	MSTRG.21778.5	MSTRG.21778	-5,38	2239,33	55,00
18	TCP2	Transcription factor TCP2	MSTRG.21778.6	MSTRG.21778	-5,38	2239,33	55,00
19	HYH	Transcription factor HY5-like	MSTRG.15354.1	MSTRG.15354	-4,99	72,00	2,33
20	NFYB5	Nuclear transcription factor Y subunit B-5	MSTRG.31092.1	MSTRG.31092	-4,97	258,00	8,33
21	NFYB5	Nuclear transcription factor Y subunit B-5	MSTRG.31092.2	MSTRG.31092	-4,97	258,00	8,33
22	MYB61	Transcription factor MYB61	MSTRG.32874.1	MSTRG.32874	-4,73	101,67	4,00
23	MYB26	Transcription factor MYB26	MSTRG.32874.2	MSTRG.32874	-4,73	101,67	4,00
24	PHL5	Myb family transcription factor PHL5	MSTRG.13735.1	MSTRG.13735	-4,69	25,33	1,00
25	NFYB3	Nuclear transcription factor Y subunit B-3	MSTRG.5885.1	MSTRG.5885	-4,69	111,00	4,33

26	WRK43	Probable WRKY transcription factor 43	MSTRG.11159.1	MSTRG.11159	-4,55	918,33	39,67
27	MYB52	Transcription factor MYB52	MSTRG.24374.1	MSTRG.24374	-4,51	44,67	2,00
28	MYB1	Transcription factor MYB1	MSTRG.5460.1	MSTRG.5460	-4,51	8,33	0,33
29	WRK56	Probable WRKY transcription factor 56	MSTRG.32004.1	MSTRG.32004	-4,40	165,67	8,00
30	RAX3	Transcription factor RAX3	MSTRG.2669.1	MSTRG.2669	-4,14	23,33	1,33
31	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.11938.1	MSTRG.11938	-4,11	536,67	32,00
32	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.11938.2	MSTRG.11938	-4,11	536,67	32,00
33	BH120	Transcription factor bHLH120	MSTRG.31546.1	MSTRG.31546	-4,10	87,33	5,33
34	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.33457.1	MSTRG.33457	-4,07	967,00	59,33
35	BH111	Transcription factor bHLH111	MSTRG.9033.1	MSTRG.9033	-3,91	1542,33	105,00
36	BH111	Transcription factor bHLH111	MSTRG.9033.2	MSTRG.9033	-3,91	1542,33	105,00
37	BH111	Transcription factor bHLH111	MSTRG.9033.3	MSTRG.9033	-3,91	1542,33	105,00
38	BH111	Transcription factor bHLH111	MSTRG.9033.4	MSTRG.9033	-3,91	1542,33	105,00
39	BH111	Transcription factor bHLH111	MSTRG.9033.5	MSTRG.9033	-3,91	1542,33	105,00
40	BH111	Transcription factor bHLH111	MSTRG.9033.6	MSTRG.9033	-3,91	1542,33	105,00
41	BH111	Transcription factor bHLH111	MSTRG.9033.7	MSTRG.9033	-3,91	1542,33	105,00
42	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.33443.1	MSTRG.33443	-3,89	24,33	1,67
43	PIL15	Transcription factor PHYTOCHROME INTERACTING FACTOR-LIKE 15	MSTRG.34248.1	MSTRG.34248	-3,86	51,67	3,67
44	WRK74	Probable WRKY transcription factor 74	MSTRG.21830.1	MSTRG.21830	-3,78	717,67	52,67
45	WRK74	Probable WRKY transcription factor 74	MSTRG.21830.2	MSTRG.21830	-3,78	717,67	52,67
46	MYB86	Transcription factor MYB86	MSTRG.27862.1	MSTRG.27862	-3,76	66,00	5,00
47	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.26257.1	MSTRG.26257	-3,64	258,33	21,67
48	ODO1	MYB-like transcription factor ODO1	MSTRG.24008.1	MSTRG.24008	-3,58	260,00	22,33
49	NFYC4	Nuclear transcription factor Y subunit C-4	MSTRG.32241.1	MSTRG.32241	-3,51	41,00	3,67
50	ODO1	MYB-like transcription factor ODO1	MSTRG.30090.1	MSTRG.30090	-3,49	549,67	50,00
51	MYB93	Transcription factor MYB93	MSTRG.3372.1	MSTRG.3372	-3,41	198,33	19,00
52	MYB93	Transcription factor MYB93	MSTRG.17206.1	MSTRG.17206	-3,39	366,67	35,67
53	IBH1	Transcription factor IBH1	MSTRG.16011.1	MSTRG.16011	-3,35	177,67	18,00
54	IBH1	Transcription factor IBH1	MSTRG.16011.2	MSTRG.16011	-3,35	177,67	18,00

55	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.1	MSTRG.5571	-3,32	126,67	13,00
56	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.2	MSTRG.5571	-3,32	126,67	13,00
57	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.3	MSTRG.5571	-3,32	126,67	13,00
58	TCP13	Transcription factor TCP13	MSTRG.8313.1	MSTRG.8313	-3,31	44,67	4,67
59	RA211	Ethylene-responsive transcription factor RAP2-11	MSTRG.22022.1	MSTRG.22022	-3,29	80,33	8,67
60	BZIP2	bZIP transcription factor 2	MSTRG.16355.1	MSTRG.16355	-3,28	1561,33	167,00
61	AP2L1	AP2-like ethylene-responsive transcription factor At1g16060	MSTRG.7763.1	MSTRG.7763	-3,25	68,00	7,33
62	AP2L1	AP2-like ethylene-responsive transcription factor At1g16060	MSTRG.7763.2	MSTRG.7763	-3,25	68,00	7,33
63	AP2L1	AP2-like ethylene-responsive transcription factor At1g16060	MSTRG.7763.3	MSTRG.7763	-3,25	68,00	7,33
64	MYB26	Transcription factor MYB26	MSTRG.31161.1	MSTRG.31161	-3,17	100,33	11,33
65	MYB46	Transcription factor MYB46	MSTRG.15784.1	MSTRG.15784	-3,15	69,33	8,00
66	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.1	MSTRG.544	-3,14	252,67	29,67
67	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.2	MSTRG.544	-3,14	252,67	29,67
68	MYB52	Transcription factor MYB52	MSTRG.26728.1	MSTRG.26728	-3,11	189,33	22,67
69	TGA10	bZIP transcription factor TGA10	MSTRG.18034.1	MSTRG.18034	-3,09	1937,67	234,67
70	BH030	Transcription factor bHLH30	MSTRG.13027.1	MSTRG.13027	-3,07	3106,00	379,00
71	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.10894.1	MSTRG.10894	-3,05	15,67	2,00
72	NFYA1	Nuclear transcription factor Y subunit A-1	MSTRG.4176.1	MSTRG.4176	-3,05	1047,33	130,33
73	TGA9	Transcription factor TGA9	MSTRG.6736.1	MSTRG.6736	-3,03	4304,67	543,33
74	TGA9	Transcription factor TGA9	MSTRG.6736.2	MSTRG.6736	-3,03	4304,67	543,33
75	TGA9	Transcription factor TGA9	MSTRG.6736.3	MSTRG.6736	-3,03	4304,67	543,33
76	MY113	Transcription factor MYB113	MSTRG.1431.1	MSTRG.1431	-3,03	28,67	3,67
77	MYB75	Transcription factor MYB75	MSTRG.1431.2	MSTRG.1431	-3,03	28,67	3,67
78	MYB27	Transcription factor MYB27	MSTRG.25709.1	MSTRG.25709	-2,87	25,67	3,67
79	PHL5	Myb family transcription factor PHL5	MSTRG.18051.1	MSTRG.18051	-2,84	161,67	23,33
80	ILR3	Transcription factor ILR3	MSTRG.32423.1	MSTRG.32423	-2,83	379,00	55,33

81	ILR3	Transcription factor ILR3	MSTRG.32423.2	MSTRG.32423	-2,83	379,00	55,33
82	MYB93	Transcription factor MYB93	MSTRG.24195.1	MSTRG.24195	-2,80	202,00	30,00
83	LAF1	Transcription factor LAF1	MSTRG.23733.1	MSTRG.23733	-2,76	600,00	91,33
84	ERF11	Ethylene-responsive transcription factor ERF011	MSTRG.2732.1	MSTRG.2732	-2,71	687,67	109,33
85	MYBS3	Transcription factor MYBS3	MSTRG.5695.1	MSTRG.5695	-2,70	135,67	21,33
86	WRKY6	WRKY transcription factor 6	MSTRG.20348.1	MSTRG.20348	-2,69	374,67	58,67
87	TCP3	Transcription factor TCP3	MSTRG.21481.1	MSTRG.21481	-2,62	636,00	106,67
88	TCP3	Transcription factor TCP3	MSTRG.21481.2	MSTRG.21481	-2,62	636,00	106,67
89	TCP3	Transcription factor TCP3	MSTRG.21481.3	MSTRG.21481	-2,62	636,00	106,67
90	MYB48	Transcription factor MYB48	MSTRG.346.1	MSTRG.346	-2,55	92,00	16,33
91	ERF53	Ethylene-responsive transcription factor ERF053	MSTRG.21403.1	MSTRG.21403	-2,52	374,67	67,33
92	MYB59	Transcription factor MYB59	MSTRG.13004.1	MSTRG.13004	-2,50	4519,33	826,33
93	MYB48	Transcription factor MYB48	MSTRG.13004.2	MSTRG.13004	-2,50	4519,33	826,33
94	MYB48	Transcription factor MYB48	MSTRG.13004.3	MSTRG.13004	-2,50	4519,33	826,33
95	BH130	Transcription factor bHLH130	MSTRG.10310.1	MSTRG.10310	-2,43	473,00	89,67
96	ERF38	Ethylene-responsive transcription factor ERF038	MSTRG.16468.1	MSTRG.16468	-2,43	361,00	69,00
97	NFYB5	Nuclear transcription factor Y subunit B-5	MSTRG.34546.1	MSTRG.34546	-2,42	80,00	15,33
98	FIT	Transcription factor FER-LIKE IRON DEFICIENCY-INDUCED TRANSCRIPTION FACTOR	MSTRG.895.1	MSTRG.895	-2,42	2460,00	473,33
99	PHL5	Myb family transcription factor PHL5	MSTRG.19446.1	MSTRG.19446	-2,40	71,67	14,33
100	DIV	Transcription factor DIVARICATA	MSTRG.22698.1	MSTRG.22698	-2,38	451,33	88,67
101	DIV	Transcription factor DIVARICATA	MSTRG.22698.2	MSTRG.22698	-2,38	451,33	88,67
102	RSL2	Transcription factor RSL2	MSTRG.30608.1	MSTRG.30608	-2,30	82,00	17,33
103	MYB2	Transcription factor MYB2	MSTRG.30419.1	MSTRG.30419	-2,29	102,00	21,67
104	MYB93	Transcription factor MYB93	MSTRG.29975.1	MSTRG.29975	-2,29	57,67	11,67
105	BH036	Transcription factor bHLH36	MSTRG.31547.1	MSTRG.31547	-2,25	148,33	32,00
106	NAC56	NAC transcription factor 56	MSTRG.20722.1	MSTRG.20722	-2,25	533,00	114,67
107	PHL5	Myb family transcription factor PHL5	MSTRG.18049.1	MSTRG.18049	-2,24	193,33	42,33
108	PHL5	Myb family transcription factor PHL5	MSTRG.18049.2	MSTRG.18049	-2,24	193,33	42,33
109	PHL5	Myb family transcription factor PHL5	MSTRG.18049.3	MSTRG.18049	-2,24	193,33	42,33

110	PHL5	Myb family transcription factor PHL5	MSTRG.18049.4	MSTRG.18049	-2,24	193,33	42,33
111	LHWL1	Transcription factor EMB1444	MSTRG.18533.1	MSTRG.18533	-2,23	8470,33	1842,67
112	RAX3	Transcription factor RAX3	MSTRG.4329.1	MSTRG.4329	-2,21	623,33	138,67
113	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.20675.1	MSTRG.20675	-2,17	27,67	6,33
114	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.20675.2	MSTRG.20675	-2,17	27,67	6,33
115	HSFA3	Heat stress transcription factor A-3	MSTRG.19355.1	MSTRG.19355	-2,13	50,67	12,00
116	HSFA3	Heat stress transcription factor A-3	MSTRG.19355.2	MSTRG.19355	-2,13	50,67	12,00
117	HSFA3	Heat stress transcription factor A-3	MSTRG.19355.3	MSTRG.19355	-2,13	50,67	12,00
118	TCP15	Transcription factor TCP15	MSTRG.23976.1	MSTRG.23976	-2,13	238,67	56,67
119	NFYB3	Nuclear transcription factor Y subunit B-3	MSTRG.20204.1	MSTRG.20204	-2,10	24,33	5,67
120	NFYB3	Nuclear transcription factor Y subunit B-3	MSTRG.20204.2	MSTRG.20204	-2,10	24,33	5,67
121	WRKY3	Probable WRKY transcription factor 3	MSTRG.6266.1	MSTRG.6266	-2,09	271,00	65,00
122	BH123	Transcription factor bHLH123	MSTRG.20606.1	MSTRG.20606	-2,07	218,67	53,67
123	BH123	Transcription factor bHLH123	MSTRG.20606.2	MSTRG.20606	-2,07	218,67	53,67
124	BH123	Transcription factor bHLH123	MSTRG.20606.3	MSTRG.20606	-2,07	218,67	53,67
125	KUA1	Transcription factor KUA1	MSTRG.2485.1	MSTRG.2485	-2,07	142,33	34,67
126	WRK14	Probable WRKY transcription factor 14	MSTRG.13688.1	MSTRG.13688	-2,02	1412,67	356,67
127	NFYA1	Nuclear transcription factor Y subunit A-1	MSTRG.308.1	MSTRG.308	-1,99	845,33	219,00
128	BH030	Transcription factor bHLH30	MSTRG.122.1	MSTRG.122	-1,98	203,33	52,67
129	BH030	Transcription factor bHLH30	MSTRG.122.2	MSTRG.122	-1,98	203,33	52,67
130	BH112	Transcription factor bHLH112	MSTRG.14135.1	MSTRG.14135	-1,97	337,33	88,00
131	BH112	Transcription factor bHLH112	MSTRG.14135.2	MSTRG.14135	-1,97	337,33	88,00
132	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.24071.1	MSTRG.24071	-1,95	1557,33	415,33
133	IBH1	Transcription factor IBH1	MSTRG.34050.1	MSTRG.34050	-1,94	463,00	125,33
134	IPN2	Myb family transcription factor IPN2	MSTRG.11369.1	MSTRG.11369	-1,91	75,67	20,67
135	IPN2	Myb family transcription factor IPN2	MSTRG.11369.2	MSTRG.11369	-1,91	75,67	20,67
136	IPN2	Myb family transcription factor IPN2	MSTRG.11369.3	MSTRG.11369	-1,91	75,67	20,67
137	IPN2	Myb family transcription factor IPN2	MSTRG.11369.4	MSTRG.11369	-1,91	75,67	20,67
138	WRK72	Probable WRKY transcription factor 72	MSTRG.4599.1	MSTRG.4599	-1,91	1132,00	311,00

139	RAX3	Transcription factor RAX3	MSTRG.25191.1	MSTRG.25191	-1,87	170,67	47,67
140	NAC47	NAC transcription factor 47	MSTRG.17854.1	MSTRG.17854	-1,87	146,67	41,00
141	MYB83	Transcription factor MYB83	MSTRG.10201.1	MSTRG.10201	-1,86	48,00	13,33
142	SRM1	Transcription factor SRM1	MSTRG.26383.1	MSTRG.26383	-1,85	186,33	53,33
143	ERF91	Ethylene-responsive transcription factor ERF091	MSTRG.29554.1	MSTRG.29554	-1,82	18,67	5,33
144	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.20679.1	MSTRG.20679	-1,80	26,33	8,00
145	WRK22	WRKY transcription factor 22	MSTRG.11161.1	MSTRG.11161	-1,79	438,00	129,00
146	NFYC9	Nuclear transcription factor Y subunit C-9	MSTRG.14629.1	MSTRG.14629	-1,76	2940,00	888,00
147	MYBF	Putative Myb family transcription factor At1g14600	MSTRG.18857.1	MSTRG.18857	-1,72	1326,33	414,67
148	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.32459.1	MSTRG.32459	-1,72	2429,33	755,33
149	MYB36	Transcription factor MYB36	MSTRG.919.1	MSTRG.919	-1,71	771,67	245,00
150	ASIL2	Trihelix transcription factor ASIL2	MSTRG.3056.1	MSTRG.3056	-1,70	1382,33	438,33
151	IPN2	Myb family transcription factor IPN2	MSTRG.32764.1	MSTRG.32764	-1,69	214,33	68,00
152	IPN2	Myb family transcription factor IPN2	MSTRG.32764.2	MSTRG.32764	-1,69	214,33	68,00
153	ERF10	Ethylene-responsive transcription factor ERF010	MSTRG.16619.1	MSTRG.16619	-1,64	126,00	41,33
154	HFA4A	Heat stress transcription factor A-4a	MSTRG.13140.1	MSTRG.13140	-1,64	1172,67	385,33
155	WRKY4	Probable WRKY transcription factor 4	MSTRG.6267.1	MSTRG.6267	-1,64	130,67	43,00
156	TGA7	Transcription factor TGA7	MSTRG.31376.1	MSTRG.31376	-1,63	1659,00	552,00
157	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.1	MSTRG.3750	-1,58	1229,00	423,00
158	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.2	MSTRG.3750	-1,58	1229,00	423,00
159	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.3	MSTRG.3750	-1,58	1229,00	423,00
160	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.4	MSTRG.3750	-1,58	1229,00	423,00
161	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.5	MSTRG.3750	-1,58	1229,00	423,00
162	TCP9	Transcription factor TCP9	MSTRG.22039.1	MSTRG.22039	-1,56	568,67	197,67

163	TCP9	Transcription factor TCP9	MSTRG.30295.1	MSTRG.30295	-1,53	287,67	103,67
164	EFM	Myb family transcription factor EFM	MSTRG.6466.1	MSTRG.6466	-1,52	192,33	68,67
165	PHL6	Myb family transcription factor PHL6	MSTRG.27626.1	MSTRG.27626	-1,52	253,00	89,67
166	PHL6	Myb family transcription factor PHL6	MSTRG.27626.2	MSTRG.27626	-1,52	253,00	89,67
167	PHL6	Myb family transcription factor PHL6	MSTRG.27626.3	MSTRG.27626	-1,52	253,00	89,67
168	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.4668.1	MSTRG.4668	-1,51	71,00	26,00
169	WRKY7	Probable WRKY transcription factor 7	MSTRG.2713.1	MSTRG.2713	-1,51	824,00	296,33
170	MYB88	Transcription factor MYB88	MSTRG.23953.1	MSTRG.23953	-1,51	506,67	182,67
171	MYB88	Transcription factor MYB88	MSTRG.23953.2	MSTRG.23953	-1,51	506,67	182,67
172	MYB88	Transcription factor MYB88	MSTRG.23953.3	MSTRG.23953	-1,51	506,67	182,67
173	MYB36	Transcription factor MYB36	MSTRG.19503.1	MSTRG.19503	-1,51	1792,67	642,67
174	MYB36	Transcription factor MYB36	MSTRG.19503.2	MSTRG.19503	-1,51	1792,67	642,67
175	IBL1	Transcription factor IBH1-like 1	MSTRG.5276.1	MSTRG.5276	1,54	105,00	315,33
176	IBL1	Transcription factor IBH1-like 1	MSTRG.5276.2	MSTRG.5276	1,54	105,00	315,33
177	NGA1	B3 domain-containing transcription factor NGA1	MSTRG.7200.1	MSTRG.7200	1,54	105,33	311,33
178	NGA1	B3 domain-containing transcription factor NGA1	MSTRG.7200.2	MSTRG.7200	1,54	105,33	311,33
179	NGA1	B3 domain-containing transcription factor NGA1	MSTRG.7200.3	MSTRG.7200	1,54	105,33	311,33
180	MYB73	Transcription factor MYB73	MSTRG.28397.1	MSTRG.28397	1,58	145,00	461,33
181	PAR1	Transcription factor PAR1	MSTRG.21806.1	MSTRG.21806	1,59	75,67	237,67
182	MYB1	Transcription factor MYB1	MSTRG.23325.1	MSTRG.23325	1,59	116,00	365,00
183	MYB2	Transcription factor MYB1	MSTRG.7371.1	MSTRG.7371	1,60	175,67	555,00
184	CRF4	Ethylene-responsive transcription factor CRF4	MSTRG.23591.1	MSTRG.23591	1,67	73,33	242,67
185	HSFB4	Heat stress transcription factor B-4	MSTRG.2747.1	MSTRG.2747	1,80	178,00	647,00
186	BBM	AP2-like ethylene-responsive transcription factor BBM	MSTRG.1135.1	MSTRG.1135	1,81	304,67	1117,67
187	BBM	AP2-like ethylene-responsive transcription factor BBM	MSTRG.1135.2	MSTRG.1135	1,81	304,67	1117,67
188	BBM	AP2-like ethylene-responsive transcription factor BBM	MSTRG.1135.3	MSTRG.1135	1,81	304,67	1117,67
189	WER	Transcription factor WER	MSTRG.9637.1	MSTRG.9637	1,81	44,33	163,00

190	GATA9	GATA transcription factor 9	MSTRG.31632.1	MSTRG.31632	1,82	143,67	543,00
191	AIL5	AP2-like ethylene-responsive transcription factor AIL5	MSTRG.5649.1	MSTRG.5649	1,87	115,00	433,00
192	CRF1	Ethylene-responsive transcription factor CRF1	MSTRG.35210.1	MSTRG.35210	1,89	112,00	438,67
193	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25340.1	MSTRG.25340	1,94	47,67	187,33
194	PRE3	Transcription factor PRE3	MSTRG.25650.1	MSTRG.25650	2,11	106,00	479,67
195,00	MYB77	Transcription factor MYB77	MSTRG.32755.1	MSTRG.32755	2,11	105,00	468,00
196,00	MYB77	Transcription factor MYB77	MSTRG.32755.2	MSTRG.32755	2,11	105,00	468,00
197	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.1	MSTRG.467	2,14	110,00	512,33
198	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.2	MSTRG.467	2,14	110,00	512,33
199	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.3	MSTRG.467	2,14	110,00	512,33
200	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.4	MSTRG.467	2,14	110,00	512,33
201	AIL6	AP2-like ethylene-responsive transcription factor AIL6	MSTRG.16268.1	MSTRG.16268	2,18	499,33	2395,33
202	AIL7	AP2-like ethylene-responsive transcription factor AIL7	MSTRG.16268.2	MSTRG.16268	2,18	499,33	2395,33
203	TCP8	Transcription factor TCP8	MSTRG.19238.1	MSTRG.19238	2,20	4,33	21,33
204	HEC1	Transcription factor HEC1	MSTRG.2749.1	MSTRG.2749	2,21	19,67	93,33
205	HEC1	Transcription factor HEC1	MSTRG.2749.2	MSTRG.2749	2,21	19,67	93,33
206	HSFB1	Heat stress transcription factor B-1	MSTRG.12950.1	MSTRG.12950	2,22	36,67	172,33
207	GAT22	Putative GATA transcription factor 22	MSTRG.2559.1	MSTRG.2559	2,33	19,00	98,00
208	BH087	Transcription factor bHLH87	MSTRG.33264.1	MSTRG.33264	2,37	13,67	72,67
209	BH087	Transcription factor bHLH87	MSTRG.33264.2	MSTRG.33264	2,37	13,67	72,67
210	HFB4B	Heat stress transcription factor B-4b	MSTRG.1031.1	MSTRG.1031	2,42	132,33	751,67
211	GTL2	Trihelix transcription factor GTL2	MSTRG.8422.1	MSTRG.8422	2,47	178,67	1035,00
212	GTL2	Trihelix transcription factor GTL2	MSTRG.8422.2	MSTRG.8422	2,47	178,67	1035,00

213	BH041	Putative transcription factor bHLH041	MSTRG.5733.1	MSTRG.5733	2,47	3,33	19,33
214	BH041	Putative transcription factor bHLH041	MSTRG.5733.2	MSTRG.5733	2,47	3,33	19,33
215	WRK71	WRKY transcription factor 71	MSTRG.4627.1	MSTRG.4627	2,54	9,00	54,33
216	WRK71	WRKY transcription factor 71	MSTRG.4627.2	MSTRG.4627	2,54	9,00	54,33
217	BH096	Transcription factor bHLH96	MSTRG.8073.1	MSTRG.8073	2,56	157,00	958,67
218	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.6801.1	MSTRG.6801	2,57	188,67	1169,33
219	TCP8	Transcription factor TCP8	MSTRG.21111.1	MSTRG.21111	2,64	148,67	978,00
220	BH093	Transcription factor bHLH93	MSTRG.31564.1	MSTRG.31564	2,73	144,67	981,33
221	MY123	Transcription factor MYB123	MSTRG.1827.1	MSTRG.1827	3,00	10,33	85,67
222	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.28028.1	MSTRG.28028	3,01	64,33	542,67
223	MYB2	Transcription factor MYB1	MSTRG.3779.1	MSTRG.3779	3,02	28,33	239,00
224	MYB2	Transcription factor MYB1	MSTRG.3779.2	MSTRG.3779	3,02	28,33	239,00
225	MYB2	Transcription factor MYB1	MSTRG.3779.3	MSTRG.3779	3,02	28,33	239,00
226	MYB15	Transcription factor MYB15	MSTRG.24690.1	MSTRG.24690	3,13	28,33	253,00
227	MYB2	Transcription factor MYB1	MSTRG.5581.1	MSTRG.5581	3,26	94,67	922,67
228	MYB2	Transcription factor MYB1	MSTRG.5581.2	MSTRG.5581	3,26	94,67	922,67
229	MYB2	Transcription factor MYB1	MSTRG.5581.3	MSTRG.5581	3,26	94,67	922,67
230	MYB2	Transcription factor MYB1	MSTRG.5581.4	MSTRG.5581	3,26	94,67	922,67
231	MYB2	Transcription factor MYB1	MSTRG.5581.5	MSTRG.5581	3,26	94,67	922,67
232	ERF22	Ethylene-responsive transcription factor ERF022	MSTRG.23479.1	MSTRG.23479	3,27	1,67	16,33
233	BH096	Transcription factor bHLH96	MSTRG.11440.1	MSTRG.11440	3,43	4,67	50,67
234	MYB4	Transcription factor MYB4	MSTRG.33492.1	MSTRG.33492	3,58	3,67	46,33
235	PRE6	Transcription factor PRE6	MSTRG.23961.1	MSTRG.23961	3,65	84,33	1123,67
236	BH061	Transcription factor bHLH61	MSTRG.22938.1	MSTRG.22938	3,94	29,67	473,67
237	ERF99	Ethylene-responsive transcription factor 13	MSTRG.10673.1	MSTRG.10673	4,15	4,33	79,67
238	ERF99	Ethylene-responsive transcription factor 13	MSTRG.10673.2	MSTRG.10673	4,15	4,33	79,67
239	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.34676.1	MSTRG.34676	4,53	4,00	94,00

240	RAV1	AP2/ERF and B3 domain-containing transcription factor RAV1	MSTRG.1319.1	MSTRG.1319	4,55	1,33	31,33
241	BH096	Transcription factor bHLH96	MSTRG.29985.1	MSTRG.29985	4,56	17,67	432,67
242	MY123	Transcription factor MYB123	MSTRG.3781.1	MSTRG.3781	4,87	0,33	11,00
243	WIN1	Ethylene-responsive transcription factor WIN1	MSTRG.6626.1	MSTRG.6626	5,02	0,67	22,33
244	MY113	Transcription factor MYB113	MSTRG.1796.1	MSTRG.1796	5,03	0,00	6,33
245	BH146	Transcription factor bHLH146	MSTRG.27597.1	MSTRG.27597	5,45	0,67	30,00
246	WER	Transcription factor WER	MSTRG.20889.1	MSTRG.20889	6,04	0,33	24,67
247	MYB2	Transcription factor MYB1	MSTRG.5586.1	MSTRG.5586	6,07	2,67	177,67
248	ABI4	Ethylene-responsive transcription factor ABI4	MSTRG.21719.1	MSTRG.21719	10,02	0,00	200,33
249	ABI4	Ethylene-responsive transcription factor ABI4	MSTRG.21719.2	MSTRG.21719	10,02	0,00	200,33

LTR vs. LLR

No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	LLR Genes Results	LTR Genes Results
250	NFYB4	Nuclear transcription factor Y subunit B-4	MSTRG.7981.1	MSTRG.7981	-9,38	148,67	0,00
251	NFYB4	Nuclear transcription factor Y subunit B-4	MSTRG.7602.1	MSTRG.7602	-9,21	131,33	0,00
252	MOF1	Myb family transcription factor MOF1	MSTRG.21728.1	MSTRG.21728	-8,81	100,00	0,00
253	WRK56	Probable WRKY transcription factor 56	MSTRG.32004.1	MSTRG.32004	-8,60	170,00	0,33
254	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.1	MSTRG.18391	-8,06	541,33	1,67
255	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.2	MSTRG.18391	-8,06	541,33	1,67
256	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.3	MSTRG.18391	-8,06	541,33	1,67
257	NFYAA	Nuclear transcription factor Y subunit A-10	MSTRG.18391.4	MSTRG.18391	-8,06	541,33	1,67
258	ORG2	Transcription factor ORG2	MSTRG.13172.1	MSTRG.13172	-7,73	690,00	2,67
259	ORG2	Transcription factor ORG2	MSTRG.13172.2	MSTRG.13172	-7,73	690,00	2,67
260	MYB93	Transcription factor MYB93	MSTRG.3372.1	MSTRG.3372	-7,15	230,67	1,33
261	TCP2	Transcription factor TCP2	MSTRG.21778.1	MSTRG.21778	-7,10	2112,33	12,67
262	TCP2	Transcription factor TCP2	MSTRG.21778.2	MSTRG.21778	-7,10	2112,33	12,67
263	TCP2	Transcription factor TCP2	MSTRG.21778.3	MSTRG.21778	-7,10	2112,33	12,67

264	TCP2	Transcription factor TCP2	MSTRG.21778.4	MSTRG.21778	-7,10	2112,33	12,67
265	TCP2	Transcription factor TCP2	MSTRG.21778.5	MSTRG.21778	-7,10	2112,33	12,67
266	TCP2	Transcription factor TCP2	MSTRG.21778.6	MSTRG.21778	-7,10	2112,33	12,67
267	HYH	Transcription factor HY5-like	MSTRG.15354.1	MSTRG.15354	-7,09	30,67	0,00
268	WRK43	Probable WRKY transcription factor 43	MSTRG.11159.1	MSTRG.11159	-6,80	766,33	5,67
269	MYB52	Transcription factor MYB52	MSTRG.24374.1	MSTRG.24374	-6,79	48,33	0,33
270	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.1	MSTRG.5571	-6,78	178,00	1,33
271	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.2	MSTRG.5571	-6,78	178,00	1,33
272	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.5571.3	MSTRG.5571	-6,78	178,00	1,33
273	RAX3	Transcription factor RAX3	MSTRG.2669.1	MSTRG.2669	-6,58	76,67	0,67
274	GAT22	Putative GATA transcription factor 22	MSTRG.5711.1	MSTRG.5711	-6,58	21,67	0,00
275	ORG2	Transcription factor ORG2	MSTRG.20832.1	MSTRG.20832	-6,26	33,33	0,33
276	UNE10	Transcription factor UNE10	MSTRG.26111.1	MSTRG.26111	-6,16	16,00	0,00
277	MYB61	Transcription factor MYB61	MSTRG.32874.1	MSTRG.32874	-6,00	105,67	1,33
278	MYB26	Transcription factor MYB26	MSTRG.32874.2	MSTRG.32874	-6,00	105,67	1,33
279	MYB59	Transcription factor MYB59	MSTRG.347.1	MSTRG.347	-5,93	13,67	0,00
280	BH120	Transcription factor bHLH120	MSTRG.31548.1	MSTRG.31548	-5,84	25,00	0,33
281	BH111	Transcription factor bHLH111	MSTRG.9033.1	MSTRG.9033	-5,62	2404,00	40,00
282	BH111	Transcription factor bHLH111	MSTRG.9033.2	MSTRG.9033	-5,62	2404,00	40,00
283	BH111	Transcription factor bHLH111	MSTRG.9033.3	MSTRG.9033	-5,62	2404,00	40,00
284	BH111	Transcription factor bHLH111	MSTRG.9033.4	MSTRG.9033	-5,62	2404,00	40,00
285	BH111	Transcription factor bHLH111	MSTRG.9033.5	MSTRG.9033	-5,62	2404,00	40,00
286	BH111	Transcription factor bHLH111	MSTRG.9033.6	MSTRG.9033	-5,62	2404,00	40,00
287	BH111	Transcription factor bHLH111	MSTRG.9033.7	MSTRG.9033	-5,62	2404,00	40,00
288	NFYB5	Nuclear transcription factor Y subunit B-5	MSTRG.31092.1	MSTRG.31092	-5,28	266,33	5,67
289	NFYB5	Nuclear transcription factor Y subunit B-5	MSTRG.31092.2	MSTRG.31092	-5,28	266,33	5,67
290	MY102	Transcription factor MYB102	MSTRG.21375.1	MSTRG.21375	-5,24	31,00	0,67
291	MYB86	Transcription factor MYB86	MSTRG.27862.1	MSTRG.27862	-5,21	76,00	1,67
292	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.11938.1	MSTRG.11938	-4,98	615,33	16,00
293	NFYA3	Nuclear transcription factor Y subunit A-3	MSTRG.11938.2	MSTRG.11938	-4,98	615,33	16,00

294	BZIP2	bZIP transcription factor 2	MSTRG.16355.1	MSTRG.16355	-4,71	2647,00	82,67
295	IPN2	Myb family transcription factor IPN2	MSTRG.11369.1	MSTRG.11369	-4,40	153,67	6,00
296	IPN2	Myb family transcription factor IPN2	MSTRG.11369.2	MSTRG.11369	-4,40	153,67	6,00
297	IPN2	Myb family transcription factor IPN2	MSTRG.11369.3	MSTRG.11369	-4,40	153,67	6,00
298	IPN2	Myb family transcription factor IPN2	MSTRG.11369.4	MSTRG.11369	-4,40	153,67	6,00
299	MYB48	Transcription factor MYB48	MSTRG.346.1	MSTRG.346	-4,34	175,00	7,00
300	TCP13	Transcription factor TCP13	MSTRG.8313.1	MSTRG.8313	-4,34	74,00	3,00
301	DIV	Transcription factor DIVARICATA	MSTRG.22698.1	MSTRG.22698	-4,31	830,00	34,33
302	DIV	Transcription factor DIVARICATA	MSTRG.22698.2	MSTRG.22698	-4,31	830,00	34,33
303	AP2L1	AP2-like ethylene-responsive transcription factor At1g16060	MSTRG.7763.1	MSTRG.7763	-4,29	64,33	2,67
304	AP2L1	AP2-like ethylene-responsive transcription factor At1g16060	MSTRG.7763.2	MSTRG.7763	-4,29	64,33	2,67
305	AP2L1	AP2-like ethylene-responsive transcription factor At1g16060	MSTRG.7763.3	MSTRG.7763	-4,29	64,33	2,67
306	TCP3	Transcription factor TCP3	MSTRG.21481.1	MSTRG.21481	-4,26	920,33	39,67
307	TCP3	Transcription factor TCP3	MSTRG.21481.2	MSTRG.21481	-4,26	920,33	39,67
308	TCP3	Transcription factor TCP3	MSTRG.21481.3	MSTRG.21481	-4,26	920,33	39,67
309	MYB52	Transcription factor MYB52	MSTRG.26728.1	MSTRG.26728	-4,17	219,67	10,00
310	TGA10	bZIP transcription factor TGA10	MSTRG.18034.1	MSTRG.18034	-4,14	2332,33	108,67
311	NFYB3	Nuclear transcription factor Y subunit B-3	MSTRG.5885.1	MSTRG.5885	-4,09	138,00	6,67
312	WRK74	Probable WRKY transcription factor 74	MSTRG.21830.1	MSTRG.21830	-4,01	587,33	30,67
313	WRK74	Probable WRKY transcription factor 74	MSTRG.21830.2	MSTRG.21830	-4,01	587,33	30,67
314	NFYA1	Nuclear transcription factor Y subunit A-1	MSTRG.4176.1	MSTRG.4176	-3,97	1813,67	96,33
315	MYB93	Transcription factor MYB93	MSTRG.29975.1	MSTRG.29975	-3,95	89,33	4,67
316	BH030	Transcription factor bHLH30	MSTRG.13027.1	MSTRG.13027	-3,81	4250,33	248,00
317	LHWL1	Transcription factor EMB1444	MSTRG.18533.1	MSTRG.18533	-3,81	17005,00	993,67
318	MYB93	Transcription factor MYB93	MSTRG.17206.1	MSTRG.17206	-3,78	409,67	24,00
319	BH160	Transcription factor bHLH160	MSTRG.35374.1	MSTRG.35374	-3,71	53,00	3,33
320	BH160	Transcription factor bHLH160	MSTRG.35374.2	MSTRG.35374	-3,71	53,00	3,33

321	BH160	Transcription factor bHLH160	MSTRG.35374.3	MSTRG.35374	-3,71	53,00	3,33
322	BH160	Transcription factor bHLH160	MSTRG.35374.4	MSTRG.35374	-3,71	53,00	3,33
323	BH160	Transcription factor bHLH160	MSTRG.35374.5	MSTRG.35374	-3,71	53,00	3,33
324	BH112	Transcription factor bHLH112	MSTRG.14135.1	MSTRG.14135	-3,69	873,33	55,33
325	BH112	Transcription factor bHLH112	MSTRG.14135.2	MSTRG.14135	-3,69	873,33	55,33
326	MYB93	Transcription factor MYB93	MSTRG.24195.1	MSTRG.24195	-3,63	303,67	20,00
327	ERF11	Ethylene-responsive transcription factor ERF011	MSTRG.2732.1	MSTRG.2732	-3,51	1047,00	76,33
328	ODO1	MYB-like transcription factor ODO1	MSTRG.24008.1	MSTRG.24008	-3,47	175,33	13,00
329	TGA9	Transcription factor TGA9	MSTRG.6736.1	MSTRG.6736	-3,44	5423,00	409,67
330	TGA9	Transcription factor TGA9	MSTRG.6736.2	MSTRG.6736	-3,44	5423,00	409,67
331	TGA9	Transcription factor TGA9	MSTRG.6736.3	MSTRG.6736	-3,44	5423,00	409,67
332	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.33443.1	MSTRG.33443	-3,44	26,33	2,00
333	WRK12	Probable WRKY transcription factor 12	MSTRG.10638.1	MSTRG.10638	-3,38	17,00	1,33
334	KUA1	Transcription factor KUA1	MSTRG.2485.1	MSTRG.2485	-3,37	146,00	11,67
335	WRKY6	WRKY transcription factor 6	MSTRG.20348.1	MSTRG.20348	-3,36	584,33	47,00
336	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.33457.1	MSTRG.33457	-3,35	823,67	65,67
337	PAR2	Transcription factor PAR2	MSTRG.5275.1	MSTRG.5275	-3,34	12,00	1,00
338	PHL5	Myb family transcription factor PHL5	MSTRG.18049.1	MSTRG.18049	-3,32	258,67	21,33
339	PHL5	Myb family transcription factor PHL5	MSTRG.18049.2	MSTRG.18049	-3,32	258,67	21,33
340	PHL5	Myb family transcription factor PHL5	MSTRG.18049.3	MSTRG.18049	-3,32	258,67	21,33
341	PHL5	Myb family transcription factor PHL5	MSTRG.18049.4	MSTRG.18049	-3,32	258,67	21,33
342	PHL5	Myb family transcription factor PHL5	MSTRG.13735.1	MSTRG.13735	-3,32	73,33	6,00
343	MYBS3	Transcription factor MYBS3	MSTRG.5695.1	MSTRG.5695	-3,30	95,00	8,00
344	ERF10	Ethylene-responsive transcription factor ERF010	MSTRG.16619.1	MSTRG.16619	-3,26	240,33	20,67
345	MYB26	Transcription factor MYB26	MSTRG.31161.1	MSTRG.31161	-3,23	71,00	6,00
346	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.24071.1	MSTRG.24071	-3,18	1884,67	174,00
347	HYH	Transcription factor HY5-like	MSTRG.15305.1	MSTRG.15305	-3,13	14,00	1,33
348	ASIL2	Trihelix transcription factor ASIL2	MSTRG.3056.1	MSTRG.3056	-3,11	1781,67	170,33
349	NFYB5	Nuclear transcription factor Y subunit B-5	MSTRG.34546.1	MSTRG.34546	-3,10	80,33	7,67

350	MYB59	Transcription factor MYB59	MSTRG.13004.1	MSTRG.13004	-3,09	3743,67	363,67
351	MYB48	Transcription factor MYB48	MSTRG.13004.2	MSTRG.13004	-3,09	3743,67	363,67
352	MYB48	Transcription factor MYB48	MSTRG.13004.3	MSTRG.13004	-3,09	3743,67	363,67
353	NFYC4	Nuclear transcription factor Y subunit C-4	MSTRG.32241.1	MSTRG.32241	-2,93	55,33	6,00
354	BH154	Transcription factor bHLH154	MSTRG.22604.1	MSTRG.22604	-2,92	57,00	6,33
355	BH123	Transcription factor bHLH123	MSTRG.22604.2	MSTRG.22604	-2,92	57,00	6,33
356	BH123	Transcription factor bHLH123	MSTRG.22604.3	MSTRG.22604	-2,92	57,00	6,33
357	BH123	Transcription factor bHLH123	MSTRG.22604.4	MSTRG.22604	-2,92	57,00	6,33
358	WRK18	WRKY transcription factor 18	MSTRG.12932.1	MSTRG.12932	-2,92	105,33	11,67
359	WRK18	WRKY transcription factor 18	MSTRG.12932.2	MSTRG.12932	-2,92	105,33	11,67
360	WRK40	Probable WRKY transcription factor 40	MSTRG.12932.3	MSTRG.12932	-2,92	105,33	11,67
361	ODO1	MYB-like transcription factor ODO1	MSTRG.30090.1	MSTRG.30090	-2,87	398,67	45,00
362	NFYB3	Nuclear transcription factor Y subunit B-3	MSTRG.20204.1	MSTRG.20204	-2,81	37,33	4,33
363	NFYB3	Nuclear transcription factor Y subunit B-3	MSTRG.20204.2	MSTRG.20204	-2,81	37,33	4,33
364	BH123	Transcription factor bHLH123	MSTRG.20606.1	MSTRG.20606	-2,79	446,33	53,00
365	BH123	Transcription factor bHLH123	MSTRG.20606.2	MSTRG.20606	-2,79	446,33	53,00
366	BH123	Transcription factor bHLH123	MSTRG.20606.3	MSTRG.20606	-2,79	446,33	53,00
367	NAC56	NAC transcription factor 56	MSTRG.28986.1	MSTRG.28986	-2,77	29,67	3,67
368	MYB27	Transcription factor MYB27	MSTRG.25709.1	MSTRG.25709	-2,74	21,33	2,67
369	ERF53	Ethylene-responsive transcription factor ERF053	MSTRG.21403.1	MSTRG.21403	-2,72	1010,33	125,67
370	MB3R5	Transcription factor MYB3R-5	MSTRG.30355.1	MSTRG.30355	-2,72	85,67	10,67
371	MB3R5	Transcription factor MYB3R-5	MSTRG.30355.2	MSTRG.30355	-2,72	85,67	10,67
372	RAX3	Transcription factor RAX3	MSTRG.25191.1	MSTRG.25191	-2,70	303,33	38,33
373	IBH1	Transcription factor IBH1	MSTRG.16011.1	MSTRG.16011	-2,67	213,00	27,33
374	IBH1	Transcription factor IBH1	MSTRG.16011.2	MSTRG.16011	-2,67	213,00	27,33
375	HFA4B	Heat stress transcription factor A-4b	MSTRG.14253.1	MSTRG.14253	-2,65	198,00	25,67
376	BH051	Transcription factor bHLH51	MSTRG.21715.1	MSTRG.21715	-2,65	80,33	10,67
377	WK72A	WRKY transcription factor 72A	MSTRG.25671.1	MSTRG.25671	-2,61	806,33	108,33
378	WK72A	WRKY transcription factor 72A	MSTRG.25671.2	MSTRG.25671	-2,61	806,33	108,33
379	WRKY7	Probable WRKY transcription factor 7	MSTRG.2713.1	MSTRG.2713	-2,60	1450,67	197,33

380	ILR3	Transcription factor ILR3	MSTRG.32423.1	MSTRG.32423	-2,58	441,67	62,33
381	ILR3	Transcription factor ILR3	MSTRG.32423.2	MSTRG.32423	-2,58	441,67	62,33
382	EF109	Ethylene-responsive transcription factor ERF109	MSTRG.28648.1	MSTRG.28648	-2,58	21,33	3,00
383	UNE10	Transcription factor UNE10	MSTRG.15488.1	MSTRG.15488	-2,56	144,00	19,67
384	UNE10	Transcription factor UNE10	MSTRG.15488.2	MSTRG.15488	-2,56	144,00	19,67
385	MYB2	Transcription factor MYB2	MSTRG.30419.1	MSTRG.30419	-2,54	112,00	15,67
386	PIL15	Transcription factor PHYTOCHROME INTERACTING FACTOR-LIKE 15	MSTRG.34248.1	MSTRG.34248	-2,54	32,67	4,67
387	RAX3	Transcription factor RAX3	MSTRG.4329.1	MSTRG.4329	-2,53	888,67	126,33
388	NFYA1	Nuclear transcription factor Y subunit A-1	MSTRG.308.1	MSTRG.308	-2,53	1249,00	180,33
389	LAF1	Transcription factor LAF1	MSTRG.23733.1	MSTRG.23733	-2,52	827,33	118,33
390	PHL5	Myb family transcription factor PHL5	MSTRG.19446.1	MSTRG.19446	-2,47	97,33	14,33
391	NFYC9	Nuclear transcription factor Y subunit C-9	MSTRG.14629.1	MSTRG.14629	-2,46	4474,33	664,00
392	NAC56	NAC transcription factor 56	MSTRG.20722.1	MSTRG.20722	-2,42	478,00	73,67
393	WRK22	WRKY transcription factor 22	MSTRG.11161.1	MSTRG.11161	-2,41	613,67	95,00
394	MYB46	Transcription factor MYB46	MSTRG.15784.1	MSTRG.15784	-2,40	84,00	13,00
395	BH130	Transcription factor bHLH130	MSTRG.10310.1	MSTRG.10310	-2,39	375,00	59,00
396	TCP9	Transcription factor TCP9	MSTRG.22039.1	MSTRG.22039	-2,38	711,00	112,00
397	MYB15	Transcription factor MYB15	MSTRG.2089.1	MSTRG.2089	-2,37	154,33	24,33
398	BH068	Transcription factor bHLH68	MSTRG.12478.1	MSTRG.12478	-2,37	2636,33	419,33
399	BH068	Transcription factor bHLH68	MSTRG.12478.2	MSTRG.12478	-2,37	2636,33	419,33
400	BH068	Transcription factor bHLH68	MSTRG.12478.3	MSTRG.12478	-2,37	2636,33	419,33
401	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.32459.1	MSTRG.32459	-2,34	3323,67	539,00
402	WRK75	Probable WRKY transcription factor 75	MSTRG.29989.1	MSTRG.29989	-2,33	22,33	3,67
403	PHL5	Myb family transcription factor PHL5	MSTRG.18051.1	MSTRG.18051	-2,31	164,67	27,33
404	VRN1	B3 domain-containing transcription factor VRN1	MSTRG.24276.1	MSTRG.24276	-2,31	26,00	4,33
405	PHL6	Myb family transcription factor PHL6	MSTRG.27626.1	MSTRG.27626	-2,29	299,33	50,33
406	PHL6	Myb family transcription factor PHL6	MSTRG.27626.2	MSTRG.27626	-2,29	299,33	50,33
407	PHL6	Myb family transcription factor PHL6	MSTRG.27626.3	MSTRG.27626	-2,29	299,33	50,33

408	FIT	Transcription factor FER-LIKE IRON DEFICIENCY-INDUCED TRANSCRIPTION FACTOR	MSTRG.895.1	MSTRG.895	-2,25	1953,67	338,67
409	ERF38	Ethylene-responsive transcription factor ERF038	MSTRG.16468.1	MSTRG.16468	-2,25	302,33	51,33
410	HSFA3	Heat stress transcription factor A-3	MSTRG.19355.1	MSTRG.19355	-2,24	65,00	11,33
411	HSFA3	Heat stress transcription factor A-3	MSTRG.19355.2	MSTRG.19355	-2,24	65,00	11,33
412	HSFA3	Heat stress transcription factor A-3	MSTRG.19355.3	MSTRG.19355	-2,24	65,00	11,33
413	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.26257.1	MSTRG.26257	-2,23	202,67	35,67
414	ERF86	Ethylene-responsive transcription factor ERF086	MSTRG.24331.1	MSTRG.24331	-2,22	55,00	9,67
415	CRL5	AP2-like ethylene-responsive transcription factor CRL5	MSTRG.16361.1	MSTRG.16361	-2,18	533,00	97,33
416	CRL5	AP2-like ethylene-responsive transcription factor CRL5	MSTRG.16361.2	MSTRG.16361	-2,18	533,00	97,33
417	CRL5	AP2-like ethylene-responsive transcription factor CRL5	MSTRG.16361.3	MSTRG.16361	-2,18	533,00	97,33
418	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.1	MSTRG.3750	-2,15	1367,33	256,33
419	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.2	MSTRG.3750	-2,15	1367,33	256,33
420	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.3	MSTRG.3750	-2,15	1367,33	256,33
421	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.4	MSTRG.3750	-2,15	1367,33	256,33
422	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.3750.5	MSTRG.3750	-2,15	1367,33	256,33
423	TGA7	Transcription factor TGA7	MSTRG.31376.1	MSTRG.31376	-2,14	2016,67	376,00
424	MYB36	Transcription factor MYB36	MSTRG.19503.1	MSTRG.19503	-2,14	2123,33	396,67
425	MYB36	Transcription factor MYB36	MSTRG.19503.2	MSTRG.19503	-2,14	2123,33	396,67
426	EBIII	MYB-like transcription factor 4	MSTRG.21876.1	MSTRG.21876	-2,11	143,33	27,00
427	MY111	Transcription factor MYB111	MSTRG.21876.2	MSTRG.21876	-2,11	143,33	27,00
428	WRKY1	WRKY transcription factor 1	MSTRG.21093.1	MSTRG.21093	-2,10	1452,33	279,00
429	WRK46	WRKY transcription factor SUSIBA2	MSTRG.21093.2	MSTRG.21093	-2,10	1452,33	279,00
430	WRKY1	WRKY transcription factor 1	MSTRG.21093.3	MSTRG.21093	-2,10	1452,33	279,00

431	WRKY1	WRKY transcription factor 1	MSTRG.21093.4	MSTRG.21093	-2,10	1452,33	279,00
432	HSFB3	Heat stress transcription factor B-3	MSTRG.17389.1	MSTRG.17389	-2,08	334,00	65,33
433	ILR3	Transcription factor ILR3	MSTRG.14109.1	MSTRG.14109	-2,07	1189,00	235,33
434	ILR3	Transcription factor ILR3	MSTRG.14109.2	MSTRG.14109	-2,07	1189,00	235,33
435	ILR3	Transcription factor ILR3	MSTRG.14109.3	MSTRG.14109	-2,07	1189,00	235,33
436	ILR3	Transcription factor ILR3	MSTRG.14109.4	MSTRG.14109	-2,07	1189,00	235,33
437	TGA1	Transcription factor TGA1	MSTRG.16154.1	MSTRG.16154	-2,06	3269,67	647,33
438	TGA1	Transcription factor TGA1	MSTRG.16154.2	MSTRG.16154	-2,06	3269,67	647,33
439	HFA4A	Heat stress transcription factor A-4a	MSTRG.13140.1	MSTRG.13140	-2,06	1474,00	290,33
440	WRK72	Probable WRKY transcription factor 72	MSTRG.4599.1	MSTRG.4599	-2,04	1218,67	245,33
441	WRK14	Probable WRKY transcription factor 14	MSTRG.13688.1	MSTRG.13688	-2,03	1984,67	401,00
442	IPN2	Myb family transcription factor IPN2	MSTRG.32764.1	MSTRG.32764	-2,02	268,00	54,33
443	IPN2	Myb family transcription factor IPN2	MSTRG.32764.2	MSTRG.32764	-2,02	268,00	54,33
444	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.1	MSTRG.30184	-2,02	692,00	140,00
445	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.2	MSTRG.30184	-2,02	692,00	140,00
446	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.3	MSTRG.30184	-2,02	692,00	140,00
447	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.4	MSTRG.30184	-2,02	692,00	140,00
448	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.5	MSTRG.30184	-2,02	692,00	140,00
449	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.6	MSTRG.30184	-2,02	692,00	140,00
450	ERF5	Ethylene-responsive transcription factor 5	MSTRG.30184.7	MSTRG.30184	-2,02	692,00	140,00
451	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.8	MSTRG.30184	-2,02	692,00	140,00
452	MYB36	Transcription factor MYB36	MSTRG.7134.1	MSTRG.7134	-2,01	622,00	125,00
453	MY102	Transcription factor MYB102	MSTRG.14278.1	MSTRG.14278	-2,01	151,33	31,33
454	WRKY3	Probable WRKY transcription factor 3	MSTRG.6266.1	MSTRG.6266	-2,01	207,00	42,00
455	BH035	Transcription factor bHLH35	MSTRG.5369.1	MSTRG.5369	-1,98	1699,67	354,00
456	TCP20	Transcription factor TCP20	MSTRG.9215.1	MSTRG.9215	-1,97	601,33	126,33
457	TCP20	Transcription factor TCP20	MSTRG.9215.2	MSTRG.9215	-1,97	601,33	126,33
458	TCP20	Transcription factor TCP20	MSTRG.9215.3	MSTRG.9215	-1,97	601,33	126,33
459	TCP20	Transcription factor TCP20	MSTRG.9215.4	MSTRG.9215	-1,97	601,33	126,33
460	TCP20	Transcription factor TCP20	MSTRG.9215.5	MSTRG.9215	-1,97	601,33	126,33

461	TCP20	Transcription factor TCP20	MSTRG.9215.6	MSTRG.9215	-1,97	601,33	126,33
462	PHL8	Myb family transcription factor PHL8	MSTRG.15885.1	MSTRG.15885	-1,94	216,67	46,33
463	PHL8	Myb family transcription factor PHL8	MSTRG.15885.2	MSTRG.15885	-1,94	216,67	46,33
464	MYB36	Transcription factor MYB36	MSTRG.919.1	MSTRG.919	-1,90	821,00	179,67
465	WRKY4	Probable WRKY transcription factor 4	MSTRG.6267.1	MSTRG.6267	-1,89	120,33	26,67
466	PTL	Trihelix transcription factor PTL	MSTRG.19364.1	MSTRG.19364	-1,87	83,67	19,00
467	RAP24	Ethylene-responsive transcription factor RAP2-4	MSTRG.17263.1	MSTRG.17263	-1,86	12995,00	2960,00
468	MY113	Transcription factor MYB113	MSTRG.1431.1	MSTRG.1431	-1,86	21,00	4,67
469	MYB75	Transcription factor MYB75	MSTRG.1431.2	MSTRG.1431	-1,86	21,00	4,67
470	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.1	MSTRG.544	-1,84	273,67	62,00
471	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.2	MSTRG.544	-1,84	273,67	62,00
472	WRK27	Probable WRKY transcription factor 27	MSTRG.21919.1	MSTRG.21919	-1,83	534,33	125,00
473	WRK27	Probable WRKY transcription factor 27	MSTRG.21919.2	MSTRG.21919	-1,83	534,33	125,00
474	MY102	Transcription factor MYB102	MSTRG.13316.1	MSTRG.13316	-1,83	248,67	58,00
475	PIF4	Transcription factor PIF4	MSTRG.11272.1	MSTRG.11272	-1,80	26,67	6,33
476	NAC47	NAC transcription factor 47	MSTRG.17854.1	MSTRG.17854	-1,80	170,67	41,00
477	WRK57	Probable WRKY transcription factor 57	MSTRG.21649.1	MSTRG.21649	-1,75	149,00	36,00
478	BH068	Transcription factor bHLH68	MSTRG.5234.1	MSTRG.5234	-1,75	1771,33	431,67
479	BH068	Transcription factor bHLH68	MSTRG.5234.2	MSTRG.5234	-1,75	1771,33	431,67
480	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.20674.1	MSTRG.20674	-1,75	83,33	20,33
481	WRK51	Probable WRKY transcription factor 51	MSTRG.16082.1	MSTRG.16082	-1,74	150,00	36,67
482	WRK51	Probable WRKY transcription factor 51	MSTRG.16082.2	MSTRG.16082	-1,74	150,00	36,67
483	WRK51	Probable WRKY transcription factor 51	MSTRG.16082.3	MSTRG.16082	-1,74	150,00	36,67
484	PHL6	Myb family transcription factor PHL6	MSTRG.33506.1	MSTRG.33506	-1,69	103,67	26,67
485	ASR3	Trihelix transcription factor ASR3	MSTRG.9196.1	MSTRG.9196	-1,68	398,67	101,33
486	EFM	Myb family transcription factor EFM	MSTRG.6466.1	MSTRG.6466	-1,66	241,67	62,67
487	WRK19	Probable WRKY transcription factor 19	MSTRG.28166.1	MSTRG.28166	-1,64	11921,67	3162,33
488	WRK19	Probable WRKY transcription factor 19	MSTRG.28166.2	MSTRG.28166	-1,64	11921,67	3162,33
489	BH143	Transcription factor bHLH143	MSTRG.32581.1	MSTRG.32581	-1,64	11963,00	3153,67

490	MYBF	Putative Myb family transcription factor At1g14600	MSTRG.18857.1	MSTRG.18857	-1,62	1631,67	431,33
491	HSFB1	Heat stress transcription factor B-1	MSTRG.12950.1	MSTRG.12950	-1,62	101,00	27,33
492	UNE12	Transcription factor UNE12	MSTRG.8503.1	MSTRG.8503	-1,61	1260,00	338,00
493	WRK47	Probable WRKY transcription factor 47	MSTRG.31313.1	MSTRG.31313	-1,60	1233,67	335,00
494	MYB83	Transcription factor MYB83	MSTRG.10201.1	MSTRG.10201	-1,59	60,00	16,33
495	BH106	Transcription factor bHLH106	MSTRG.7850.1	MSTRG.7850	-1,58	334,00	92,00
496	BH106	Transcription factor bHLH106	MSTRG.7850.2	MSTRG.7850	-1,58	334,00	92,00
497	DPB	Transcription factor-like protein DPB	MSTRG.19725.1	MSTRG.19725	-1,57	110,67	30,67
498	DPB	Transcription factor-like protein DPB	MSTRG.19725.2	MSTRG.19725	-1,57	110,67	30,67
499	WRK70	Probable WRKY transcription factor 70	MSTRG.22918.1	MSTRG.22918	-1,55	202,33	56,33
500	MYB88	Transcription factor MYB88	MSTRG.23953.1	MSTRG.23953	-1,55	542,00	151,67
501	MYB88	Transcription factor MYB88	MSTRG.23953.2	MSTRG.23953	-1,55	542,00	151,67
502	MYB88	Transcription factor MYB88	MSTRG.23953.3	MSTRG.23953	-1,55	542,00	151,67
503	MOF1	Myb family transcription factor MOF1	MSTRG.35373.1	MSTRG.35373	-1,55	28,33	8,00
504	MOF1	Myb family transcription factor MOF1	MSTRG.35373.2	MSTRG.35373	-1,55	28,33	8,00
505	MOF1	Myb family transcription factor MOF1	MSTRG.35373.3	MSTRG.35373	-1,55	28,33	8,00
506	MOF1	Myb family transcription factor MOF1	MSTRG.35373.4	MSTRG.35373	-1,55	28,33	8,00
507	LHWL3	Transcription factor bHLH155	MSTRG.24661.1	MSTRG.24661	-1,51	4461,33	1290,67
508	LHWL3	Transcription factor bHLH155	MSTRG.24661.2	MSTRG.24661	-1,51	4461,33	1290,67
509	IBL1	Transcription factor IBH1-like 1	MSTRG.5276.1	MSTRG.5276	1,50	136,67	317,33
510	IBL1	Transcription factor IBH1-like 1	MSTRG.5276.2	MSTRG.5276	1,50	136,67	317,33
511	BH093	Transcription factor bHLH93	MSTRG.16326.1	MSTRG.16326	1,53	641,67	1535,00
512	MYB2	Transcription factor MYB1	MSTRG.5581.1	MSTRG.5581	1,53	99,33	233,00
513	MYB2	Transcription factor MYB1	MSTRG.5581.2	MSTRG.5581	1,53	99,33	233,00
514	MYB2	Transcription factor MYB1	MSTRG.5581.3	MSTRG.5581	1,53	99,33	233,00
515	MYB2	Transcription factor MYB1	MSTRG.5581.4	MSTRG.5581	1,53	99,33	233,00
516	MYB2	Transcription factor MYB1	MSTRG.5581.5	MSTRG.5581	1,53	99,33	233,00
517	BH151	Transcription factor UPBEAT1	MSTRG.33941.1	MSTRG.33941	1,59	90,00	223,67
518	BH025	Transcription factor bHLH25	MSTRG.16343.1	MSTRG.16343	1,61	57,33	144,67

519	ERF34	Ethylene-responsive transcription factor ERF034	MSTRG.12338.1	MSTRG.12338	1,66	61,00	158,33
520	GAT11	GATA transcription factor 11	MSTRG.1362.1	MSTRG.1362	1,75	554,00	1532,67
521	GAT11	GATA transcription factor 11	MSTRG.1362.2	MSTRG.1362	1,75	554,00	1532,67
522	GATA8	GATA transcription factor 8	MSTRG.1362.3	MSTRG.1362	1,75	554,00	1532,67
523	GTL1	Trihelix transcription factor GTL1	MSTRG.4360.1	MSTRG.4360	1,77	1356,67	3813,67
524	GTL1	Trihelix transcription factor GTL1	MSTRG.4360.2	MSTRG.4360	1,77	1356,67	3813,67
525	KAN4	Probable transcription factor KAN4	MSTRG.2851.1	MSTRG.2851	1,79	8,67	24,67
526	MYB77	Transcription factor MYB77	MSTRG.32755.1	MSTRG.32755	1,93	88,33	275,00
527	MYB77	Transcription factor MYB77	MSTRG.32755.2	MSTRG.32755	1,93	88,33	275,00
528	TCP8	Transcription factor TCP8	MSTRG.19238.1	MSTRG.19238	1,94	5,67	17,67
529	MYB2	Transcription factor MYB1	MSTRG.3779.1	MSTRG.3779	1,95	33,67	103,33
530	MYB2	Transcription factor MYB1	MSTRG.3779.2	MSTRG.3779	1,95	33,67	103,33
531	MYB2	Transcription factor MYB1	MSTRG.3779.3	MSTRG.3779	1,95	33,67	103,33
532	BBM	AP2-like ethylene-responsive transcription factor BBM	MSTRG.1135.1	MSTRG.1135	2,01	399,67	1306,00
533	BBM	AP2-like ethylene-responsive transcription factor BBM	MSTRG.1135.2	MSTRG.1135	2,01	399,67	1306,00
534	BBM	AP2-like ethylene-responsive transcription factor BBM	MSTRG.1135.3	MSTRG.1135	2,01	399,67	1306,00
535	BH094	Transcription factor BHLH094	MSTRG.33538.1	MSTRG.33538	2,02	309,33	1025,00
536	CRF4	Ethylene-responsive transcription factor CRF4	MSTRG.23591.1	MSTRG.23591	2,08	75,00	257,00
537	GAT22	Putative GATA transcription factor 22	MSTRG.2559.1	MSTRG.2559	2,09	18,33	64,00
538	HSFB4	Heat stress transcription factor B-4	MSTRG.2747.1	MSTRG.2747	2,12	177,00	621,00
539	CRF1	Ethylene-responsive transcription factor CRF1	MSTRG.35210.1	MSTRG.35210	2,22	130,33	493,00
540	MYB73	Transcription factor MYB73	MSTRG.28397.1	MSTRG.28397	2,36	99,67	419,67
541	BH096	Transcription factor bHLH96	MSTRG.2645.1	MSTRG.2645	2,42	457,00	2013,00
542	BH096	Transcription factor bHLH96	MSTRG.2645.2	MSTRG.2645	2,42	457,00	2013,00
543	BH096	Transcription factor bHLH96	MSTRG.8073.1	MSTRG.8073	2,50	130,67	603,00
544	GATA9	GATA transcription factor 9	MSTRG.12389.1	MSTRG.12389	2,50	361,33	1679,33
545	AMS	Transcription factor ABORTED MICROSPORES	MSTRG.35221.1	MSTRG.35221	2,56	10,67	52,33

546	GATA2	GATA transcription factor 2	MSTRG.26685.1	MSTRG.26685	2,67	37,67	193,67
547	MYB1	Transcription factor MYB1	MSTRG.23325.1	MSTRG.23325	2,68	90,33	478,00
548	AIL6	AP2-like ethylene-responsive transcription factor AIL6	MSTRG.16268.1	MSTRG.16268	2,71	535,00	2852,33
549	AIL7	AP2-like ethylene-responsive transcription factor AIL7	MSTRG.16268.2	MSTRG.16268	2,71	535,00	2852,33
550	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.1	MSTRG.467	2,73	127,67	696,67
551	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.2	MSTRG.467	2,73	127,67	696,67
552	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.3	MSTRG.467	2,73	127,67	696,67
553	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.4	MSTRG.467	2,73	127,67	696,67
554	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.6801.1	MSTRG.6801	2,81	193,00	1101,67
555	PAR1	Transcription factor PAR1	MSTRG.21806.1	MSTRG.21806	2,81	58,33	336,67
556	GATA4	GATA transcription factor 4	MSTRG.10803.1	MSTRG.10803	2,94	75,33	468,00
557	GTL2	Trihelix transcription factor GTL2	MSTRG.8422.1	MSTRG.8422	2,99	172,67	1131,33
558	GTL2	Trihelix transcription factor GTL2	MSTRG.8422.2	MSTRG.8422	2,99	172,67	1131,33
559	GATA9	GATA transcription factor 9	MSTRG.31632.1	MSTRG.31632	3,02	127,67	845,67
560	BH093	Transcription factor bHLH93	MSTRG.31564.1	MSTRG.31564	3,10	81,33	571,67
561	BH146	Transcription factor bHLH146	MSTRG.27597.1	MSTRG.27597	3,13	6,33	45,67
562	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.34676.1	MSTRG.34676	3,15	8,33	60,33
563	HFB4B	Heat stress transcription factor B-4b	MSTRG.1031.1	MSTRG.1031	3,25	123,33	961,00
564	BH096	Transcription factor bHLH96	MSTRG.11440.1	MSTRG.11440	3,28	2,67	21,67
565	WIN1	Ethylene-responsive transcription factor WIN1	MSTRG.6626.1	MSTRG.6626	3,58	3,00	29,33
566	MY123	Transcription factor MYB123	MSTRG.1827.1	MSTRG.1827	3,65	7,33	76,00
567	PRE3	Transcription factor PRE3	MSTRG.25650.1	MSTRG.25650	3,80	76,00	870,33
568	WER	Transcription factor WER	MSTRG.20889.1	MSTRG.20889	3,88	0,67	8,33

569	RAV1	AP2/ERF and B3 domain-containing transcription factor RAV1	MSTRG.1319.1	MSTRG.1319	3,93	2,33	29,00
570	TCP8	Transcription factor TCP8	MSTRG.21111.1	MSTRG.21111	3,98	56,00	722,33
571	BH061	Transcription factor bHLH61	MSTRG.22938.1	MSTRG.22938	4,29	13,33	214,00
572	RITF1	Protein RGF1 INDUCIBLE TRANSCRIPTION FACTOR 1	MSTRG.28028.1	MSTRG.28028	4,35	39,33	650,67
573	PRE6	Transcription factor PRE6	MSTRG.23961.1	MSTRG.23961	4,49	77,33	1420,00
574	ERF81	Ethylene-responsive transcription factor 12	MSTRG.12007.1	MSTRG.12007	4,89	0,00	4,33
575	BH096	Transcription factor bHLH96	MSTRG.29985.1	MSTRG.29985	4,96	14,67	375,67
576	ABI4	Ethylene-responsive transcription factor ABI4	MSTRG.21719.1	MSTRG.21719	8,56	0,67	203,67
577	ABI4	Ethylene-responsive transcription factor ABI4	MSTRG.21719.2	MSTRG.21719	8,56	0,67	203,67

Supplementary Table 6. DEGs related to hormones identified in MTR vs. MLR and LTR vs. LLR comparisons.

MTR vs. MLR

Hormone	No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	MLR Genes Results	MTR Genes Results	Function
IAA	1	YUC2	Indole-3-pyruvate monooxygenase YUCCA2	MSTRG.6281.1	MSTRG.6281	-5,2112	187	6	Biosynthesis
	2	YUC6	Indole-3-pyruvate monooxygenase YUCCA6	MSTRG.30679.1	MSTRG.30679	-3,5704	172	19	Biosynthesis
	3	YUC10	Probable indole-3-pyruvate monooxygenase YUCCA10	MSTRG.3084.1	MSTRG.3084	3,7961	32	257	Biosynthesis
	4	YUC10	Probable indole-3-pyruvate monooxygenase YUCCA10	MSTRG.12291.1	MSTRG.12291	4,8133	16	319	Biosynthesis
	5	GH39	Putative indole-3-acetic acid-amido synthetase GH3.9	MSTRG.32140.1	MSTRG.32140	-2,8943	36	7	Conjugate synthesis
	6	GH31	Probable indole-3-acetic acid-amido synthetase GH3.1	MSTRG.16511.1	MSTRG.16511	-2,0903	514	131	Conjugate synthesis
	7	IAMT1	Indole-3-acetate O-methyltransferase 1	MSTRG.20288.1	MSTRG.20288	2,3815	21	96	Conjugate synthesis
	8	ILL1	IAA-amino acid hydrolase ILR1-like 1	MSTRG.9014.1	MSTRG.9014	-4,1824	450	45	Conjugate degradation
	9	ILR1	IAA-amino acid hydrolase ILR1	MSTRG.19241.1	MSTRG.19241	-2,0252	800	274	Conjugate degradation
	10	AB15B	ABC transporter B family member 15	MSTRG.4010.1	MSTRG.4010	-2,7268	2543	668	Transport
	11	AB9B	ABC transporter B family member 9	MSTRG.13237.1	MSTRG.13237	-2,5044	98	31	Transport
	12	AB21B	ABC transporter B family member 21	MSTRG.31320.1	MSTRG.31320	-2,1974	1160	418	Transport
	13	AB11B	ABC transporter B family member 11	MSTRG.31322.1	MSTRG.31322	-1,8567	9258	3176	Transport
	14	AB29B	ABC transporter B family member 29	MSTRG.19185.1	MSTRG.19185	-1,5476	193	75	Transport
	15	PILS3	Protein PIN-LIKES 3	MSTRG.3734.1	MSTRG.3734	1,6496	46	164	Transport
	16	PILS1	Protein PIN-LIKES 1	MSTRG.17183.1	MSTRG.17183	2,1618	17	109	Transport

17	PIN2	Auxin efflux carrier component 2	MSTRG.5844.1	MSTRG.5844	2,2286	284	1333	Transport
18	PID	Protein kinase PINOID	MSTRG.31243.1	MSTRG.31243	2,8869	38	220	Transport
19	SAU40	Auxin-responsive protein SAUR40	MSTRG.1959.1	MSTRG.1959	-6,7452	59	2	Signal transduction-related
20	SAU71	Auxin-responsive protein SAUR71	MSTRG.32207.1	MSTRG.32207	-5,9003	8	0	Signal transduction-related
21	C87A3	Cytochrome P450 87A3	MSTRG.4894.1	MSTRG.4894	-5,1444	34	0	Signal transduction-related
22	AFB3	Protein AUXIN SIGNALING F-BOX 3	MSTRG.14228.1	MSTRG.14228	-4,943	31	2	Signal transduction-related
23	ARFQ	Auxin response factor 17	MSTRG.12405.1	MSTRG.12405	-4,1832	12	0	Signal transduction-related
24	SAU72	Auxin-responsive protein SAUR72	MSTRG.19194.1	MSTRG.19194	-3,1102	17	3	Signal transduction-related
25	SAU71	Auxin-responsive protein SAUR71	MSTRG.9206.1	MSTRG.9206	-2,8056	4388	814	Signal transduction-related
26	SAU32	Auxin-responsive protein SAUR32	MSTRG.25422.1	MSTRG.25422	-2,6683	152	40	Signal transduction-related
27	A115	Auxin-induced protein PCNT115	MSTRG.9859.1	MSTRG.9859	-2,4989	10	1	Signal transduction-related
28	SAU32	Auxin-responsive protein SAUR32	MSTRG.2293.1	MSTRG.2293	-2,2686	1750	384	Signal transduction-related
29	ARFK	Auxin response factor 11	MSTRG.4376.1	MSTRG.4376	-2,1838	183	52	Signal transduction-related
30	WOX4	WUSCHEL-related homeobox 4	MSTRG.2733.1	MSTRG.2733	-2,0738	648	157	Signal transduction-related
31	ARFI	Auxin response factor 9	MSTRG.4754.1	MSTRG.4754	-1,8694	2099	614	Signal transduction-related
32	SAU32	Auxin-responsive protein SAUR32	MSTRG.26612.1	MSTRG.26612	-1,8577	254	61	Signal transduction-related
33	SAU32	Auxin-responsive protein SAUR32	MSTRG.21851.1	MSTRG.21851	-1,8368	464	117	Signal transduction-related

	34	ARFQ	Auxin response factor 17	MSTRG.34776.1	MSTRG.34776	-1,7786	110	39	Signal transduction-related
	35	SAU10	Protein SMALL AUXIN UP-REGULATED RNA 10	MSTRG.790.1	MSTRG.790	1,6404	267	725	Signal transduction-related
	36	IAA17	Auxin-responsive protein IAA17	MSTRG.12703.1	MSTRG.12703	1,6512	90	403	Signal transduction-related
	37	SAU50	Auxin-responsive protein SAUR50	MSTRG.3446.1	MSTRG.3446	1,9482	10	67	Signal transduction-related
	38	ARFH	Auxin response factor 8	MSTRG.5433.1	MSTRG.5433	1,9664	823	3119	Signal transduction-related
	39	SAU71	Auxin-responsive protein SAUR71	MSTRG.33530.1	MSTRG.33530	2,0792	37	83	Signal transduction-related
	40	AX22D	Auxin-induced protein 22D	MSTRG.8528.1	MSTRG.8528	2,1204	607	2439	Signal transduction-related
	41	C87A3	Cytochrome P450 87A3	MSTRG.12706.1	MSTRG.12706	2,3679	8	37	Signal transduction-related
	42	IAA30	Auxin-responsive protein IAA30	MSTRG.34246.1	MSTRG.34246	2,6419	4	28	Signal transduction-related
	43	SAU76	Auxin-responsive protein SAUR76	MSTRG.788.1	MSTRG.788	2,7078	236	1291	Signal transduction-related
	44	SAU39	Auxin-responsive protein SAUR36	MSTRG.3550.1	MSTRG.3550	3,6682	1	17	Signal transduction-related
	45	SAU23	Auxin-responsive protein SAUR23	MSTRG.29253.1	MSTRG.29253	3,9579	6	60	Signal transduction-related
	46	A10A5	Auxin-induced protein 10A5	MSTRG.29215.1	MSTRG.29215	5,4677	0	14	Signal transduction-related
	47	WOX10	WUSCHEL-related homeobox 10	MSTRG.17988.1	MSTRG.17988	5,6645	18	463	Signal transduction-related
CK	48	LOGL1	Probable cytokinin riboside 5'-monophosphate phosphoribohydrolase LOGL1	MSTRG.537.1	MSTRG.537	-2,5339	349	63	Biosynthesis

	49	LOG3	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG3	MSTRG.3451.1	MSTRG.3451	-1,5704	153	55	Biosynthesis
	50	ZOG	Zeatin O-glucosyltransferase	MSTRG.17299.1	MSTRG.17299	-2,0938	33	6	Conjugate synthesis
	51	CKX3	Cytokinin dehydrogenase 3	MSTRG.13748.1	MSTRG.13748	-3,8728	415	42	Degradation/ Inactivation
	52	CKX7	Cytokinin dehydrogenase 7	MSTRG.3787.1	MSTRG.3787	-3,5133	366	41	Degradation/ Inactivation
	53	CKX1	Cytokinin dehydrogenase 1	MSTRG.8622.1	MSTRG.8622	-2,1654	19	2	Degradation/ Inactivation
	54	CKX3	Cytokinin dehydrogenase 3	MSTRG.5730.1	MSTRG.5730	2,6401	3	41	Degradation/ Inactivation
	55	ORR26	Two-component response regulator ORR26	MSTRG.9399.1	MSTRG.9399	-2,564	2618	565	Signal transduction-related
	56	PRR95	Two-component response regulator-like PRR95	MSTRG.345.1	MSTRG.345	-1,7649	313	63	Signal transduction-related
ABA	57	ABA2	Zeaxanthin epoxidase	MSTRG.33024.1	MSTRG.33024	-2,1044	26	6	Biosynthesis
	58	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	MSTRG.32782.1	MSTRG.32782	1,5634	16	32	Biosynthesis
	59	ABAH2	Abscisic acid 8'-hydroxylase 2	MSTRG.16243.1	MSTRG.16243	-5,2787	31	1	Degradation/ Inactivation
	60	P2C04	Probable protein phosphatase 2C 4	MSTRG.29129.1	MSTRG.29129	-5,0248	71	3	Signal transduction-related
	61	P2C73	Probable protein phosphatase 2C 73	MSTRG.15095.1	MSTRG.15095	-3,9349	4180	220	Signal transduction-related
	62	P2C04	Probable protein phosphatase 2C 4	MSTRG.19739.1	MSTRG.19739	-3,4172	170	21	Signal transduction-related
	63	P2C08	Probable protein phosphatase 2C 8	MSTRG.23547.1	MSTRG.23547	-3,3572	17	1	Signal transduction-related
	64	AHK1	Histidine kinase 1	MSTRG.17005.1	MSTRG.17005	-3,3636	3604	655	Signal transduction-related
	65	PYL2	Abscisic acid receptor PYL2	MSTRG.12250.1	MSTRG.12250	-2,6911	137	20	Signal transduction-related

66	IPP2	Protein phosphatase inhibitor 2	MSTRG.30358.1	MSTRG.30358	-2,6803	106	18	Signal transduction-related
67	AHK1	Histidine kinase 1	MSTRG.13834.1	MSTRG.13834	-2,6154	24	13	Signal transduction-related
68	PPP7L	Serine/threonine-protein phosphatase 7 long form homolog	MSTRG.3095.1	MSTRG.3095	-2,5412	9	4	Signal transduction-related
69	DSP1	Tyrosine-protein phosphatase DSP1	MSTRG.13847.1	MSTRG.13847	-2,3627	836	199	Signal transduction-related
70	P2C11	Probable protein phosphatase 2C 11	MSTRG.27361.1	MSTRG.27361	-2,3433	48	5	Signal transduction-related
71	P2C72	Probable protein phosphatase 2C 72	MSTRG.2465.1	MSTRG.2465	-2,3163	508	115	Signal transduction-related
72	ANR44	Serine/threonine-protein phosphatase 6 regulatory ankyrin repeat subunit B	MSTRG.26225.2	MSTRG.26225	-2,1305	74	20	Signal transduction-related
73	P2C44	Putative protein phosphatase 2C-like protein 44	MSTRG.14692.1	MSTRG.14692	-2,0556	23	6	Signal transduction-related
74	P2C57	Protein phosphatase 2C 57	MSTRG.23434.1	MSTRG.23434	-2,0249	81	15	Signal transduction-related
75	PPP7L	Serine/threonine-protein phosphatase 7 long form homolog	MSTRG.3104.1	MSTRG.3104	-1,8351	47	16	Signal transduction-related
76	DSP1	Tyrosine-protein phosphatase DSP1	MSTRG.21152.1	MSTRG.21152	-1,7454	2181	624	Signal transduction-related
77	2A5A	Serine/threonine protein phosphatase 2A 57 kDa regulatory subunit B' alpha isoform	MSTRG.28433.1	MSTRG.28433	-1,5233	84	37	Signal transduction-related
78	PPP7L	Serine/threonine-protein phosphatase 7 long form homolog	MSTRG.1260.1	MSTRG.1260	1,8142	39	132	Signal transduction-related
79	PPP7	Serine/threonine-protein phosphatase 7	MSTRG.35018.1	MSTRG.35018	1,8771	21	80	Signal transduction-related
80	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.4145.1	MSTRG.4145	1,8744	85	246	Signal transduction-related

	81	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.1675.1	MSTRG.1675	2,0499	60	196	Signal transduction-related
	82	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.4144.1	MSTRG.4144	2,5733	88	491	Signal transduction-related
	83	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.1674.1	MSTRG.1674	2,6003	15	89	Signal transduction-related
	84	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.4140.1	MSTRG.4140	3,9077	1	11	Signal transduction-related
	85	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.4496.1	MSTRG.4496	4,6994	7	168	Signal transduction-related
	86	ABI4	Ethylene-responsive transcription factor ABI4	MSTRG.21719.1	MSTRG.21719	10,0248	0	163	Signal transduction-related
ET	87	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	MSTRG.15400.1	MSTRG.15400	-3,7395	952	58	Biosynthesis
	88	1A17	1-aminocyclopropane-1-carboxylate synthase 7	MSTRG.5769.1	MSTRG.5769	-3,0484	30	2	Biosynthesis
	89	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	MSTRG.15404.1	MSTRG.15404	-2,7215	381	59	Biosynthesis
	90	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	MSTRG.24860.1	MSTRG.24860	-2,1475	128	24	Biosynthesis
	91	1A12	1-aminocyclopropane-1-carboxylate synthase CMA101	MSTRG.25190.1	MSTRG.25190	1,7534	25	41	Biosynthesis
	92	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	MSTRG.19206.1	MSTRG.19206	2,0938	243	959	Biosynthesis
	93	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	MSTRG.17225.1	MSTRG.17225	4,0847	56	1063	Biosynthesis
	94	1A1C	1-aminocyclopropane-1-carboxylate synthase	MSTRG.14325.1	MSTRG.14325	5,6266	0	12	Biosynthesis
	95	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.33457.1	MSTRG.33457	-4,0729	823	71	Signal transduction-related
	96	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.33443.1	MSTRG.33443	-3,8892	23	4	Signal transduction-related

97	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.26257.1	MSTRG.26257	-3,6383	214	13	Signal transduction-related
98	RA211	Ethylene-responsive transcription factor RAP2-11	MSTRG.22022.1	MSTRG.22022	-3,2922	62	6	Signal transduction-related
99	AP2L1	AP2-like ethylene-responsive transcription factor At1g16060	MSTRG.7763.1	MSTRG.7763	-3,2455	78	7	Signal transduction-related
100	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.1	MSTRG.544	-3,1413	240	29	Signal transduction-related
101	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.2	MSTRG.544.2	-3,1413	240	29	Signal transduction-related
102	ERF11	Ethylene-responsive transcription factor ERF011	MSTRG.2732.1	MSTRG.2732	-2,7087	734	112	Signal transduction-related
103	ERF53	Ethylene-responsive transcription factor ERF053	MSTRG.21403.1	MSTRG.21403	-2,5207	320	51	Signal transduction-related
104	ERF38	Ethylene-responsive transcription factor ERF038	MSTRG.16468.1	MSTRG.16468	-2,4293	354	83	Signal transduction-related
105	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.20675.1	MSTRG.20675	-2,1674	45	5	Signal transduction-related
106	ERF91	Ethylene-responsive transcription factor ERF091	MSTRG.29554.1	MSTRG.29554	-1,8152	20	5	Signal transduction-related
107	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.20679.1	MSTRG.20679	-1,7974	27	14	Signal transduction-related
108	ERF10	Ethylene-responsive transcription factor ERF010	MSTRG.16619.1	MSTRG.16619	-1,6439	149	44	Signal transduction-related
109	CRF4	Ethylene-responsive transcription factor CRF4	MSTRG.23591.1	MSTRG.23591	1,6727	85	204	Signal transduction-related
110	BBM	AP2-like ethylene-responsive transcription factor BBM	MSTRG.1135.1	MSTRG.1135	1,8106	315	1038	Signal transduction-related
111	AIL5	AP2-like ethylene-responsive transcription factor AIL5	MSTRG.5649.1	MSTRG.5649	1,8727	114	454	Signal transduction-related
112	CRF1	Ethylene-responsive transcription factor CRF1	MSTRG.35210.1	MSTRG.35210	1,8865	122	352	Signal transduction-related

	113	EF115	Ethylene-responsive transcription factor ERF115	MSTRG.25340.1	MSTRG.25340	1,9423	57	244	Signal transduction-related
	114	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.1	MSTRG.467	2,1391	95	411	Signal transduction-related
	115	AIL6	AP2-like ethylene-responsive transcription factor AIL6	MSTRG.16268.1	MSTRG.16268	2,1817	484	1900	Signal transduction-related
	116	ERF22	Ethylene-responsive transcription factor ERF022	MSTRG.23479.1	MSTRG.23479	3,2691	0	22	Signal transduction-related
	117	ERF99	Ethylene-responsive transcription factor 13	MSTRG.10673.1	MSTRG.10673	4,1533	5	86	Signal transduction-related
	118	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.34676.1	MSTRG.34676	4,5284	4	117	Signal transduction-related
	119	WIN1	Ethylene-responsive transcription factor WIN1	MSTRG.6626.1	MSTRG.6626	5,0208	0	22	Signal transduction-related
	120	ABI4	Ethylene-responsive transcription factor ABI4	MSTRG.21719.1	MSTRG.21719	10,0248	0	163	Signal transduction-related
JA	121	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.570.1	MSTRG.570	-7,3351	25	0	Biosynthesis
	122	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.575.1	MSTRG.575	-6,0066	11	0	Biosynthesis
	123	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.572.1	MSTRG.572	-5,4695	3	0	Biosynthesis
	124	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34848.1	MSTRG.34848	-4,3946	7	1	Biosynthesis
	125	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34849.1	MSTRG.34849	-3,6309	21	1	Biosynthesis
	126	OPR1	12-oxophytodienoate reductase 1	MSTRG.3282.1	MSTRG.3282	-2,6852	18	4	Biosynthesis
	127	AOS3	Allene oxide synthase 3	MSTRG.9496.1	MSTRG.9496	-2,1794	227	67	Biosynthesis
	128	AOC	Allene oxide cyclase	MSTRG.1321.1	MSTRG.1321	1,8831	811	2730	Biosynthesis
	129	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34851.1	MSTRG.34851	2,3805	40	176	Biosynthesis
	130	OPR2	12-oxophytodienoate reductase 2	MSTRG.7230.1	MSTRG.7230	3,2298	0	40	Biosynthesis
	131	JOX2	Jasmonate-induced oxygenase 2	MSTRG.28807.2	MSTRG.28807	-2,0109	1270	420	Degradation/ Inactivation
GA	132	G3OX	Gibberellin 3-beta-dioxygenase 1	MSTRG.31144.1	MSTRG.31144	-3,7558	205	19	Biosynthesis
	133	GAOX2	Gibberellin 20 oxidase 2	MSTRG.13536.1	MSTRG.13536	-3,6861	15	3	Biosynthesis
	134	G2OX2	Gibberellin 2-beta-dioxygenase 2	MSTRG.33954.1	MSTRG.33954	-2,1582	304	116	Biosynthesis
	135	KO1	Ent-kaurene oxidase	MSTRG.32736.1	MSTRG.32736	2,2311	30	147	Biosynthesis

	136	KAO2	Ent-kaurenoic acid oxidase 2	MSTRG.9502.1	MSTRG.9502	2,2388	208	1043	Biosynthesis
	137	G3OX	Gibberellin 3-beta-dioxygenase 1	MSTRG.22681.1	MSTRG.22681	4,3047	18	154	Biosynthesis
	138	G2OX2	Gibberellin 2-beta-dioxygenase 2	MSTRG.33954.1	MSTRG.33954	-2,1582	304	116	Degradation/ Inactivation
	139	G2OX2	Gibberellin 2-beta-dioxygenase 2	MSTRG.13439.1	MSTRG.13439	-1,6799	736	361	Degradation/ Inactivation
	140	SCL3	Scarecrow-like protein 3	MSTRG.344.1	MSTRG.344	-4,0357	18	3	Signal transduction-related
	141	SCL1	Scarecrow-like protein 1	MSTRG.24375.1	MSTRG.24375	-2,0956	2465	743	Signal transduction-related
	142	GID1B	Gibberellin receptor GID1B	MSTRG.29907.1	MSTRG.29907	-1,5264	3338	1464	Signal transduction-related
	143	GASA4	Gibberellin-regulated protein 4	MSTRG.6190.1	MSTRG.6190	2,2115	923	2381	Signal transduction-related
	144	GASA4	Gibberellin-regulated protein 4	MSTRG.25978.1	MSTRG.25978	2,4045	1720	5952	Signal transduction-related
	145	SCL3	Scarecrow-like protein 3	MSTRG.10288.1	MSTRG.10288	5,4626	0	13	Signal transduction-related
BR	146	C85A	Cytochrome P450 85A	MSTRG.335.1	MSTRG.335	1,8951	149	575	Biosynthesis
	147	C90A1	Cytochrome P450 90A1	MSTRG.22789.1	MSTRG.22789	2,0283	125	456	Biosynthesis
	148	C85A1	Cytochrome P450 85A1	MSTRG.8718.1	MSTRG.8718	3,1355	5	49	Biosynthesis
	149	BRAT1	Brassinosteroid-related acyltransferase 1	MSTRG.8870.1	MSTRG.8870	-6,8251	321	6	Degradation/ Inactivation
	150	C734A	Cytochrome P450 734A1	MSTRG.2961.1	MSTRG.2961	-2,9751	293	50	Degradation/ Inactivation
	151	C734A	Cytochrome P450 734A1	MSTRG.2962.1	MSTRG.2962	-1,5833	350	143	Degradation/ Inactivation
	152	BRAT1	Brassinosteroid-related acyltransferase 1	MSTRG.3982.1	MSTRG.3982	-1,5529	75	33	Degradation/ Inactivation
	153	BKI1	BRI1 kinase inhibitor 1	MSTRG.2804.1	MSTRG.2804	-3,65	24	3	Signal transduction-related
	154	BKI1	BRI1 kinase inhibitor 1	MSTRG.11804.1	MSTRG.11804	-3,2586	26	1	Signal transduction-related

155	BRH1	Brassinosteroid-responsive RING protein	MSTRG.15844.1	MSTRG.15844	-2,6418	36	4	Signal transduction-related
156	BRH1	Brassinosteroid-responsive RING protein	MSTRG.34457.1	MSTRG.34457	-2,5713	35	8	Signal transduction-related
157	BRH1	Brassinosteroid-responsive RING protein	MSTRG.21943.1	MSTRG.21943	-2,2395	215	70	Signal transduction-related
158	BRH1	Brassinosteroid-responsive RING protein	MSTRG.23290.1	MSTRG.23290	-2,0071	172	50	Signal transduction-related
159	BKI1	BRI1 kinase inhibitor 1	MSTRG.11805.1	MSTRG.11805	-1,8912	112	15	Signal transduction-related
160	BRH1	Brassinosteroid-responsive RING protein	MSTRG.31175.1	MSTRG.31175	1,7577	243	664	Signal transduction-related
161	BRH1	Brassinosteroid-responsive RING protein	MSTRG.11139.1	MSTRG.11139	1,8539	121	351	Signal transduction-related
162	BSK2	Serine/threonine-protein kinase BSK2	MSTRG.13335.1	MSTRG.13335	2,265	7	46	Signal transduction-related

LTR vs. LLR

Hormone	No.	Symbol	Gene description	Transcript ID	Gene ID	log2FC	LLR Genes Results	LTR Genes Results	Function
IAA	163	YUC2	Indole-3-pyruvate monooxygenase YUCCA2	MSTRG.6281.1	MSTRG.6281	-8,7453	325	1	Biosynthesis
	164	YUC6	Indole-3-pyruvate monooxygenase YUCCA6	MSTRG.30679.1	MSTRG.30679	-3,176	218	15	Biosynthesis
	165	YUC10	Probable indole-3-pyruvate monooxygenase YUCCA10	MSTRG.3084.1	MSTRG.3084	2,8535	38	154	Biosynthesis
	166	YUC10	Probable indole-3-pyruvate monooxygenase YUCCA10	MSTRG.12291.1	MSTRG.12291	3,0725	24	132	Biosynthesis
	167	TAA1	L-tryptophan--pyruvate aminotransferase 1	MSTRG.11988.1	MSTRG.11988	3,088	3	53	Biosynthesis

168	TAA1	L-tryptophan--pyruvate aminotransferase 1	MSTRG.9561.1	MSTRG.9561	5,1882	1	12	Biosynthesis
169	GH31	Probable indole-3-acetic acid-amido synthetase GH3.1	MSTRG.16511.1	MSTRG.16511	-3,8623	1016	42	Conjugate synthesis
170	GH39	Putative indole-3-acetic acid-amido synthetase GH3.9	MSTRG.32140.1	MSTRG.32140	-3,0447	44	6	Conjugate synthesis
171	ILL1	IAA-amino acid hydrolase ILR1-like 1	MSTRG.9014.1	MSTRG.9014	-5,1796	780	10	Conjugate degradation
172	ILL3	IAA-amino acid hydrolase ILR1-like 3	MSTRG.19114.1	MSTRG.19114	-2,6383	348	50	Conjugate degradation
173	PIN5	Auxin efflux carrier component 5	MSTRG.34102.1	MSTRG.34102	-7,3284	1689	10	Transport
174	AB15B	ABC transporter B family member 15	MSTRG.4010.1	MSTRG.4010	-3,8849	5337	281	Transport
175	AB9B	ABC transporter B family member 9	MSTRG.13237.1	MSTRG.13237	-3,5417	251	9	Transport
176	PIN6	Auxin efflux carrier component 6	MSTRG.35377.1	MSTRG.35377	-3,5369	130	7	Transport
177	AB8B	Putative ABC transporter B family member 8	MSTRG.5121.1	MSTRG.5121	-3,4517	833	75	Transport
178	AB21B	ABC transporter B family member 21	MSTRG.31320.1	MSTRG.31320	-3,2566	2835	264	Transport
179	PIN6	Auxin efflux carrier component 6	MSTRG.4274.1	MSTRG.4274	-3,1862	151	12	Transport
180	AB2B	ABC transporter B family member 2	MSTRG.29974.1	MSTRG.29974	-2,5927	62	12	Transport
181	AB11B	ABC transporter B family member 11	MSTRG.31322.1	MSTRG.31322	-1,6601	14346	2960	Transport
182	AB29B	ABC transporter B family member 29	MSTRG.19185.1	MSTRG.19185	-1,6265	148	34	Transport
183	AB19B	ABC transporter B family member 19	MSTRG.6163.1	MSTRG.6163	1,8265	2155	6644	Transport
184	PID	Protein kinase PINOID	MSTRG.31243.1	MSTRG.31243	2,038	68	250	Transport
185	PIN2	Auxin efflux carrier component 2	MSTRG.5844.1	MSTRG.5844	3,0375	378	2348	Transport
186	C87A3	Cytochrome P450 87A3	MSTRG.22004.1	MSTRG.22004	-6,2261	31	0	Signal transduction-related
187	SAU40	Auxin-responsive protein SAUR40	MSTRG.1959.1	MSTRG.1959	-5,3609	2	0	Signal transduction-related

188	C87A3	Cytochrome P450 87A3	MSTRG.12626.1	MSTRG.12626	-4,9975	89	1	Signal transduction-related
189	WOX4	WUSCHEL-related homeobox 4	MSTRG.2733.1	MSTRG.2733	-4,8334	850	11	Signal transduction-related
190	SAU71	Auxin-responsive protein SAUR71	MSTRG.32207.1	MSTRG.32207	-4,599	19	2	Signal transduction-related
191	SAU71	Auxin-responsive protein SAUR71	MSTRG.9206.1	MSTRG.9206	-3,8397	6107	234	Signal transduction-related
192	SAU32	Auxin-responsive protein SAUR32	MSTRG.25422.1	MSTRG.25422	-3,078	199	20	Signal transduction-related
193	SAU32	Auxin-responsive protein SAUR32	MSTRG.26612.1	MSTRG.26612	-2,4708	295	58	Signal transduction-related
194	SAU32	Auxin-responsive protein SAUR32	MSTRG.21851.1	MSTRG.21851	-2,2644	480	67	Signal transduction-related
195	ARFD	Auxin response factor 4	MSTRG.1419.1	MSTRG.1419	-2,237	498	72	Signal transduction-related
196	ARFK	Auxin response factor 11	MSTRG.4376.1	MSTRG.4376	-2,2075	414	56	Signal transduction-related
197	IAA27	Auxin-responsive protein IAA27	MSTRG.5231.1	MSTRG.5231	-2,1835	871	174	Signal transduction-related
198	IAA27	Auxin-responsive protein IAA27	MSTRG.5231.1	MSTRG.5231	-2,1835	871	174	Signal transduction-related
199	C87A3	Cytochrome P450 87A3	MSTRG.12706.1	MSTRG.12706	-1,9858	145	15	Signal transduction-related
200	ARFD	Auxin response factor 4	MSTRG.1418.1	MSTRG.1418	-1,8902	78	21	Signal transduction-related
201	SAU36	Auxin-responsive protein SAUR36	MSTRG.10889.1	MSTRG.10889	-1,8725	636	155	Signal transduction-related
202	SAU32	Auxin-responsive protein SAUR32	MSTRG.2293.1	MSTRG.2293	-1,8589	1463	327	Signal transduction-related
203	ARFI	Auxin response factor 9	MSTRG.4754.1	MSTRG.4754	-1,852	2426	514	Signal transduction-related

	204	SAU76	Auxin-responsive protein SAUR76	MSTRG.32895.1	MSTRG.32895	-1,764	15	5	Signal transduction-related
	205	ARF2A	Auxin response factor 2A	MSTRG.9199.1	MSTRG.9199	-1,63	1543	335	Signal transduction-related
	206	ARFH	Auxin response factor 8	MSTRG.5433.1	MSTRG.5433	2,0734	964	3074	Signal transduction-related
	207	SAU71	Auxin-responsive protein SAUR71	MSTRG.30867.1	MSTRG.30867	2,332	28	144	Signal transduction-related
	208	SAU71	Auxin-responsive protein SAUR71	MSTRG.33530.1	MSTRG.33530	2,5824	24	129	Signal transduction-related
	209	SAU39	Auxin-responsive protein SAUR36	MSTRG.3550.1	MSTRG.3550	2,7205	9	43	Signal transduction-related
	210	SAU76	Auxin-responsive protein SAUR76	MSTRG.788.1	MSTRG.788	2,885	187	1297	Signal transduction-related
	211	SAU40	Auxin-responsive protein SAUR40	MSTRG.3770.1	MSTRG.3770	3,8148	0	14	Signal transduction-related
	212	WOX10	WUSCHEL-related homeobox 10	MSTRG.17988.1	MSTRG.17988	3,8582	31	226	Signal transduction-related
	213	SAU67	Auxin-responsive protein SAUR67	MSTRG.35217.1	MSTRG.35217	4,069	0	3	Signal transduction-related
	214	SAU23	Auxin-responsive protein SAUR23	MSTRG.29253.1	MSTRG.29253	4,7464	1	40	Signal transduction-related
CK	215	LOGL1	Probable cytokinin riboside 5'-monophosphate phosphoribohydrolase LOGL1	MSTRG.537.1	MSTRG.537	-4,2714	422	11	Biosynthesis
	216	LOG3	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG3	MSTRG.3451.1	MSTRG.3451	-1,9212	258	47	Biosynthesis
	217	LOG7	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG7	MSTRG.19148.1	MSTRG.19148	1,9641	28	95	Biosynthesis
	218	C7351	Cytokinin hydroxylase	MSTRG.5409.1	MSTRG.5409	1,5491	59	159	Biosynthesis
	219	ZOG	Zeatin O-glucosyltransferase	MSTRG.17299.1	MSTRG.17299	-2,5678	68	11	Conjugate synthesis

	220	CKX7	Cytokinin dehydrogenase 7	MSTRG.3787.1	MSTRG.3787	-5,947	1117	4	Degradation/ Inactivation
	221	CKX3	Cytokinin dehydrogenase 3	MSTRG.13748.1	MSTRG.13748	-4,182	878	32	Degradation/ Inactivation
	222	CKX1	Cytokinin dehydrogenase 1	MSTRG.8622.1	MSTRG.8622	-2,6915	43	5	Degradation/ Inactivation
	223	CKX6	Cytokinin dehydrogenase 6	MSTRG.14015.1	MSTRG.14015	-2,5807	80	9	Degradation/ Inactivation
	224	ORR26	Two-component response regulator ORR26	MSTRG.9399.1	MSTRG.9399	-4,2516	5950	244	Signal transduction-related
	225	APRR2	Two-component response regulator-like APRR2	MSTRG.9487.1	MSTRG.9487	-2,0726	107	19	Signal transduction-related
	226	AHK3	Histidine kinase 3	MSTRG.9310.1	MSTRG.9310	-1,7102	3418	743	Signal transduction-related
ABA	227	ABA2	Zeaxanthin epoxidase	MSTRG.33024.1	MSTRG.33024	-3,6424	23	1	Biosynthesis
	228	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	MSTRG.13453.1	MSTRG.13453	-3,5926	1435	42	Biosynthesis
	229	ABA2	Zeaxanthin epoxidase	MSTRG.16651.1	MSTRG.16651	-2,2749	6358	827	Biosynthesis
	230	ABAH2	Abscisic acid 8'-hydroxylase 2	MSTRG.16243.1	MSTRG.16243	-6,7264	38	0	Degradation/ Inactivation
	231	ABAH4	Abscisic acid 8'-hydroxylase 4	MSTRG.187.1	MSTRG.187	-4,7085	10	0	Degradation/ Inactivation
	232	P2C73	Probable protein phosphatase 2C 73	MSTRG.15095.1	MSTRG.15095	-5,7669	8661	116	Signal transduction-related
	233	PPP7L	Serine/threonine-protein phosphatase 7 long form homolog	MSTRG.29017.1	MSTRG.29017	-5,3952	96	3	Signal transduction-related
	234	P2C44	Putative protein phosphatase 2C-like protein 44	MSTRG.14692.1	MSTRG.14692	-4,9284	41	1	Signal transduction-related
	235	AHK1	Histidine kinase 1	MSTRG.17005.1	MSTRG.17005	-4,5512	5406	175	Signal transduction-related
	236	AHK1	Histidine kinase 1	MSTRG.13834.1	MSTRG.13834	-4,1166	30	5	Signal transduction-related

237	P2C57	Protein phosphatase 2C 57	MSTRG.23434.1	MSTRG.23434	-3,9435	76	1	Signal transduction-related
238	P2C04	Probable protein phosphatase 2C 4	MSTRG.29129.1	MSTRG.29129	-3,9275	105	8	Signal transduction-related
239	P2C08	Probable protein phosphatase 2C 8	MSTRG.23547.1	MSTRG.23547	-3,8654	290	3	Signal transduction-related
240	P2C02	Probable protein phosphatase 2C 2	MSTRG.23158.1	MSTRG.23158	-3,5667	11	2	Signal transduction-related
241	P2C04	Probable protein phosphatase 2C 4	MSTRG.19739.1	MSTRG.19739	-3,5594	224	13	Signal transduction-related
242	DSP1	Tyrosine-protein phosphatase DSP1	MSTRG.13847.1	MSTRG.13847	-3,4038	1210	85	Signal transduction-related
243	P2C25	Probable protein phosphatase 2C 25	MSTRG.21711.1	MSTRG.21711	-3,2027	388	38	Signal transduction-related
244	IPP2	Protein phosphatase inhibitor 2	MSTRG.30358.1	MSTRG.30358	-2,6108	64	6	Signal transduction-related
245	P2C04	Probable protein phosphatase 2C 4	MSTRG.33271.1	MSTRG.33271	-2,4472	210	33	Signal transduction-related
246	LEA29	Late embryogenesis abundant protein D-29;	MSTRG.23000.1	MSTRG.23000	-2,4337	35	3	Signal transduction-related
247	P2C24	Probable protein phosphatase 2C 24	MSTRG.1695.1	MSTRG.1695	-2,3478	1174	132	Signal transduction-related
248	P2C75	Probable protein phosphatase 2C 75	MSTRG.31540.2	MSTRG.31540	-2,0984	344	63	Signal transduction-related
249	LEA65	Late embryogenesis abundant protein At5g17165	MSTRG.24262.1	MSTRG.24262	-2,0417	10717	1964	Signal transduction-related
250	P2C72	Probable protein phosphatase 2C 72	MSTRG.2465.1	MSTRG.2465	-1,9901	543	92	Signal transduction-related
251	PP1	Serine/threonine-protein phosphatase PP1	MSTRG.15433.1	MSTRG.15433	-1,9078	1861	333	Signal transduction-related
252	PYL2	Abscisic acid receptor PYL2	MSTRG.12250.1	MSTRG.12250	-1,7962	48	15	Signal transduction-related

253	LEA7	Late embryogenesis abundant protein 7	MSTRG.12711.1	MSTRG.12711	-1,7657	23	2	Signal transduction-related
254	P2C44	Probable protein phosphatase 2C 44	MSTRG.27615.1	MSTRG.27615	-1,7571	1384	277	Signal transduction-related
255	LEA29	Late embryogenesis abundant protein D-29	MSTRG.16902.1	MSTRG.16902	-1,753	99	17	Signal transduction-related
256	PP1	Serine/threonine-protein phosphatase PP1	MSTRG.24450.1	MSTRG.24450	-1,7491	400	57	Signal transduction-related
257	P2C04	Probable protein phosphatase 2C 4	MSTRG.1917.1	MSTRG.1917	-1,7444	2479	569	Signal transduction-related
258	DSP1	Tyrosine-protein phosphatase DSP1	MSTRG.21152.1	MSTRG.21152	-1,7306	2271	521	Signal transduction-related
259	ANR28	Serine/threonine-protein phosphatase 6 regulatory ankyrin repeat subunit A	MSTRG.4914.1	MSTRG.4914	-1,6752	70	33	Signal transduction-related
260	P2C77	Protein phosphatase 2C 77	MSTRG.5548.1	MSTRG.5548	-1,6207	926	196	Signal transduction-related
261	2ABB	Serine/threonine protein phosphatase 2A 55 kDa regulatory subunit B beta isoform	MSTRG.15575.1	MSTRG.15575	-1,5888	259	65	Signal transduction-related
262	P2C13	Probable protein phosphatase 2C 13	MSTRG.15212.1	MSTRG.15212	-1,5751	1177	270	Signal transduction-related
263	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.4805.1	MSTRG.4805	-1,5656	62	28	Signal transduction-related
264	P2C10	Probable protein phosphatase 2C 10	MSTRG.3374.1	MSTRG.3374	-1,5496	1377	360	Signal transduction-related
265	P2C60	Probable protein phosphatase 2C 60	MSTRG.29368.1	MSTRG.29368	-1,5471	7322	1787	Signal transduction-related
266	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.1675.1	MSTRG.1675	2,1116	67	204	Signal transduction-related
267	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.4144.1	MSTRG.4144	2,5489	67	277	Signal transduction-related

	268	2A5B	Serine/threonine protein phosphatase 2A 57 kDa regulatory subunit B' beta isoform	MSTRG.29451.1	MSTRG.29451	2,756	55	295	Signal transduction-related
	269	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.4496.1	MSTRG.4496	3,5263	9	129	Signal transduction-related
	270	Y1465	Late embryogenesis abundant protein At1g64065	MSTRG.4140.1	MSTRG.4140	4,0971	0	6	Signal transduction-related
	271	PPP7L	Serine/threonine-protein phosphatase 7 long form homolog	MSTRG.17531.1	MSTRG.17531	5,5809	0	0	Signal transduction-related
	272	ABI4	Ethylene-responsive transcription factor ABI4	MSTRG.21719.1	MSTRG.21719	8,5609	1	257	Signal transduction-related
ET	273	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	MSTRG.15403.1	MSTRG.15403	-4,5356	335	14	Biosynthesis
	274	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	MSTRG.15400.1	MSTRG.15400	-4,0416	1292	29	Biosynthesis
	275	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	MSTRG.15404.1	MSTRG.15404	-3,8592	659	19	Biosynthesis
	276	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	MSTRG.24860.1	MSTRG.24860	-3,5711	325	35	Biosynthesis
	277	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	MSTRG.24659.1	MSTRG.24659	-3,0726	5497	548	Biosynthesis
	278	ACCH4	1-aminocyclopropane-1-carboxylate oxidase homolog 4	MSTRG.8813.1	MSTRG.8813	-2,5054	8	3	Biosynthesis
	279	1A11	1-aminocyclopropane-1-carboxylate synthase 1	MSTRG.11166.1	MSTRG.11166	-2,297	93	16	Biosynthesis
	280	1A17	1-aminocyclopropane-1-carboxylate synthase 7	MSTRG.5769.1	MSTRG.5769	-1,756	27	14	Biosynthesis
	281	ACCH3	1-aminocyclopropane-1-carboxylate oxidase homolog	MSTRG.6490.11	MSTRG.64901	-1,7103	2384	570	Biosynthesis
	282	1A1C	1-aminocyclopropane-1-carboxylate synthase	MSTRG.32014.1	MSTRG.32014	-1,6589	265	85	Biosynthesis
	283	1A12	1-aminocyclopropane-1-carboxylate synthase CMA101	MSTRG.25190.1	MSTRG.25190	1,7992	12	52	Biosynthesis

284	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	MSTRG.17222.1	MSTRG.17222	2,1656	734	3142	Biosynthesis
285	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	MSTRG.17225.1	MSTRG.17225	3,1515	58	898	Biosynthesis
286	AP2L1	AP2-like ethylene-responsive transcription factor At1g16060	MSTRG.7763.1	MSTRG.7763	-4,2933	43	4	Signal transduction-related
287	ERF11	Ethylene-responsive transcription factor ERF011	MSTRG.2732.1	MSTRG.2732	-3,5119	1157	52	Signal transduction-related
288	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.33443.1	MSTRG.33443	-3,4402	13	1	Signal transduction-related
289	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.33457.1	MSTRG.33457	-3,345	890	90	Signal transduction-related
290	ERF10	Ethylene-responsive transcription factor ERF010	MSTRG.16619.1	MSTRG.16619	-3,2628	247	18	Signal transduction-related
291	ERF53	Ethylene-responsive transcription factor ERF053	MSTRG.21403.1	MSTRG.21403	-2,7219	937	112	Signal transduction-related
292	EF109	Ethylene-responsive transcription factor ERF109	MSTRG.28648.1	MSTRG.28648	-2,5811	23	0	Signal transduction-related
293	ERF38	Ethylene-responsive transcription factor ERF038	MSTRG.16468.1	MSTRG.16468	-2,2457	284	73	Signal transduction-related
294	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.26257.1	MSTRG.26257	-2,2319	181	24	Signal transduction-related
295	ERF86	Ethylene-responsive transcription factor ERF086	MSTRG.24331.1	MSTRG.24331	-2,2162	45	9	Signal transduction-related
296	CRL5	AP2-like ethylene-responsive transcription factor CRL5	MSTRG.16361.1	MSTRG.16361	-2,1792	516	68	Signal transduction-related
297	EF102	Ethylene-responsive transcription factor 5	MSTRG.30184.1	MSTRG.30184	-2,0174	691	149	Signal transduction-related
298	RAP24	Ethylene-responsive transcription factor RAP2-4	MSTRG.17263.1	MSTRG.17263	-1,8595	14307	2549	Signal transduction-related
299	ERN1	Ethylene-responsive transcription factor ERN1	MSTRG.544.1	MSTRG.544	-1,8374	229	76	Signal transduction-related

300	ERF25	Ethylene-responsive transcription factor ERF025	MSTRG.20674.1	MSTRG.20674	-1,7457	91	23	Signal transduction-related
301	ERF34	Ethylene-responsive transcription factor ERF034	MSTRG.12338.1	MSTRG.12338	1,6582	49	131	Signal transduction-related
302	BBM	AP2-like ethylene-responsive transcription factor BBM	MSTRG.1135.1	MSTRG.1135	2,0063	431	1446	Signal transduction-related
303	CRF4	Ethylene-responsive transcription factor CRF4	MSTRG.23591.1	MSTRG.23591	2,0763	86	291	Signal transduction-related
304	CRF1	Ethylene-responsive transcription factor CRF1	MSTRG.35210.1	MSTRG.35210	2,2212	105	561	Signal transduction-related
305	AIL6	AP2-like ethylene-responsive transcription factor AIL6	MSTRG.16268.1	MSTRG.16268	2,7109	517	2960	Signal transduction-related
306	PLET2	AP2-like ethylene-responsive transcription factor PLT2	MSTRG.467.1	MSTRG.467	2,7311	141	585	Signal transduction-related
307	ERF03	Ethylene-responsive transcription factor ERF003	MSTRG.34676.1	MSTRG.34676	3,1525	14	67	Signal transduction-related
308	WIN1	Ethylene-responsive transcription factor WIN1	MSTRG.6626.1	MSTRG.6626	3,5759	2	21	Signal transduction-related
309	ERF81	Ethylene-responsive transcription factor 12	MSTRG.12007.1	MSTRG.12007	4,894	0	8	Signal transduction-related
310	ABI4	Ethylene-responsive transcription factor ABI4	MSTRG.21719.1	MSTRG.21719	8,5609	1	257	Signal transduction-related
311	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.570.1	MSTRG.570	-8,1767	146	0	Biosynthesis
312	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.575.1	MSTRG.575	-8,1349	44	0	Biosynthesis
313	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34848.1	MSTRG.34848	-7,4783	52	0	Biosynthesis
314	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34851.1	MSTRG.34851	-7,4451	154	3	Biosynthesis
315	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.572.1	MSTRG.572	-7,431	44	0	Biosynthesis
316	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.34849.1	MSTRG.34849	-5,6925	149	1	Biosynthesis
317	OPR2	12-oxophytodienoate reductase 2	MSTRG.24084.1	MSTRG.24084	-4,2969	730	22	Biosynthesis
318	LOX6	Lipoxygenase 6	MSTRG.9345.1	MSTRG.9345	-2,9783	194	17	Biosynthesis
319	OPR2	12-oxophytodienoate reductase 2	MSTRG.24102.1	MSTRG.24102	-2,3321	118	39	Biosynthesis
320	LOX5	Linoleate 9S-lipoxygenase 5	MSTRG.25250.1	MSTRG.25250	-1,7499	101	21	Biosynthesis

	321	AOS1	Allene oxide synthase 1	MSTRG.2880.1	MSTRG.2880	1,6233	21	36	Biosynthesis
	322	LOXB	Linoleate 9S-lipoxygenase B	MSTRG.14581.1	MSTRG.14581	2,1709	16	32	Biosynthesis
	323	LOX21	Linoleate 13S-lipoxygenase 2-1	MSTRG.424.1	MSTRG.424	2,1959	14	121	Biosynthesis
	324	AOS1	Allene oxide synthase 1	MSTRG.9495.1	MSTRG.9495	3,9974	0	5	Biosynthesis
	325	JMT2	Probable jasmonic acid carboxyl methyltransferase 2	MSTRG.34341.2	MSTRG.34341	-3,6156	379	10	Conjugate synthesis
	326	JOX2	Jasmonate-induced oxygenase 2	MSTRG.22752.1	MSTRG.22752	-2,9211	507	50	Degradation/ Inactivation
	327	JOX2	Jasmonate-induced oxygenase 2	MSTRG.28807.2	MSTRG.28807	-2,0591	1915	316	Degradation/ Inactivation
	328	JOX2	Jasmonate-induced oxygenase 2	MSTRG.34582.1	MSTRG.34582	-1,8026	17	7	Degradation/ Inactivation
	329	JOX4	Jasmonate-induced oxygenase 4	MSTRG.6775.3	MSTRG.6775	-1,7182	1106	208	Degradation/ Inactivation
	330	JOX2	Jasmonate-induced oxygenase	MSTRG.22753.1	MSTRG.22753	2,8056	4	19	Degradation/ Inactivation
GA	331	G3OX	Gibberellin 3-beta-dioxygenase 1	MSTRG.31144.1	MSTRG.31144	-3,7043	124	19	Biosynthesis
	332	G3OX	Gibberellin 3-beta-dioxygenase 1	MSTRG.22681.1	MSTRG.22681	4,5645	15	283	Biosynthesis
	333	G2OX1	Gibberellin 2-beta-dioxygenase 1	MSTRG.13439.1	MSTRG.13439	-2,549	2121	356	Degradation/ Inactivation
	334	SCL3	Scarecrow-like protein 3	MSTRG.344.1	MSTRG.344	-3,4055	38	8	Signal transduction-related
	335	SCL1	Scarecrow-like protein 1	MSTRG.24375.1	MSTRG.24375	-2,5893	2989	389	Signal transduction-related
	336	GID1B	Gibberellin receptor GID1B	MSTRG.29907.1	MSTRG.29907	-2,2134	4093	712	Signal transduction-related
	337	GASA9	Gibberellin-regulated protein 9	MSTRG.771.1	MSTRG.771	1,9038	8	35	Signal transduction-related
BR	338	C90A1	Cytochrome P450 90A1	MSTRG.22789.1	MSTRG.22789	1,9349	150	448	Biosynthesis
	339	C85A	Cytochrome P450 85A	MSTRG.335.1	MSTRG.335	1,9812	193	501	Biosynthesis
	340	C85A1	Cytochrome P450 85A1	MSTRG.8718.1	MSTRG.8718	5,5727	0	14	Biosynthesis

341	BRAT1	Brassinosteroid-related acyltransferase 1	MSTRG.8870.1	MSTRG.8870	-6,105	591	0	Degradation/ Inactivation
342	C734A	Cytochrome P450 734A1	MSTRG.2961.1	MSTRG.2961	-2,8978	554	49	Degradation/ Inactivation
343	BRAT1	Brassinosteroid-related acyltransferase 1	MSTRG.3982.1	MSTRG.3982	-2,2785	120	20	Degradation/ Inactivation
344	C734A	Cytochrome P450 734A1	MSTRG.2962.1	MSTRG.2962	-2,2289	457	73	Degradation/ Inactivation
345	C734A	Cytochrome P450 734A1	MSTRG.2960.1	MSTRG.2960	1,806	227	549	Degradation/ Inactivation
346	BRH1	Brassinosteroid-responsive RING protein 1	MSTRG.27141.1	MSTRG.27141	-3,9998	8	1	Signal transduction-related
347	BRH1	Brassinosteroid-responsive RING protein 1	MSTRG.27142.1	MSTRG.27142	-2,3922	17	5	Signal transduction-related
348	BRH1	Brassinosteroid-responsive RING protein 1	MSTRG.34457.1	MSTRG.34457	-2,0747	34	5	Signal transduction-related
349	BRH1	Brassinosteroid-responsive RING protein 1	MSTRG.21943.1	MSTRG.21943	-1,9125	134	30	Signal transduction-related
350	BRH1	Brassinosteroid-responsive RING protein 1	MSTRG.30042.1	MSTRG.30042	-1,6646	800	178	Signal transduction-related
351	BRH1	Brassinosteroid-responsive RING protein 1	MSTRG.11139.1	MSTRG.11139	1,9438	56	197	Signal transduction-related
352	BSK2	Serine/threonine-protein kinase BSK2	MSTRG.10788.1	MSTRG.10788	1,5758	659	1403	Signal transduction-related

Supplementary table 7. The list of genes represented in each cluster.

Transcript ID	Gene ID	Cluster	Symbol	Gene description
MSTRG.13000.1	MSTRG.13000	1	TIP13	Aquaporin TIP1-3
MSTRG.14041.1	MSTRG.14041	1	PER27	Peroxidase 27
MSTRG.14041.2	MSTRG.14041	1	PER27	Peroxidase 27
MSTRG.14041.3	MSTRG.14041	1	PER27	Peroxidase 27
MSTRG.31072.1	MSTRG.31072	1	GSTF	Glutathione S-transferase
MSTRG.31072.2	MSTRG.31072	1	GSTF	Glutathione S-transferase
MSTRG.31072.3	MSTRG.31072	1	GSTF	Glutathione S-transferase
MSTRG.31072.4	MSTRG.31072	1	GSTF	Glutathione S-transferase
MSTRG.10906.1	MSTRG.10906	2	14KD	14 kDa proline-rich protein DC2.15
MSTRG.10906.2	MSTRG.10906	2	14KD	14 kDa proline-rich protein DC2.15
MSTRG.10906.3	MSTRG.10906	2	14KD	14 kDa proline-rich protein DC2.15
MSTRG.10906.4	MSTRG.10906	2	14KD	14 kDa proline-rich protein DC2.15
MSTRG.10906.5	MSTRG.10906	2	14KD	14 kDa proline-rich protein DC2.15
MSTRG.10906.6	MSTRG.10906	2	ERLI1	Lipid transfer protein EARLI 1
MSTRG.11426.1	MSTRG.11426	2	AGP	Arabinogalactan protein
MSTRG.12515.1	MSTRG.12515	2	AGP	Arabinogalactan protein
MSTRG.12515.2	MSTRG.12515	2	AGP	Arabinogalactan protein
MSTRG.12515.3	MSTRG.12515	2	AGP	Arabinogalactan protein
MSTRG.12515.4	MSTRG.12515	2	AGP	Arabinogalactan protein
MSTRG.12724.1	MSTRG.12724	2	AGP	Arabinogalactan protein
MSTRG.16521.1	MSTRG.16521	2	AGP	Arabinogalactan protein
MSTRG.18395.1	MSTRG.18395	2	TBB8	Tubulin beta-8 chain
MSTRG.18522.1	MSTRG.18522	2	XTHB	Probable xyloglucan endotransglucosyl
MSTRG.1949.1	MSTRG.1949	2	RSSA	40S ribosomal protein SA
MSTRG.20255.1	MSTRG.20255	2	TBA	Tubulin alpha chain
MSTRG.20691.1	MSTRG.20691	2	GASAE	Gibberellin-regulated protein 14
MSTRG.22579.1	MSTRG.22579	2	HSP72	Heat shock cognate 70 kDa protein 2
MSTRG.22579.2	MSTRG.22579	2	HSP72	Heat shock cognate 70 kDa protein 2
MSTRG.22579.3	MSTRG.22579	2	PGTB1	Geranylgeranyl transferase type-1 sub
MSTRG.22716.1	MSTRG.22716	2	RLA0	60S acidic ribosomal protein P0
MSTRG.22716.2	MSTRG.22716	2	RLA0	60S acidic ribosomal protein P0
MSTRG.2355.1	MSTRG.2355	2	R27A3	60S ribosomal protein L27a-3
MSTRG.2355.2	MSTRG.2355	2	R27A3	60S ribosomal protein L27a-3
MSTRG.25978.1	MSTRG.25978	2	GASA6	Gibberellin-regulated protein 6
MSTRG.28291.1	MSTRG.28291	2	TBA	Tubulin alpha chain
MSTRG.3040.1	MSTRG.3040	2	AED3	Aspartyl protease AED3

MSTRG.31431.1	MSTRG.31431	2	DFC	Protein DOWNSTREAM OF FLC
MSTRG.3332.1	MSTRG.3332	2	RS27A	Ubiquitin-40S ribosomal protein S27a
MSTRG.336.1	MSTRG.336	2	RGP2	Probable UDP-arabinopyranose mutase 2
MSTRG.3387.1	MSTRG.3387	2	TBB6	Tubulin beta-6 chain
MSTRG.5580.1	MSTRG.5580	2	RS33	40S ribosomal protein S3-3
MSTRG.622.1	MSTRG.622	2	AGP	Arabinogalactan protein
MSTRG.6649.1	MSTRG.6649	2	PRF1	36.4 kDa proline-rich protein
MSTRG.6649.2	MSTRG.6649	2	PRF1	36.4 kDa proline-rich protein
MSTRG.6649.3	MSTRG.6649	2	PRF1	36.4 kDa proline-rich protein
MSTRG.6649.4	MSTRG.6649	2	PRF1	36.4 kDa proline-rich protein
MSTRG.12321.1	MSTRG.12321	3	PPA1	Acid phosphatase 1
MSTRG.12321.2	MSTRG.12321	3	PPA1	Acid phosphatase 1
MSTRG.12321.3	MSTRG.12321	3	PPA1	Acid phosphatase 1
MSTRG.12488.1	MSTRG.12488	3	TIP21	Aquaporin TIP2-1
MSTRG.14479.1	MSTRG.14479	3	C7A17	Beta-amyrin 28-monooxygenase
MSTRG.15985.1	MSTRG.15985	3	AROF	Phospho-2-dehydro-3-deoxyheptonate aldolase 1
MSTRG.16430.1	MSTRG.16430	3	BGL17	Beta-glucosidase 17
MSTRG.16430.2	MSTRG.16430	3	F26G	Furostanol glycoside 26-O-beta-glucosidase
MSTRG.16430.3	MSTRG.16430	3	F26G	Furostanol glycoside 26-O-beta-glucosidase
MSTRG.16430.4	MSTRG.16430	3	F26G	Furostanol glycoside 26-O-beta-glucosidase
MSTRG.16430.5	MSTRG.16430	3	BGL13	Beta-glucosidase 13
MSTRG.16430.6	MSTRG.16430	3	BGL17	Beta-glucosidase 17
MSTRG.16430.7	MSTRG.16430	3	BGL10	Beta-glucosidase 10
MSTRG.16953.1	MSTRG.16953	3	AROF	Phospho-2-dehydro-3-deoxyheptonate aldolase 1
MSTRG.17731.1	MSTRG.17731	3	BGL12	Beta-glucosidase 12
MSTRG.17731.2	MSTRG.17731	3	BGL12	Beta-glucosidase 12
MSTRG.17731.3	MSTRG.17731	3	BGL12	Beta-glucosidase 12
MSTRG.17731.4	MSTRG.17731	3	BGL12	Beta-glucosidase 12
MSTRG.19169.1	MSTRG.19169	3	R10A	60S ribosomal protein L10a
MSTRG.19169.10	MSTRG.19169	3	R10A	60S ribosomal protein L10a
MSTRG.19169.2	MSTRG.19169	3	R10A	60S ribosomal protein L10a
MSTRG.19169.3	MSTRG.19169	3	R10A	60S ribosomal protein L10a
MSTRG.19169.4	MSTRG.19169	3	R10A	60S ribosomal protein L10a
MSTRG.19169.5	MSTRG.19169	3	R10A	60S ribosomal protein L10a
MSTRG.19169.6	MSTRG.19169	3	RL10A	60S ribosomal protein L10a
MSTRG.19169.7	MSTRG.19169	3	R10A	60S ribosomal protein L10a
MSTRG.19169.8	MSTRG.19169	3	R10A	60S ribosomal protein L10a
MSTRG.19169.9	MSTRG.19169	3	R10A	60S ribosomal protein L10a
MSTRG.21079.1	MSTRG.21079	3	ALL5	Major latex allergen Hev b 5
MSTRG.21934.1	MSTRG.21934	3	RLA1	60S acidic ribosomal protein P1
MSTRG.26851.1	MSTRG.26851	3	SAHH	Adenosylhomocysteinase

MSTRG.28897.1	MSTRG.28897	3	DIRL1	Putative lipid-transfer protein DIR1
MSTRG.30246.1	MSTRG.30246	3	14KD	14 kDa proline-rich protein DC2.15
MSTRG.30246.2	MSTRG.30246	3	14KD	14 kDa proline-rich protein DC2.15
MSTRG.30959.1	MSTRG.30959	3	PHR2	Blue-light photoreceptor PHR2
MSTRG.32389.1	MSTRG.32389	3	ANX4	Annexin-like protein RJ4
MSTRG.32389.2	MSTRG.32389	3	ANX4	Annexin-like protein RJ4
MSTRG.33064.1	MSTRG.33064	3	BGL11	Beta-glucosidase 11
MSTRG.33064.10	MSTRG.33064	3	BGL24	Beta-glucosidase 24
MSTRG.33064.11	MSTRG.33064	3	F26G	Furostanol glycoside 26-O-beta-glucosidase
MSTRG.33064.12	MSTRG.33064	3	F26G	Furostanol glycoside 26-O-beta-glucosidase
MSTRG.33064.13	MSTRG.33064	3	BGL29	Beta-glucosidase 29
MSTRG.33064.14	MSTRG.33064	3	BGL13	Beta-glucosidase 13
MSTRG.33064.15	MSTRG.33064	3	BGL29	Beta-glucosidase 29
MSTRG.33064.2	MSTRG.33064	3	BGL13	Beta-glucosidase 13
MSTRG.33064.3	MSTRG.33064	3	BGL13	Beta-glucosidase 13
MSTRG.33064.4	MSTRG.33064	3	BGL13	Beta-glucosidase 13
MSTRG.33064.5	MSTRG.33064	3	BGL13	Beta-glucosidase 13
MSTRG.33064.6	MSTRG.33064	3	BGL11	Beta-glucosidase 11
MSTRG.33064.7	MSTRG.33064	3	BGL24	Beta-glucosidase 24
MSTRG.33064.8	MSTRG.33064	3	BGL13	Beta-glucosidase 13
MSTRG.33064.9	MSTRG.33064	3	F26G	Furostanol glycoside 26-O-beta-glucosidase
MSTRG.34606.1	MSTRG.34606	3	ALL5	Major latex allergen Hev b 5
MSTRG.34606.2	MSTRG.34606	3	ALL5	Major latex allergen Hev b 5
MSTRG.34606.3	MSTRG.34606	3	ALL5	Major latex allergen Hev b 5
MSTRG.3689.1	MSTRG.3689	3	RL222	60S ribosomal protein L22-2
MSTRG.6176.1	MSTRG.6176	3	RS92	40S ribosomal protein S9-2
MSTRG.6431.1	MSTRG.6431	3	ODD19	2-oxoglutarate-dependent dioxygenase 19
MSTRG.6431.10	MSTRG.6431	3	ODD19	2-oxoglutarate-dependent dioxygenase 19
MSTRG.6431.11	MSTRG.6431	3	ODD19	2-oxoglutarate-dependent dioxygenase 19
MSTRG.6431.12	MSTRG.6431	3	ODD19	2-oxoglutarate-dependent dioxygenase 19
MSTRG.6431.2	MSTRG.6431	3	ODD19	2-oxoglutarate-dependent dioxygenase 19
MSTRG.6431.3	MSTRG.6431	3	ODD19	2-oxoglutarate-dependent dioxygenase 19
MSTRG.6431.4	MSTRG.6431	3	ODD19	2-oxoglutarate-dependent dioxygenase 19
MSTRG.6431.5	MSTRG.6431	3	ODD19	2-oxoglutarate-dependent dioxygenase 19

MSTRG.6431.6	MSTRG.6431	3	ODD19	2-oxoglutarate-dependent dioxygenase 19
MSTRG.6431.7	MSTRG.6431	3	ODD19	2-oxoglutarate-dependent dioxygenase 19
MSTRG.6431.8	MSTRG.6431	3	ODD19	2-oxoglutarate-dependent dioxygenase 19
MSTRG.6431.9	MSTRG.6431	3	ODD19	2-oxoglutarate-dependent dioxygenase 19
MSTRG.697.1	MSTRG.697	3	Y5258	Stress-response A/B barrel domain-containing protein At5g22580
MSTRG.697.2	MSTRG.697	3	Y5258	Stress-response A/B barrel domain-containing protein At5g22580
MSTRG.697.3	MSTRG.697	3	Y5258	Stress-response A/B barrel domain-containing protein At5g22580
MSTRG.9026.1	MSTRG.9026	3	DEF	Defensin-like protein
MSTRG.9026.2	MSTRG.9026	3	DEF	Defensin-like protein
MSTRG.11346.1	MSTRG.11346	4	-	no hit
MSTRG.11346.2	MSTRG.11346	4	-	no hit
MSTRG.11346.3	MSTRG.11346	4	-	no hit
MSTRG.1345.1	MSTRG.1345	4	PIP27	Aquaporin PIP2-7
MSTRG.1345.2	MSTRG.1345	4	PIP21	Aquaporin PIP2-1
MSTRG.14200.1	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.10	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.11	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.12	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.13	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.14	MSTRG.14200	4	GL113	Germin-like protein subfamily 1 member 13
MSTRG.14200.15	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.16	MSTRG.14200	4	GL116	Germin-like protein subfamily 1 member 16
MSTRG.14200.17	MSTRG.14200	4	GL116	Germin-like protein subfamily 1 member 16
MSTRG.14200.18	MSTRG.14200	4	GL116	Germin-like protein subfamily 1 member 16
MSTRG.14200.19	MSTRG.14200	4	GL116	Germin-like protein subfamily 1 member 16
MSTRG.14200.2	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.20	MSTRG.14200	4	GL113	Germin-like protein subfamily 1 member 13

MSTRG.14200.21	MSTRG.14200	4	GL113	Germin-like protein subfamily 1 member 13
MSTRG.14200.22	MSTRG.14200	4	GL113	Germin-like protein subfamily 1 member 13
MSTRG.14200.23	MSTRG.14200	4	GL116	Germin-like protein subfamily 1 member 16
MSTRG.14200.24	MSTRG.14200	4	GL113	Germin-like protein subfamily 1 member 13
MSTRG.14200.25	MSTRG.14200	4	GL117	Germin-like protein subfamily 1 member 17
MSTRG.14200.26	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.27	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.3	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.4	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.5	MSTRG.14200	4	GL116	Germin-like protein subfamily 1 member 16
MSTRG.14200.6	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.7	MSTRG.14200	4	GL116	Germin-like protein subfamily 1 member 16
MSTRG.14200.8	MSTRG.14200	4	GL17	Germin-like protein subfamily 1 member 7
MSTRG.14200.9	MSTRG.14200	4	GL116	Germin-like protein subfamily 1 member 16
MSTRG.14754.1	MSTRG.14754	4	E134	Endo-1,3
MSTRG.14809.1	MSTRG.14809	4	PER24	Peroxidase 24
MSTRG.14809.2	MSTRG.14809	4	PER3	Peroxidase 3
MSTRG.14809.3	MSTRG.14809	4	PER24	Peroxidase 24
MSTRG.1768.1	MSTRG.1768	4	GLNA2	Glutamine synthetase cytosolic isozyme 2
MSTRG.18445.1	MSTRG.18445	4	-	no hit
MSTRG.18445.2	MSTRG.18445	4	-	no hit
MSTRG.18445.3	MSTRG.18445	4	-	no hit
MSTRG.18445.4	MSTRG.18445	4	-	no hit
MSTRG.18445.5	MSTRG.18445	4	-	no hit
MSTRG.18445.6	MSTRG.18445	4	-	no hit
MSTRG.18445.7	MSTRG.18445	4	-	no hit
MSTRG.18531.1	MSTRG.18531	4	TRNH	Tropinone reductase homolog
MSTRG.18531.2	MSTRG.18531	4	TRNH	Tropinone reductase homolog
MSTRG.18531.3	MSTRG.18531	4	TRN1	Tropinone reductase 1
MSTRG.18531.4	MSTRG.18531	4	TRNH	Tropinone reductase homolog
MSTRG.18531.5	MSTRG.18531	4	TRNH	Tropinone reductase homolog
MSTRG.18531.6	MSTRG.18531	4	TRNH	Tropinone reductase homolog
MSTRG.1907.1	MSTRG.1907	4	MT2	Metallothionein-like protein 2
MSTRG.1907.2	MSTRG.1907	4	MT2	Metallothionein-like protein 2

MSTRG.1907.3	MSTRG.1907	4	MT2	Metallothionein-like protein 2
MSTRG.1907.4	MSTRG.1907	4	MT2	Metallothionein-like protein 2
MSTRG.1907.5	MSTRG.1907	4	MT2	Metallothionein-like protein 2
MSTRG.1907.6	MSTRG.1907	4	MT2	Metallothionein-like protein 2
MSTRG.1907.7	MSTRG.1907	4	MT2	Metallothionein-like protein 2
MSTRG.19077.1	MSTRG.19077	4	ML328	MLP-like protein 328
MSTRG.19077.2	MSTRG.19077	4	MLP43	MLP-like protein 43
MSTRG.19077.3	MSTRG.19077	4	ML328	MLP-like protein 328
MSTRG.19077.4	MSTRG.19077	4	MLP43	MLP-like protein 43
MSTRG.19080.1	MSTRG.19080	4	MLP31	MLP-like protein 31
MSTRG.19080.2	MSTRG.19080	4	MLP31	MLP-like protein 31
MSTRG.19080.3	MSTRG.19080	4	MLP31	MLP-like protein 31
MSTRG.1910.1	MSTRG.1910	4	MT1	Metallothionein-like protein 1
MSTRG.19533.1	MSTRG.19533	4	PIP24	Aquaporin PIP2-4
MSTRG.19638.1	MSTRG.19638	4	CYC2	(S)-8-oxocitronellyl enol synthase CYC2
MSTRG.19638.10	MSTRG.19638	4	VEP1	3-oxo-Delta(4,5)-steroid 5-beta-reductase
MSTRG.19638.2	MSTRG.19638	4	CYC2	(S)-8-oxocitronellyl enol synthase CYC2
MSTRG.19638.3	MSTRG.19638	4	CYC2	(S)-8-oxocitronellyl enol synthase CYC2
MSTRG.19638.4	MSTRG.19638	4	CYC2	(S)-8-oxocitronellyl enol synthase CYC2
MSTRG.19638.5	MSTRG.19638	4	CYC2	(S)-8-oxocitronellyl enol synthase CYC2
MSTRG.19638.6	MSTRG.19638	4	CYC2	(S)-8-oxocitronellyl enol synthase CYC2
MSTRG.19638.7	MSTRG.19638	4	CYC2	(S)-8-oxocitronellyl enol synthase CYC2
MSTRG.19638.8	MSTRG.19638	4	CYC2	(S)-8-oxocitronellyl enol synthase CYC2
MSTRG.19638.9	MSTRG.19638	4	VEP1	3-oxo-Delta(4,5)-steroid 5-beta-reductase
MSTRG.19742.1	MSTRG.19742	4	MT2	Metallothionein-like protein type 2
MSTRG.20607.1	MSTRG.20607	4	FQRL1	Probable NAD(P)H dehydrogenase (quinone) FQR1-like 1
MSTRG.22731.1	MSTRG.22731	4	PIP12	Probable aquaporin PIP1-2
MSTRG.27598.1	MSTRG.27598	4	PMA4	Plasma membrane ATPase 4
MSTRG.28393.1	MSTRG.28393	4	CADH1	Probable cinnamyl alcohol dehydrogenase 1
MSTRG.28864.1	MSTRG.28864	4	HBP2	Hemoglobin-2
MSTRG.29067.1	MSTRG.29067	4	OSS2	Organ-specific protein S2
MSTRG.32454.1	MSTRG.32454	4	GRP2	Glycine-rich cell wall structural protein 1.8
MSTRG.32454.10	MSTRG.32454	4	GRP3	Glycine-rich cell wall structural protein 1.9

MSTRG.32454.11	MSTRG.32454	4	GRP4	Glycine-rich cell wall structural protein 1.10
MSTRG.32454.2	MSTRG.32454	4	GRP5	Glycine-rich cell wall structural protein 1.11
MSTRG.32454.3	MSTRG.32454	4	GRP6	Glycine-rich cell wall structural protein 1.12
MSTRG.32454.4	MSTRG.32454	4	GRP7	Glycine-rich cell wall structural protein 1.13
MSTRG.32454.5	MSTRG.32454	4	GRP8	Glycine-rich cell wall structural protein 1.14
MSTRG.32454.6	MSTRG.32454	4	GRP9	Glycine-rich cell wall structural protein 1.15
MSTRG.32454.7	MSTRG.32454	4	GRP10	Glycine-rich cell wall structural protein 1.16
MSTRG.32454.8	MSTRG.32454	4	GRP11	Glycine-rich cell wall structural protein 1.17
MSTRG.32454.9	MSTRG.32454	4	GRP12	Glycine-rich cell wall structural protein 1.18
MSTRG.3415.1	MSTRG.3415	4	PCBER	Phenylcoumaran benzylic ether reductase POP1
MSTRG.3415.10	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3415.11	MSTRG.3415	4	EGS2	Eugenol synthase 2
MSTRG.3415.12	MSTRG.3415	4	EGS1	Eugenol synthase 1
MSTRG.3415.13	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3415.14	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3415.15	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3415.16	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3415.17	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3415.18	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3415.19	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3415.2	MSTRG.3415	4	PCBER	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3415.20	MSTRG.3415	4	IFRH	Isoflavone reductase homolog A622
MSTRG.3415.3	MSTRG.3415	4	PCBER	Phenylcoumaran benzylic ether reductase POP1
MSTRG.3415.4	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3415.5	MSTRG.3415	4	PCBER	Phenylcoumaran benzylic ether reductase POP1
MSTRG.3415.6	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6

MSTRG.3415.7	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3415.8	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3415.9	MSTRG.3415	4	BETV6	Phenylcoumaran benzylic ether reductase Betv6
MSTRG.3541.1	MSTRG.3541	4	ABP13	Arabinogalactan protein 13-like
MSTRG.3541.10	MSTRG.3541	4	ABP14	Arabinogalactan protein 13-like
MSTRG.3541.11	MSTRG.3541	4	ABP15	Arabinogalactan protein 13-like
MSTRG.3541.12	MSTRG.3541	4	ABP16	Arabinogalactan protein 13-like
MSTRG.3541.13	MSTRG.3541	4	ABP17	Arabinogalactan protein 13-like
MSTRG.3541.14	MSTRG.3541	4	ABP18	Arabinogalactan protein 13-like
MSTRG.3541.15	MSTRG.3541	4	ABP19	Arabinogalactan protein 13-like
MSTRG.3541.16	MSTRG.3541	4	ABP20	Arabinogalactan protein 13-like
MSTRG.3541.17	MSTRG.3541	4	ABP21	Arabinogalactan protein 13-like
MSTRG.3541.18	MSTRG.3541	4	ABP22	Arabinogalactan protein 13-like
MSTRG.3541.19	MSTRG.3541	4	ABP23	Arabinogalactan protein 13-like
MSTRG.3541.2	MSTRG.3541	4	ABP24	Arabinogalactan protein 13-like
MSTRG.3541.20	MSTRG.3541	4	ABP25	Arabinogalactan protein 13-like
MSTRG.3541.21	MSTRG.3541	4	ABP26	Arabinogalactan protein 13-like
MSTRG.3541.22	MSTRG.3541	4	ABP27	Arabinogalactan protein 13-like
MSTRG.3541.23	MSTRG.3541	4	ABP28	Arabinogalactan protein 13-like
MSTRG.3541.3	MSTRG.3541	4	ABP29	Arabinogalactan protein 13-like
MSTRG.3541.4	MSTRG.3541	4	ABP30	Arabinogalactan protein 13-like
MSTRG.3541.5	MSTRG.3541	4	ABP31	Arabinogalactan protein 13-like
MSTRG.3541.6	MSTRG.3541	4	ABP32	Arabinogalactan protein 13-like
MSTRG.3541.7	MSTRG.3541	4	ABP33	Arabinogalactan protein 13-like
MSTRG.3541.8	MSTRG.3541	4	ABP34	Arabinogalactan protein 13-like
MSTRG.3541.9	MSTRG.3541	4	ABP35	Arabinogalactan protein 13-like
MSTRG.4557.1	MSTRG.4557	4	ABP36	Arabinogalactan protein 13-like
MSTRG.7654.1	MSTRG.7654	4	NAS	Nicotianamine synthase
MSTRG.7890.1	MSTRG.7890	4	DRMH3	Dormancy-associated protein homolog 3
MSTRG.7890.2	MSTRG.7890	4	DRMH3	Dormancy-associated protein homolog 3
MSTRG.9584.1	MSTRG.9584	4	TBL2	Protein trichome birefringence-like 2
MSTRG.9831.1	MSTRG.9831	4	GSTUA	Glutathione S-transferase U10
MSTRG.9831.2	MSTRG.9831	4	GSTUA	Glutathione S-transferase U10
MSTRG.9831.3	MSTRG.9831	4	GSTUA	Glutathione S-transferase U10
MSTRG.9831.4	MSTRG.9831	4	GSTUA	Glutathione S-transferase U10
MSTRG.9831.5	MSTRG.9831	4	GSTUA	Glutathione S-transferase U10
MSTRG.9831.6	MSTRG.9831	4	GSTUA	Glutathione S-transferase U10
MSTRG.9831.7	MSTRG.9831	4	GSTUA	Glutathione S-transferase U10
MSTRG.9897.1	MSTRG.9897	4	ALKR4	Probable aldo-keto reductase 4
MSTRG.9897.2	MSTRG.9897	4	AKR2	Probable aldo-keto reductase 2
MSTRG.9897.3	MSTRG.9897	4	AKR2	Probable aldo-keto reductase 2

MSTRG.9897.4	MSTRG.9897	4	AKR2	Probable aldo-keto reductase 2
MSTRG.9897.5	MSTRG.9897	4	AKR2	Probable aldo-keto reductase 2
MSTRG.9897.6	MSTRG.9897	4	AKR2	Probable aldo-keto reductase 2
MSTRG.9897.7	MSTRG.9897	4	AKR2	Probable aldo-keto reductase 2
MSTRG.9897.8	MSTRG.9897	4	ALKR4	Probable aldo-keto reductase 4
MSTRG.9897.9	MSTRG.9897	4	AKR2	Probable aldo-keto reductase 2
MSTRG.10657.1	MSTRG.10657	5	BCB3	Uclacyanin-3
MSTRG.11087.1	MSTRG.11087	5	GL17	Germin-like protein subfamily 1 member 7
MSTRG.20316.1	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.10	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.11	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.12	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.13	MSTRG.20316	5	CSPLC	CASP-like protein 2B1
MSTRG.20316.14	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.15	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.16	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.17	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.18	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.19	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.2	MSTRG.20316	5	CSPLC	CASP-like protein 2B1
MSTRG.20316.20	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.21	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.22	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.23	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.24	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.3	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.4	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.5	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.6	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.7	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.8	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.20316.9	MSTRG.20316	5	RL30	50S ribosomal protein L30
MSTRG.21488.1	MSTRG.21488	5	CLE6	CLAVATA3/ESR (CLE)-related protein 6
MSTRG.2308.1	MSTRG.2308	5	ASNS	Asparagine synthetase [glutamine-hydrolyzing]
MSTRG.2308.2	MSTRG.2308	5	ASNS	Asparagine synthetase [glutamine-hydrolyzing]
MSTRG.2308.3	MSTRG.2308	5	ASNS	Asparagine synthetase [glutamine-hydrolyzing]
MSTRG.2308.4	MSTRG.2308	5	ASNS	Asparagine synthetase [glutamine-hydrolyzing]
MSTRG.32149.1	MSTRG.32149	5	GSTF	Glutathione S-transferase
MSTRG.32149.2	MSTRG.32149	5	GSTF	Glutathione S-transferase
MSTRG.32149.3	MSTRG.32149	5	GSTF	Glutathione S-transferase
MSTRG.32149.4	MSTRG.32149	5	GSTF	Glutathione S-transferase

MSTRG.4297.1	MSTRG.4297	5	-	no hit
MSTRG.4297.2	MSTRG.4297	5	-	no hit
MSTRG.4297.3	MSTRG.4297	5	-	no hit
MSTRG.4297.4	MSTRG.4297	5	-	no hit
MSTRG.4297.5	MSTRG.4297	5	-	no hit
MSTRG.4297.6	MSTRG.4297	5	-	no hit
MSTRG.4297.7	MSTRG.4297	5	-	no hit
MSTRG.4297.8	MSTRG.4297	5	-	no hit
MSTRG.6109.1	MSTRG.6109	5	FDH	Formate dehydrogenase
MSTRG.6109.10	MSTRG.6109	5	FDH1	Formate dehydrogenase 1
MSTRG.6109.11	MSTRG.6109	5	FDH	Formate dehydrogenase
MSTRG.6109.12	MSTRG.6109	5	FDH	Formate dehydrogenase
MSTRG.6109.2	MSTRG.6109	5	FDH	Formate dehydrogenase
MSTRG.6109.3	MSTRG.6109	5	FDH	Formate dehydrogenase
MSTRG.6109.4	MSTRG.6109	5	FDH	Formate dehydrogenase
MSTRG.6109.5	MSTRG.6109	5	FDH	Formate dehydrogenase
MSTRG.6109.6	MSTRG.6109	5	FDH	Formate dehydrogenase
MSTRG.6109.7	MSTRG.6109	5	FDH	Formate dehydrogenase
MSTRG.6109.8	MSTRG.6109	5	FDH	Formate dehydrogenase
MSTRG.6109.9	MSTRG.6109	5	FDH	Formate dehydrogenase
MSTRG.15019.1	MSTRG.15019	6	LEA5	Late embryogenesis abundant protein Lea5
MSTRG.15114.1	MSTRG.15114	6	PRU1	Major allergen Pru ar 1
MSTRG.15114.10	MSTRG.15114	6	PRU1	Major allergen Pru ar 1
MSTRG.15114.11	MSTRG.15114	6	PRU1	Major allergen Pru ar 1
MSTRG.15114.12	MSTRG.15114	6	PRU1	Major allergen Pru ar 1
MSTRG.15114.13	MSTRG.15114	6	PRU1	Major allergen Pru ar 1
MSTRG.15114.14	MSTRG.15114	6	PRU1	Major allergen Pru ar 1
MSTRG.15114.2	MSTRG.15114	6	FRA12	Major strawberry allergen Fra a 1-2
MSTRG.15114.3	MSTRG.15114	6	PRU1	Major allergen Pru ar 1
MSTRG.15114.4	MSTRG.15114	6	PRU1	Major allergen Pru ar 1
MSTRG.15114.5	MSTRG.15114	6	PRU1	Major allergen Pru av 1
MSTRG.15114.6	MSTRG.15114	6	PRU1	Major allergen Pru ar 1
MSTRG.15114.7	MSTRG.15114	6	PRU1	Major allergen Pru ar 1
MSTRG.15114.8	MSTRG.15114	6	PRU1	Major allergen Pru ar 1
MSTRG.15114.9	MSTRG.15114	6	-	no hit
MSTRG.15118.1	MSTRG.15118	6	PRU1	Major allergen Pru ar 1
MSTRG.15118.2	MSTRG.15118	6	PRU1	Major allergen Pru ar 1
MSTRG.15118.3	MSTRG.15118	6	PRU1	Major allergen Pru ar 1
MSTRG.15118.4	MSTRG.15118	6	PRU1	Major allergen Pru ar 1
MSTRG.15118.5	MSTRG.15118	6	PRU1	Major allergen Pru ar 1
MSTRG.15987.1	MSTRG.15987	6	PR1	Pathogenesis-related protein 1
MSTRG.15987.2	MSTRG.15987	6	PR1	Pathogenesis-related protein 1
MSTRG.17808.1	MSTRG.17808	6	SRC1	Steroid Receptor Coactivator 1
MSTRG.29484.1	MSTRG.29484	6	CHI1	Endochitinase 1

MSTRG.29484.2	MSTRG.29484	6	CHI1	Endochitinase 1
MSTRG.29484.3	MSTRG.29484	6	CHI1	Endochitinase 1
MSTRG.30527.1	MSTRG.30527	6	GIP2	Probable aspartic proteinase GIP2
MSTRG.30527.2	MSTRG.30527	6	GIP2	Probable aspartic proteinase GIP2
MSTRG.4927.1	MSTRG.4927	6	PER12	Peroxidase 12
MSTRG.8525.1	MSTRG.8525	6	WIN1	Wound-induced protein WIN1
MSTRG.8525.2	MSTRG.8525	6	WIN1	Wound-induced protein WIN1
MSTRG.8525.3	MSTRG.8525	6	WIN1	Wound-induced protein WIN1
MSTRG.12958.1	MSTRG.12958	7	EGC	EG45-like domain containing protein
MSTRG.15154.1	MSTRG.15154	7	E13B	Glucan endo-1,3-beta-glucosidase, basic vacuolar isoform
MSTRG.15154.2	MSTRG.15154	7	E13B	Glucan endo-1,3-beta-glucosidase, basic vacuolar isoform
MSTRG.15154.3	MSTRG.15154	7	E13B	Glucan endo-1,3-beta-glucosidase, basic vacuolar isoform
MSTRG.15154.4	MSTRG.15154	7	E13B	Glucan endo-1,3-beta-glucosidase, basic vacuolar isoform
MSTRG.15420.1	MSTRG.15420	7	PRP1	Repetitive proline-rich cell wall protein
MSTRG.15420.10	MSTRG.15420	7	PRP2	Repetitive proline-rich cell wall protein
MSTRG.15420.11	MSTRG.15420	7	PRP3	Repetitive proline-rich cell wall protein
MSTRG.15420.12	MSTRG.15420	7	PRP4	Repetitive proline-rich cell wall protein
MSTRG.15420.13	MSTRG.15420	7	PRP5	Repetitive proline-rich cell wall protein
MSTRG.15420.14	MSTRG.15420	7	PRP6	Repetitive proline-rich cell wall protein
MSTRG.15420.15	MSTRG.15420	7	PRP7	Repetitive proline-rich cell wall protein
MSTRG.15420.16	MSTRG.15420	7	PRP8	Repetitive proline-rich cell wall protein
MSTRG.15420.17	MSTRG.15420	7	PRP9	Repetitive proline-rich cell wall protein
MSTRG.15420.18	MSTRG.15420	7	PRP10	Repetitive proline-rich cell wall protein
MSTRG.15420.2	MSTRG.15420	7	PRP11	Repetitive proline-rich cell wall protein
MSTRG.15420.3	MSTRG.15420	7	PRP12	Repetitive proline-rich cell wall protein
MSTRG.15420.4	MSTRG.15420	7	PRP13	Repetitive proline-rich cell wall protein
MSTRG.15420.5	MSTRG.15420	7	PRP14	Repetitive proline-rich cell wall protein

MSTRG.15420.6	MSTRG.15420	7	PRP15	Repetitive proline-rich cell wall protein
MSTRG.15420.7	MSTRG.15420	7	PRP16	Repetitive proline-rich cell wall protein
MSTRG.15420.8	MSTRG.15420	7	PRP17	Repetitive proline-rich cell wall protein
MSTRG.15420.9	MSTRG.15420	7	PRP18	Repetitive proline-rich cell wall protein
MSTRG.15421.1	MSTRG.15421	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15421.2	MSTRG.15421	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15421.3	MSTRG.15421	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15421.4	MSTRG.15421	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15422.1	MSTRG.15422	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.1	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.10	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.11	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.12	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.13	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.14	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.15	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.16	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.17	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.18	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.19	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.2	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.20	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.21	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.22	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.23	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.24	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1

MSTRG.15424.25	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.26	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.27	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.28	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.29	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.3	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.30	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.31	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.32	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.33	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.34	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.35	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.36	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.37	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.38	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.39	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.4	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.40	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.41	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.42	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.43	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.44	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.45	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.46	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.47	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.48	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1

MSTRG.15424.49	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.5	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.50	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.51	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.52	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.53	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.54	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.55	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.56	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.57	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.6	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.7	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.8	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15424.9	MSTRG.15424	7	ERP1	Proline-rich extensin-like protein EPR1
MSTRG.15427.1	MSTRG.15427	7	LOC121400521	Early nodulin-75-like
MSTRG.15427.2	MSTRG.15427	7	LOC121400521	Early nodulin-75-like
MSTRG.15427.3	MSTRG.15427	7	LOC121400521	Early nodulin-75-like
MSTRG.15427.4	MSTRG.15427	7	LOC121400521	Early nodulin-75-like
MSTRG.15427.5	MSTRG.15427	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.1	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.10	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.11	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.12	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.13	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.14	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.15	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.16	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.17	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.18	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.19	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.2	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.20	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.21	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.22	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.23	MSTRG.15428	7	LOC121400521	Early nodulin-75-like

MSTRG.15428.24	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.25	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.26	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.27	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.28	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.29	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.3	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.30	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.31	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.4	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.5	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.6	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.7	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.8	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.15428.9	MSTRG.15428	7	LOC121400521	Early nodulin-75-like
MSTRG.16945.1	MSTRG.16945	7	BSP	Basic secretory protease
MSTRG.16945.2	MSTRG.16945	7	BSP	Basic secretory protease
MSTRG.16945.3	MSTRG.16945	7	BSP	Basic secretory protease
MSTRG.16945.4	MSTRG.16945	7	BSP	Basic secretory protease
MSTRG.16945.5	MSTRG.16945	7	BSP	Basic secretory protease
MSTRG.16945.6	MSTRG.16945	7	BSP	Basic secretory protease
MSTRG.16945.7	MSTRG.16945	7	BSP	Basic secretory protease
MSTRG.17329.1	MSTRG.17329	7	E13B	Glucan endo-1,3-beta-glucosidase, basic isoform
MSTRG.17515.1	MSTRG.17515	7	E13B	Glucan endo-1,3-beta-glucosidase, basic isoform
MSTRG.17515.2	MSTRG.17515	7	E13B	Glucan endo-1,3-beta-glucosidase, basic isoform
MSTRG.18073.1	MSTRG.18073	7	BGIA	Glu S.griseus protease inhibitor
MSTRG.19449.1	MSTRG.19449	7	TLP1	Thaumatin-like protein 1
MSTRG.19449.10	MSTRG.19449	7	TLP1	Thaumatin-like protein 1
MSTRG.19449.2	MSTRG.19449	7	TLP1	Thaumatin-like protein 1
MSTRG.19449.3	MSTRG.19449	7	TLP1	Thaumatin-like protein 1
MSTRG.19449.4	MSTRG.19449	7	TLP1	Thaumatin-like protein 1
MSTRG.19449.5	MSTRG.19449	7	TLP1	Thaumatin-like protein 1
MSTRG.19449.6	MSTRG.19449	7	TLP1	Thaumatin-like protein 1
MSTRG.19449.7	MSTRG.19449	7	TLP1	Thaumatin-like protein 1
MSTRG.19449.8	MSTRG.19449	7	TLP1	Thaumatin-like protein 1
MSTRG.19449.9	MSTRG.19449	7	TLP1	Thaumatin-like protein 1
MSTRG.19452.1	MSTRG.19452	7	TLP1	Thaumatin-like protein 1
MSTRG.19452.2	MSTRG.19452	7	TLP1	Thaumatin-like protein 1
MSTRG.19452.3	MSTRG.19452	7	TLP1	Thaumatin-like protein 1
MSTRG.19452.4	MSTRG.19452	7	TLP1	Thaumatin-like protein 1
MSTRG.19452.5	MSTRG.19452	7	TLP1	Thaumatin-like protein 1
MSTRG.19452.6	MSTRG.19452	7	TLP1	Thaumatin-like protein 1
MSTRG.19452.7	MSTRG.19452	7	TLP1	Thaumatin-like protein 1
MSTRG.19452.8	MSTRG.19452	7	TLP1	Thaumatin-like protein 1

MSTRG.20820.1	MSTRG.20820	7	TSJT1	Stem-specific protein TSJT1
MSTRG.20927.1	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.10	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.11	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.12	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.13	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.14	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.15	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.16	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.17	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.18	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.19	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.2	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.20	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.21	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.22	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.23	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.24	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.25	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.26	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.27	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.28	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.29	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.3	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.30	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.31	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.32	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.33	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.34	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.35	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.36	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.4	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.5	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.6	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.7	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.8	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.20927.9	MSTRG.20927	7	KI104	Kunitz type trypsin inhibitor 104
MSTRG.22869.1	MSTRG.22869	7	OSL3	Osmotin-like protein OSM34
MSTRG.22939.1	MSTRG.22939	7	PER1	Cationic peroxidase 1
MSTRG.22939.10	MSTRG.22939	7	PER1	Cationic peroxidase 1
MSTRG.22939.11	MSTRG.22939	7	PER1	Cationic peroxidase 1
MSTRG.22939.2	MSTRG.22939	7	PER1	Cationic peroxidase 1
MSTRG.22939.3	MSTRG.22939	7	PER1	Cationic peroxidase 1
MSTRG.22939.4	MSTRG.22939	7	PER1	Cationic peroxidase 1
MSTRG.22939.5	MSTRG.22939	7	PER1	Cationic peroxidase 1
MSTRG.22939.6	MSTRG.22939	7	PER1	Cationic peroxidase 1

MSTRG.22939.7	MSTRG.22939	7	PER1	Cationic peroxidase 1
MSTRG.22939.8	MSTRG.22939	7	PER1	Cationic peroxidase 1
MSTRG.22939.9	MSTRG.22939	7	PER1	Cationic peroxidase 1
MSTRG.23367.1	MSTRG.23367	7	GL17	Germin-like protein subfamily 1 member 7
MSTRG.23367.2	MSTRG.23367	7	GL114	Germin-like protein subfamily 1 member 14
MSTRG.24000.1	MSTRG.24000	7	EXTN3	Extensin-3
MSTRG.24000.2	MSTRG.24000	7	EXTN3	Extensin-3
MSTRG.24000.3	MSTRG.24000	7	EXTN3	Extensin-3
MSTRG.27246.1	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.10	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.11	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.12	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.13	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.14	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.15	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.16	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.17	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.18	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.19	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.2	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.20	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.21	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.22	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.23	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.24	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.25	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.26	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.27	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.28	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.29	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.3	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.4	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.5	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.6	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.7	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.8	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27246.9	MSTRG.27246	7	CHI5	Endochitinase EP3
MSTRG.27249.1	MSTRG.27249	7	CHI5	Endochitinase EP3
MSTRG.28025.1	MSTRG.28025	7	CRR38	Cysteine-rich repeat secretory protein 38
MSTRG.28185.1	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28185.10	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase

MSTRG.28185.11	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28185.12	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28185.13	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28185.14	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28185.2	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28185.3	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28185.4	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28185.5	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28185.6	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28185.7	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28185.8	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28185.9	MSTRG.28185	7	E13B	Glucan endo-1,3-beta-glucosidase
MSTRG.28485.1	MSTRG.28485	7	LRR2	Leucine-rich repeat protein 2
MSTRG.29108.1	MSTRG.29108	7	E13B	Glucan endo-1,3-beta-glucosidase, basic isoform
MSTRG.29116.1	MSTRG.29116	7	E13B	Glucan endo-1,3-beta-glucosidase, basic isoform
MSTRG.30351.1	MSTRG.30351	7	P21	Protein P21
MSTRG.5621.1	MSTRG.5621	7	BABL	Basic blue protein
MSTRG.5621.2	MSTRG.5621	7	BABL	Basic blue protein
MSTRG.5621.3	MSTRG.5621	7	BABL	Basic blue protein
MSTRG.5621.4	MSTRG.5621	7	BABL	Basic blue protein
MSTRG.6605.1	MSTRG.6605	7	BCB1	Blue copper protein
MSTRG.6981.1	MSTRG.6981	7	CHIC	Class V chitinase
MSTRG.6981.2	MSTRG.6981	7	CHIC	Class V chitinase
MSTRG.7309.1	MSTRG.7309	7	CHIX	Endochitinase
MSTRG.7309.2	MSTRG.7309	7	CHIX	Endochitinase
MSTRG.7309.3	MSTRG.7309	7	CHIX	Endochitinase
MSTRG.7309.4	MSTRG.7309	7	CHIC	Basic endochitinase C
MSTRG.7309.5	MSTRG.7309	7	CHIC	Basic endochitinase C
MSTRG.22495.1	MSTRG.22495	8	ART3	Putative uncharacterized protein ART3
MSTRG.22495.10	MSTRG.22495	8	-	no hit
MSTRG.22495.11	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.12	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2

MSTRG.22495.13	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.14	MSTRG.22495	8	RRT15	Regulator of rDNA transcription protein 15
MSTRG.22495.15	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.16	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.17	MSTRG.22495	8	RRT15	Regulator of rDNA transcription protein 15
MSTRG.22495.18	MSTRG.22495	8	RRT15	Regulator of rDNA transcription protein 15
MSTRG.22495.19	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.2	MSTRG.22495	8	RRT15	Regulator of rDNA transcription protein 15
MSTRG.22495.20	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.21	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.22	MSTRG.22495	8	RRT15	Regulator of rDNA transcription protein 15
MSTRG.22495.23	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.24	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.25	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.26	MSTRG.22495	8	RRT15	Regulator of rDNA transcription protein 15
MSTRG.22495.27	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.28	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.29	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.3	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.30	MSTRG.22495	8	ART3	Putative uncharacterized protein ART3
MSTRG.22495.31	MSTRG.22495	8	RRT15	Regulator of rDNA transcription protein 15
MSTRG.22495.32	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.33	MSTRG.22495	8	ART3	Putative uncharacterized protein ART3
MSTRG.22495.34	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.35	MSTRG.22495	8	RRT15	Regulator of rDNA transcription protein 15
MSTRG.22495.36	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2

MSTRG.22495.37	MSTRG.22495	8	ART3	Putative uncharacterized protein ART3
MSTRG.22495.38	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.4	MSTRG.22495	8	RRT15	Regulator of rDNA transcription protein 15
MSTRG.22495.5	MSTRG.22495	8	TAR1	Protein TAR1
MSTRG.22495.6	MSTRG.22495	8	-	no hit
MSTRG.22495.7	MSTRG.22495	8	ART2	Putative uncharacterized protein ART2
MSTRG.22495.8	MSTRG.22495	8	TAR1	Protein TAR1
MSTRG.22495.9	MSTRG.22495	8	TAR1	Protein TAR1
MSTRG.31997.1	MSTRG.31997	8	ART2	Putative uncharacterized protein ART2
MSTRG.31997.10	MSTRG.31997	8	ART2	Putative uncharacterized protein ART2
MSTRG.31997.11	MSTRG.31997	8	ART2	Putative uncharacterized protein ART2
MSTRG.31997.12	MSTRG.31997	8	-	no hit
MSTRG.31997.13	MSTRG.31997	8	ART2	Putative uncharacterized protein ART2
MSTRG.31997.14	MSTRG.31997	8	ART2	Putative uncharacterized protein ART2
MSTRG.31997.15	MSTRG.31997	8	-	no hit
MSTRG.31997.16	MSTRG.31997	8	-	no hit
MSTRG.31997.17	MSTRG.31997	8	ART2	Putative uncharacterized protein ART2
MSTRG.31997.18	MSTRG.31997	8	ART2	Putative uncharacterized protein ART2
MSTRG.31997.19	MSTRG.31997	8	ART2	Putative uncharacterized protein ART2
MSTRG.31997.2	MSTRG.31997	8	ART2	Putative uncharacterized protein ART2
MSTRG.31997.20	MSTRG.31997	8	-	no hit
MSTRG.31997.3	MSTRG.31997	8	-	no hit
MSTRG.31997.4	MSTRG.31997	8	ART2	Putative uncharacterized protein ART2
MSTRG.31997.5	MSTRG.31997	8	-	no hit
MSTRG.31997.6	MSTRG.31997	8	ART2	Putative uncharacterized protein ART2
MSTRG.31997.7	MSTRG.31997	8	-	no hit
MSTRG.31997.8	MSTRG.31997	8	-	no hit
MSTRG.31997.9	MSTRG.31997	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.1	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.10	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.11	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2

MSTRG.34873.12	MSTRG.34873	8	TAR1	Protein TAR1
MSTRG.34873.13	MSTRG.34873	8	-	no hit
MSTRG.34873.14	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.15	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.16	MSTRG.34873	8	TAR1	Protein TAR1
MSTRG.34873.17	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.18	MSTRG.34873	8	TAR1	Protein TAR1
MSTRG.34873.19	MSTRG.34873	8	-	no hit
MSTRG.34873.2	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.20	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.21	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.22	MSTRG.34873	8	-	no hit
MSTRG.34873.23	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.24	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.25	MSTRG.34873	8	TAR1	Protein TAR1
MSTRG.34873.26	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.27	MSTRG.34873	8	-	no hit
MSTRG.34873.28	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.29	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.3	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.30	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.31	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.32	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.33	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.34	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.35	MSTRG.34873	8	-	no hit
MSTRG.34873.36	MSTRG.34873	8	TAR1	Protein TAR1
MSTRG.34873.37	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.38	MSTRG.34873	8	TAR1	Protein TAR1
MSTRG.34873.39	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3

MSTRG.34873.4	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.40	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.41	MSTRG.34873	8	-	no hit
MSTRG.34873.42	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.43	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.44	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.45	MSTRG.34873	8	-	no hit
MSTRG.34873.46	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.47	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.48	MSTRG.34873	8	-	no hit
MSTRG.34873.49	MSTRG.34873	8	TAR1	Protein TAR1
MSTRG.34873.5	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.50	MSTRG.34873	8	TAR1	Protein TAR1
MSTRG.34873.51	MSTRG.34873	8	TAR1	Protein TAR1
MSTRG.34873.52	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.53	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.54	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.55	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.56	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.57	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.58	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.59	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.6	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.60	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.61	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.62	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.63	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.64	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2

MSTRG.34873.65	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.66	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.67	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.68	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.69	MSTRG.34873	8	ART2	Putative uncharacterized protein ART2
MSTRG.34873.7	MSTRG.34873	8	TAR1	Protein TAR1
MSTRG.34873.70	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.71	MSTRG.34873	8	-	no hit
MSTRG.34873.8	MSTRG.34873	8	ART3	Putative uncharacterized protein ART3
MSTRG.34873.9	MSTRG.34873	8	-	no hit
MSTRG.10749.1	MSTRG.10749	9	CRR38	Cysteine-rich repeat secretory protein 38
MSTRG.10749.10	MSTRG.10749	9	CRR38	Cysteine-rich repeat secretory protein 38
MSTRG.10749.2	MSTRG.10749	9	CRR38	Cysteine-rich repeat secretory protein 38
MSTRG.10749.3	MSTRG.10749	9	CRR38	Cysteine-rich repeat secretory protein 38
MSTRG.10749.4	MSTRG.10749	9	CRR38	Cysteine-rich repeat secretory protein 38
MSTRG.10749.5	MSTRG.10749	9	CRR38	Cysteine-rich repeat secretory protein 38
MSTRG.10749.6	MSTRG.10749	9	CRR38	Cysteine-rich repeat secretory protein 38
MSTRG.10749.7	MSTRG.10749	9	CRR38	Cysteine-rich repeat secretory protein 38
MSTRG.10749.8	MSTRG.10749	9	CRR38	Cysteine-rich repeat secretory protein 38
MSTRG.10749.9	MSTRG.10749	9	CRR38	Cysteine-rich repeat secretory protein 38
MSTRG.20275.1	MSTRG.20275	9	GRP	Glycine-rich protein DC7.1-like
MSTRG.20275.2	MSTRG.20275	9	GRP	Glycine-rich protein DC7.1-like
MSTRG.20275.3	MSTRG.20275	9	GRP	Glycine-rich protein DC7.1-like
MSTRG.20275.4	MSTRG.20275	9	GRP	Glycine-rich protein DC7.1-like
MSTRG.20275.5	MSTRG.20275	9	GRP	Glycine-rich protein DC7.1-like
MSTRG.20275.6	MSTRG.20275	9	GRP	Glycine-rich protein DC7.1-like
MSTRG.20275.7	MSTRG.20275	9	GRP	Glycine-rich protein DC7.1-like
MSTRG.20275.8	MSTRG.20275	9	GRP	Glycine-rich protein DC7.1-like
MSTRG.20275.9	MSTRG.20275	9	GRP	Glycine-rich protein DC7.1-like
MSTRG.23675.1	MSTRG.23675	9	CHIA	Acidic endochitinase
MSTRG.29800.1	MSTRG.29800	9	DIRL1	Putative lipid-transfer protein DIR1
MSTRG.30249.1	MSTRG.30249	10	ERLI1	Lipid transfer protein EARLI 1

MSTRG.9647.1	MSTRG.9647	10	GP1	Polygalacturonase-1 non-catalytic subunit beta
MSTRG.9647.2	MSTRG.9647	10	GP1	Polygalacturonase-1 non-catalytic subunit beta
MSTRG.9647.3	MSTRG.9647	10	GP1	Polygalacturonase-1 non-catalytic subunit beta
MSTRG.9647.4	MSTRG.9647	10	GP1	Polygalacturonase-1 non-catalytic subunit beta

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Kościelniak P., Glazińska P., Kęsy J., Mucha J., Zadworny M. (2023) Identification of genetics and hormonal factors involved in *Quercus robur* root growth regulation in different cultivation system.

Identification of genetics and hormonal factors involved in *Quercus robur* root growth regulation in different cultivation system

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Keywords: gene, hormone, oak, RNA-Seq, root, transcriptome

Abbreviations:

STR_RH - short taproot, meristematic zone, rhizotron

STR_C - short taproot, meristematic zone, container

STR_CRH - short taproot, meristematic zone, transplanted

MTR_RH - medium taproot, meristematic zone, rhizotron

MTR_C - medium taproot, meristematic zone, container

MTR_CRH - medium taproot, meristematic zone, transplanted

LTR_RH - long taproot, meristematic zone, rhizotron

LTR_C - long taproot, meristematic zone, container

LTR_CRH - long taproot, meristematic zone, transplanted

MEZ_RH - medium taproot, elongation zone, rhizotron

MEZ_C - medium taproot, elongation zone, container

MEZ_CRH - medium taproot, elongation zone, transplanted

LEZ_RH - long taproot, elongation zone, rhizotron

LEZ_CRH - long taproot, elongation zone, container

LEZ_CRH - long taproot, elongation zone, transplanted

MLR_RH - lateral root from medium taproot, meristematic zone, rhizotron

MLR_C - lateral root from medium taproot, meristematic zone, container

MLR_CRH - lateral root from medium taproot, meristematic zone, transplanted

LLR_RH - lateral root from long taproot, meristematic zone, rhizotron

LLR_C - lateral root from long taproot, meristematic zone, container

LLR_CRH - lateral root from long taproot, meristematic zone, transplanted

Abstract

Understanding the molecular processes and hormonal signals that govern root growth is of paramount importance for effective forest management. While Arabidopsis studies have shed light on the role of the primary root in root system development, the structure of root systems in trees is considerably more intricate, posing challenges to comprehend taproot growth in acorn-sown and nursery-cultivated seedlings. In this study, we investigated *Quercus robur* seedlings using rhizotrons, containers, and transplanted containers to rhizotrons, aiming to unravel the impact of forest nursery practices on processes governing taproot growth and root system development. Root samples were subjected to RNA-seq analysis to identify gene expression patterns and perform differential gene expression and phytohormone analysis. Among the different cultivation systems, differentially expressed genes (DEGs) exhibited significant diversity, with up-regulation observed in rhizotron-grown seedlings, and down-regulation in container-grown seedlings, implying inhibitory signals affecting root growth. Transplanted seedlings also showed downregulated DEGs, suggesting a potential difference in

taproot recovery compared to rhizotron-grown seedlings. The results imply that container cultivation triggers the activation of several genes associated with linolenic acid and peptide synthesis in root growth. Upon transplantation from containers to rhizotrons, rapid enhancement in gene expression occurs, followed by gradual reduction as root growth progresses, ultimately reaching a similar expression pattern as observed in the taproot of rhizotron-cultivated seedlings. Phytohormone analysis revealed that taproot growth patterns under different cultivation systems are regulated by the interplay between auxin and cytokinin concentrations. Moreover, the diversification of hormone levels within the root zone and cultivation systems allows for taproot growth inhibition and prompt recovery in transplanted seedlings. Our study highlights the crucial role of hormone interactions during the early stages of taproot elongation, influencing root system formation across.

1. Introduction

Periodic lowering of groundwater levels caused by prolonged droughts, and subsequent soil drying, have been linked to the premature decline of oak stands [1-4]. In naturally-regenerated oak stands, trees can cope with drought conditions by developing a robust, deep root system that accesses water from deeper soil layers. This facilitates water uptake from descending water tables and enhances the trees' ability to survive prolonged water shortages [5, 6]. As a result, seedlings with deep-rooted systems have a higher chance of surviving severe droughts compared to those with shallow root systems. Deeper rooting also improves the survival of bareroot seedlings [7]. Unfortunately, the most commonly used regeneration forestry practices, such as undercutting the taproot, which does not regenerate [8], alter root architecture and result in abundant but shallow oak root systems. These altered root systems limit above-ground development and increase vulnerability to drought, similar to the effects of coppicing [9, 10]. Root pruning management practices disrupt the natural process of further root system development and may contribute to reduced oak survival during long-term drought episodes. However, nursery practices for container-grown seedlings could enhance seedling survival after outplanting, even under drought stress, by improving root morphology and depth. Unfortunately, despite having drainage openings at the bottom of containers, root air pruning occurs, limiting outward root growth and injuring the taproots [10]. Altering seedling development in containers through taproot injury could make the seedlings more susceptible to unfavorable environmental conditions [11]. However, a decline in root system quality does not always occur, as taproots were observed within 55% of containerized seedlings after their outplanting into the experimental pots [10]. Nevertheless, it is worth noting that not all taproots

grow out of the container; some mechanism restricts taproot elongation before reaching the container's bottom. The ability to achieve a natural-like root system in a fraction of containerized seedlings could significantly improve their resistance to prolonged water shortages and enhance the overall quality of planting materials from containerized nurseries. However, information on the relationship between nursery treatments and subsequent growth, as well as the overall vitality of oak stands, is limited for seedlings produced in containers [12]. Promoting taproot regrowth in containerized seedlings upon outplanting in forests could enhance their access to water resources and positively influence oak development, increasing their ability to withstand long-term drought episodes. Thus, there is a pressing need to identify the factors that control taproot growth, cessation of growth, and regrowth.

Root growth and development are influenced by internal genetic and physiological factors as well as environmental conditions. However, most research on seedling quality in container nurseries has primarily focused on phenotypical or physiological aspects, neglecting the molecular determinants that govern root growth and development [13-15]. The level and activity of molecular and physiological factors can lead to developmental and structural diversity in seedlings growing under different cultivation systems in two ways: 1) internal signaling that shapes root growth patterns, and 2) coordination of root growth in response to environmental stimuli. Consequently, the regulation of taproot growth is multidimensional, influenced by signaling and gene expression levels that directly impact root growth dynamics. Studying these processes, from sensing environmental cues, such as those in containerized transplants, to molecular and physiological signaling cascades that initiate taproot growth (which has been inhibited in containers), presents a significant challenge. Nevertheless, fundamental questions about the role of hormonal signals and molecular processes in regulating root architecture, particularly taproot growth, remain unanswered.

Hormones are well-documented regulators of root development and growth (Casson & Lindsey, 2003). For instance, auxins are involved in initiating root formation [16], but high concentrations of auxins can inhibit root elongation [17]. Cytokinins control the cessation of root growth, preventing excessive lateral root growth [18], while ethylene inhibits root elongation, and its production is stimulated by auxins [19]. However, ethylene also inhibits auxin transport [20]. The interaction and cross-talk among these hormones regulate root growth and determine taproot dominance. For instance, ethylene's inhibition of auxin transport leads to auxin accumulation in primary root tips, effectively inhibiting root elongation [21]. Cytokinins, by modulating ethylene levels through the regulation of ACS gene family members, are also

involved in root elongation inhibition [22]. Detailed knowledge of how these hormonal signals cooperate can shed light on components of plant hormonal responses that inhibit and allow regrowth of roots. This is further supported by the observation of a wide variety of hormonal responses between different natural *Arabidopsis thaliana* (L.) accessions [23] and species, such as *Brachypodium distachyon*, which displays profound differences compared to Arabidopsis [24]. Understanding the processes that control taproot function in containerized oak seedlings requires the identification and characterization of endogenous factors regulating taproot growth and inhibition. This information is crucial for developing efficient strategies to promote taproot regrowth in containerized oak seedlings after transplantation into the field.

The objective of this study was threefold: 1) to analyze temporal changes in gene expression patterns during taproot elongation in an experimental system that mimics natural conditions, nursery containers, and transplanted containerized seedlings; 2) to investigate hormone control of root development during elongation in different nursery cultivation systems; and 3) to determine the specificity of the expression profile among different tissues, specifically the meristematic and elongation zones of the taproot and the meristematic zone of the lateral root. To achieve these goals, we conducted RNA-seq to comprehensively profile the taproot (meristematic and elongation zones) and lateral root transcriptomes. Additionally, we analyzed plant hormones to compare their activity in different nursery cultivation systems. Understanding how plants integrate internal and external signals to regulate root growth is crucial for tree cultivation. Therefore, we also discuss the implications of specific signals and signaling pathways that regulate the molecular process of taproot growth at the forest management level.

2. Materials and methods

2.1. Plant material, cultivation and sample collection

In this study, we utilized roots from *Quercus robur* seedlings grown under various cultivation systems, and acorns were purchased from a storehouse in Jarocin of the National State Forests (Jarocin forest district, Poland). The experiment took place in a large, semi-closed, and foil greenhouse situated in the Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland. Three experimental nursery cultivation systems were employed: container, rhizotron, and transplanted (wherein the seedlings were initially grown in containers and later transferred to rhizotrons). The seedlings were cultivated within transparent rhizotron chambers (30 × 50 cm) and containers (180 mm high, 5 mm wide, 0.275 dm^3). The growing medium used for both systems consisted of a peat and perlite mixture (volumetric proportion of 5:1), supplemented

with dolomite for deacidification and slow-release fertilizer (Osmocote 15-9-12-2 N-P-K-Mg, with trace nutrients) at a rate of 2.5 kg/m3. The rhizotron structure comprised two plexiglass plates separated by 2–3 cm and secured with sturdy plastic tubing to ensure adequate root space. Drainage measures were incorporated at the bottom of each rhizotron to prevent waterlogging. The use of rhizotrons enabled non-invasive monitoring of root growth in the same seedlings over time, without disrupting the root system. After 8 weeks of growth, container (C) and rhizotron (RH) seedlings were harvested. The transplanted (CRH) seedlings, however, were grown in containers for the first year, then transplanted into rhizotrons for 8 weeks, and harvested at the same time as the seedlings from both the containers and the rhizotrons. Taproots were measured and classified based on their length into three categories: S - short (5-9 cm), M - medium (9.5-15 cm), and L - long (>15.5 cm). In this study, we focused on the tips of taproots, dividing them into the meristematic zone (TR) and elongation zone (EZ) of the taproot. Lateral roots (LR) were obtained from corresponding lengths of the taproot, namely medium (MLR) and long (LLR), and consisted only of root tips of lateral roots with the meristematic zone. Lateral roots were absent when the taproot length was short (Fig. 1) [25].

For RNA-seq analysis, we extracted total RNA from the roots of seedlings grown in different cultivation systems using Ribospin (GeneAll Biotechnology, Seoul, South Korea). Subsequently, we constructed a cDNA library with a TruSeq Stranded mRNA LT Sample Prep Kit and sequenced it on a NovaSeq platform (Illumina, San Diego, CA, USA) in the 150bp PE mode. The expression of selected genes after NGS sequencing was validated through RT-qPCR reactions. The data discussed in this publication have been deposited in NCBI GEO and can be accessed through GEO Series accession number GSE181860 and the OakRootRNADB database [25]. Further information about seedling cultivation, sample collection, sequencing, and validation of sequencing results via RT-qPCR is available in detail in the work by Kościelniak et al. (2022) [25].

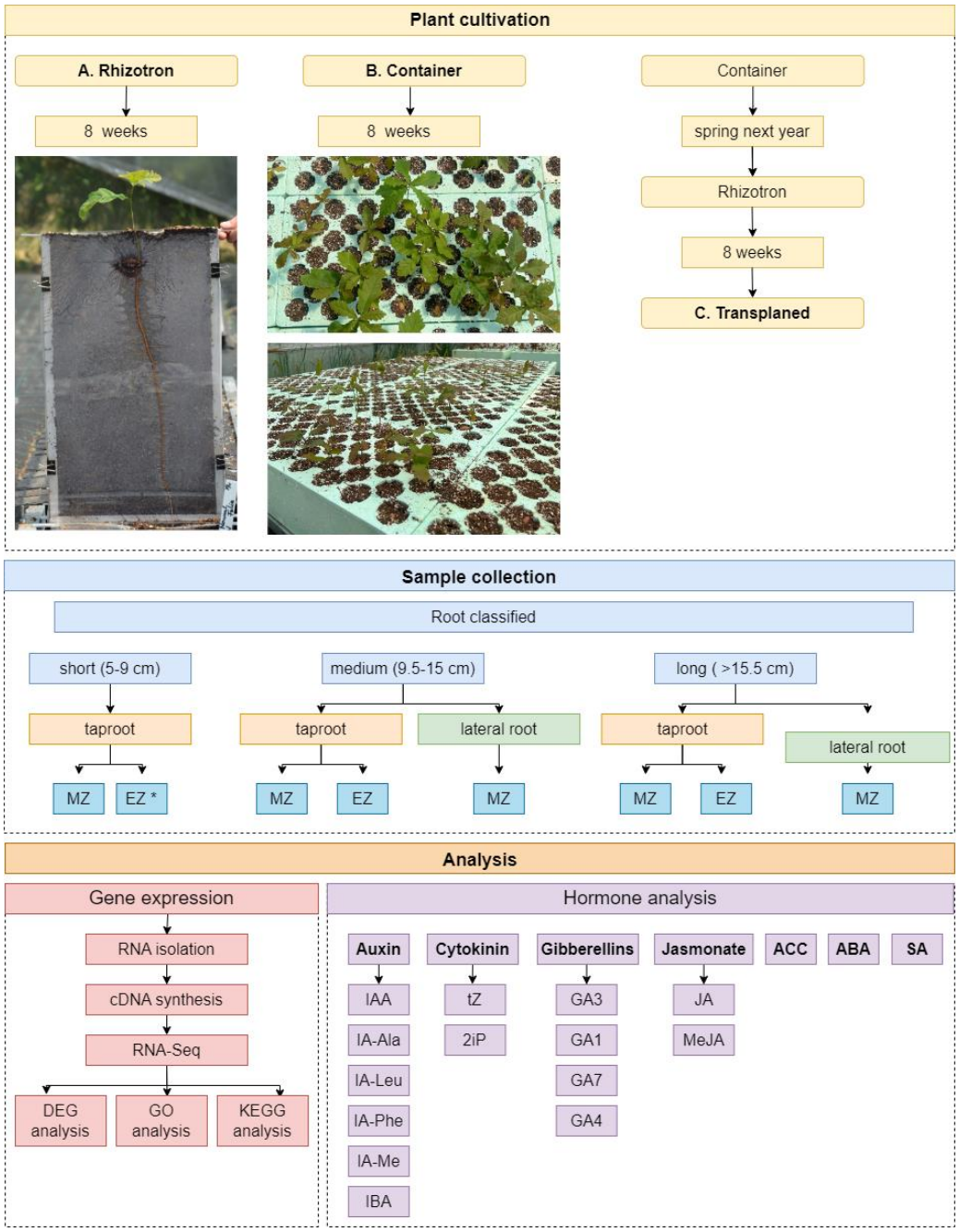

Fig. 1. General workflow of experimental steps a) sample collection, b) sequencing and c) transcriptome analysis. MZ – meristematic zone; EZ – elongation zone; DEG - Differentially expressed genes; GO – Gene Ontology; KEGG – Kyoto Encyclopedia of Genes and Genomes; IAA – indole-3-acetic acid; IBA – indole-3-butyric acid; IA-Ala – indole-3-acetyl-L-alanine; IA-Leu – indole-3-acetyl-L-leucine; IA-Phe – indole-3-acetyl-L-phenylalanine; IA-ME – indole-3-acetyl-L-methionine; tZ – trans-Zeatin; 2iP –N6-(2-Isopentenyl)adenine; GA3, GA1, GA7, GA4 – gibberellins 3,1,7,4; JA – jasmonic acid; MeJA – methyl jasmonate; ACC - 1-aminocyclopropane-1-carboxylic acid; ABA – abscisic acid; SA – salicylic acid. An asterisk (*) denotes a research variant for which the transcriptome was not sequenced.

2.2. Identification, functional and pathway enrichment for DEGs

To identify genes with different expression patterns across various cultivation systems, we conducted an analysis of differentially expressed genes (DEGs). The gene abundances for each sample were estimated using the expectation-maximization method, specifically the RSEM algorithm, and expressed as FPKM (Fragments Per Kilobase Of Exon Per Million Fragments Mapped). The differential gene expression analysis was performed at the transcript level using DESeq2, as described by MI Love, W Huber and S Anders [26]. Genes with a fold change (log2FC) greater than 1.5 and a statistically significant p-value < 0.05 were considered differentially expressed. Further analysis of the identified DEGs was carried out using the Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) databases. GO enrichment analyses were performed using the Trinotate-Trinotate-v3.2.2 package script. The Gene Ontology (GO) analysis was performed at the non-ancestral level, which is similar to the ancestral level but excludes ancestral terms from the analysis. A search was conducted to identify significantly enriched Gene Ontology (GO) terms, which were subsequently mapped. To update obsolete terms, data from the AmiGO database (amigo.geneontology.org) were utilized. Some terms in the output were marked as "none" because they had an "obsolete" status in the database. The background for the analysis comprised all the identified genes obtained using Trinotate v 3.0.2. The result files contained terms that were significantly enriched or less frequent than statistically depleted terms, with a p-value < 0.05. Similarly, the identified KEGG pathways underwent the same analysis, and the results were filtered to include only those terms derived from plants.

2.3.Plant hormone analysis

The phytohormone content analysis was performed using the QuEChERS method (quick, easy, cheap, effective, rugged, and safe) with deuterated internal standards. This method utilizes phase separation with acetonitrile and phytohormone extraction on C18 SPE columns (BAKERBOND Octadecyl spe™, Avantor, USA) designed to selectively bind and then dissociate the desired compounds [27]. The preparation of plant material followed the protocol used in the experiment of CH Pu, SK Lin, WC Chuang and TH Shyu [28] with necessary modifications. Quantification was done using high-performance liquid chromatography coupled with mass spectrometry (UHPLC-MS/MS) with a Shimadzu Nexera XR UHPLC system (Shimadzu, Kyoto, Japan) and a triple quadrupole mass spectrometer detector (LCMS-8045, Shimadzu). Analyses were carried out using a BAKERBOND Octadecyl spe™ C18 column (Avantor, USA). Chromatographic separation was achieved on an Ascentis Express

C18 column (2.7 µm, 100 × 2.1 mm, Supelco, Bellefonte, PA, USA), maintained at 35 °C, using 0.1% formic acid in water (mobile phase A) and methanol with 0.1% formic acid (mobile phase B) at a flow rate of 0.35 mL min^{-1}. The gradient started at 35% B, then increased linearly to 90% B over the next 4 minutes, and finally to 100% B over the next 2 minutes. Individual phytohormones were identified based on the decay of selected ions using a sensitive and selective mode of quantitative analysis, observing selected fragmentation reactions (MRM - multiple reaction monitoring). The recorded MRM values for individual hormones in positive (+) or negative (-) ionization are shown in Table S1. Data were analyzed using LabSolutions software 5.8 (Shimadzu, Kyoto, Japan). Log_{10} transformation of data was performed to ensure normal data distribution and homogeneous variances across treatments. Outliers were replaced by the average of valid measurements. The main effect of cultivation systems was determined using one-way ANOVA, and differences between mean values were analyzed using a post-hoc Tukey's HSD test. Statistical significance was considered at $P \leq 0.05$. All analyses were conducted using JMP Pro 13.

3. Results

3.1. Identification, functional and pathway enrichment for the DEG

In this study, we conducted an analysis of differentially expressed genes (DEGs) in the meristematic zone and elongation zone of taproots, as well as in the meristematic zone of lateral roots. This analysis allowed us to identify genes involved in the development of both root types within their respective growth zones and under different cultivation systems. Additionally, we examined the genetic profile at various stages of root elongation shortly after emergence. Subsequently, we performed an enrichment analysis of the Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) pathways for roots from different cultivation systems. The purpose of this analysis was to investigate how the growth and development of roots in different cultivation systems influence the genetic profile of taproots and lateral roots.

3.1.1. Comparative gene expression analyses of roots from rhizotrons and containers

In our study, conducted on oak roots grown in rhizotrons and containers, we identified a total of 16,120 differentially expressed genes (DEGs). Among these, 10,227 DEGs were significantly down-regulated, while 5,883 genes were significantly up-regulated in roots growing in rhizotrons. This indicates that the up-regulation of gene expression increased much more frequently than down-regulation within roots growing in the container system (Fig. 2 A). The effect of elongation on the number of DEGs was relatively consistent in both the

meristematic and elongation zones. The number of DEGs was highest when the taproots were longer during growth in containers compared to rhizotrons. This stage was also marked by a significant occurrence of DEGs specific only for the long taproot (Fig. 2 B-C). Thus, as the root grew, the number of DEGs increased in the container system. Furthermore, differences in the number of DEGs were also observed when comparing lateral roots. Lateral roots from containerized seedlings displayed a slight decrease in comparison to lateral roots harvested from rhizotrons (Fig. 2 D).

The functional analysis of these genes revealed their involvement in various metabolic pathways, including amino acid processing, ion transport, regulation of developmental processes, biosynthesis of secondary metabolites, and cell wall construction (Fig. 3).

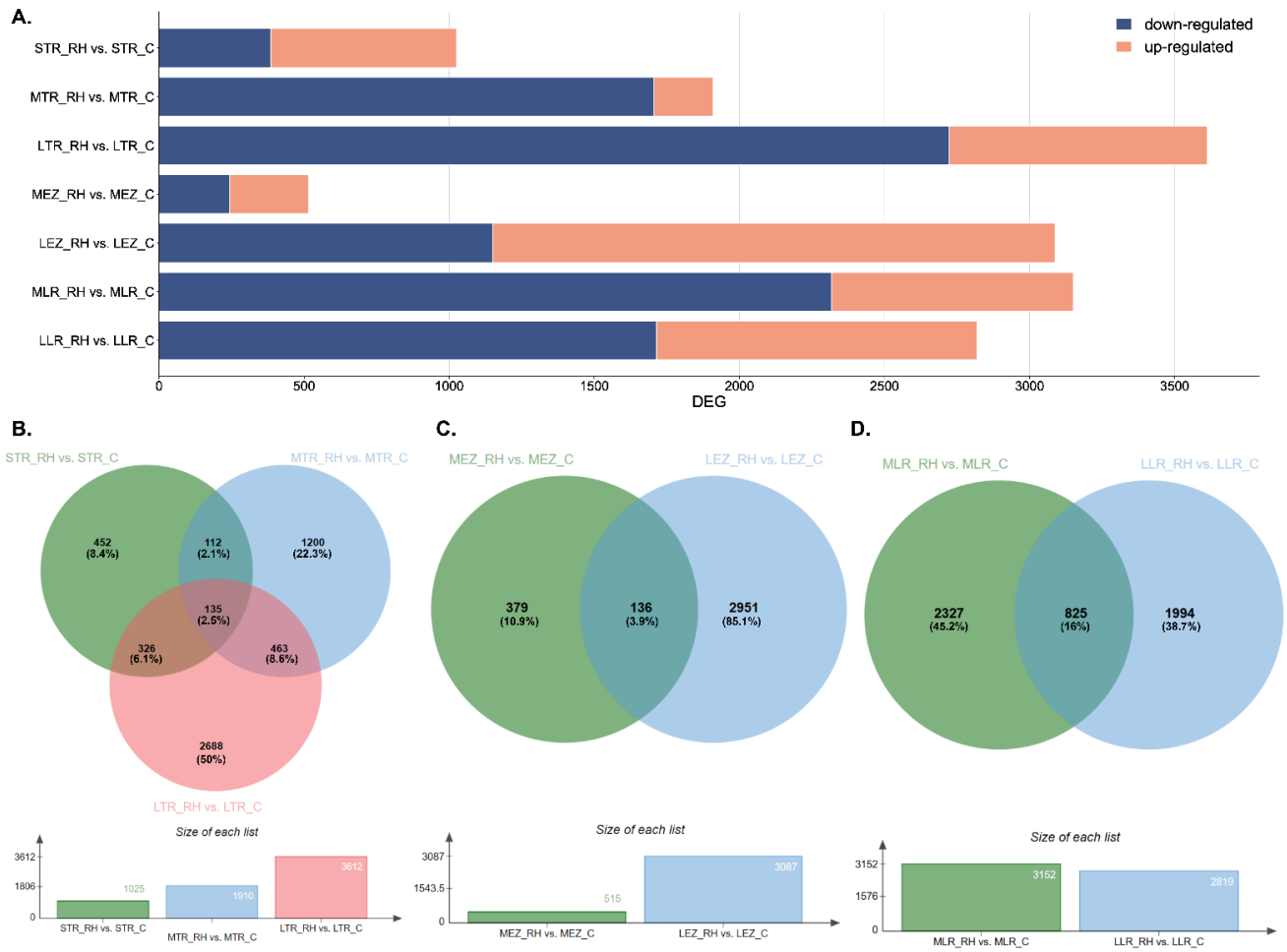

Fig. 2. A) Comparison of the number of differentially expressed genes (DEGs) in roots between rhizotron and container systems. Venn diagrams showing DEGs identified between B) short, medium, and long tips of taproots; C) elongation zone from medium and long taproots; D) and lateral roots harvested from medium and long taproots based on Bardou et al. (2014) [29]. Annotations with log2FC > 1.5 were used for the analysis of DEGs.

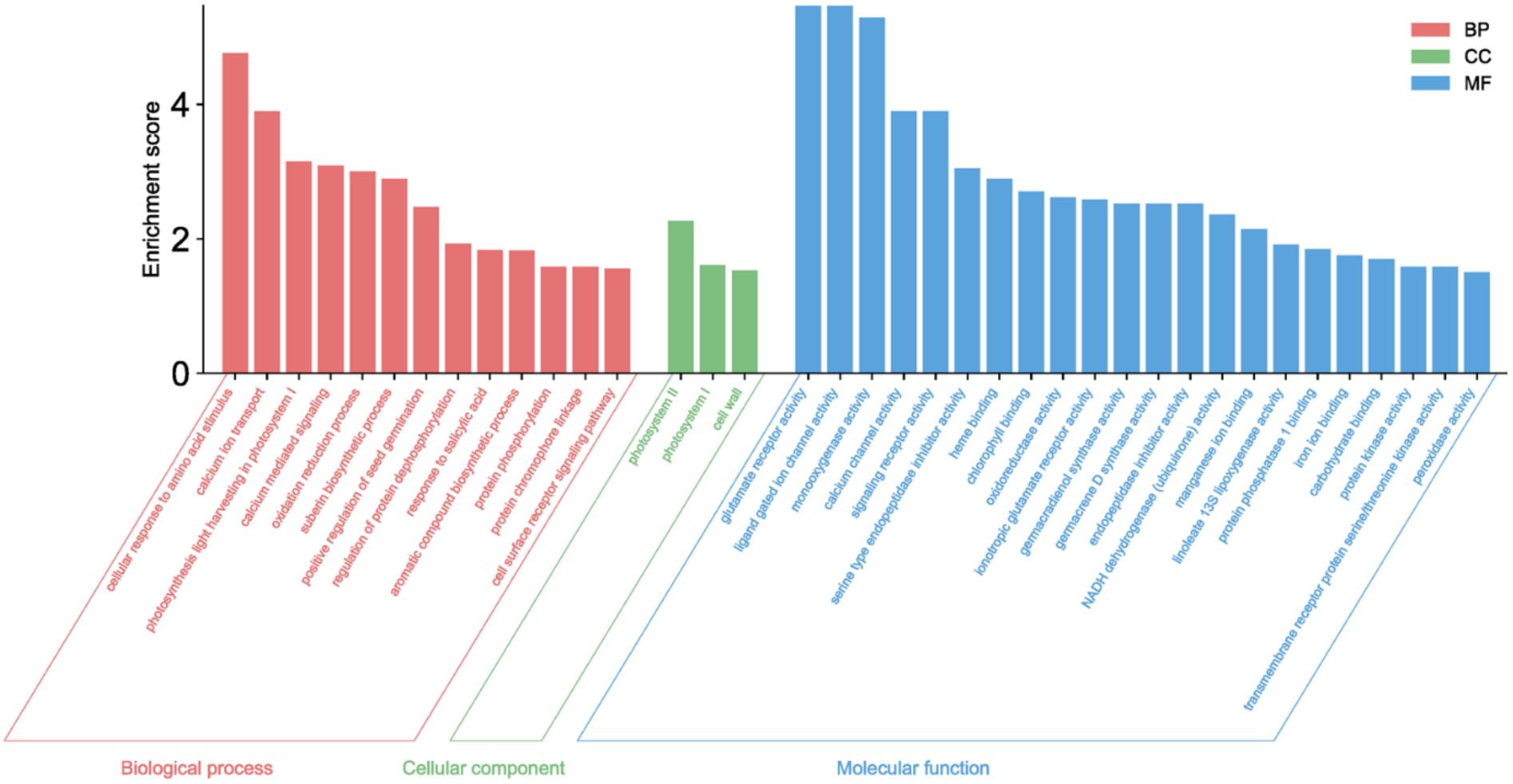

Fig. 3. The Gene Ontology (GO) enrichment analysis for the meristematic and elongation zones of taproots with different lengths, and the meristematic zone in lateral roots within the rhizotron and container comparison. Enrichment scores are represented as -log10(FDR). Enriched GO terms were selected based on an enrichment score > 1.5.

Next, we conducted KEGG pathway analysis of the differentially expressed genes (DEGs) to gain a deeper understanding of both metabolic and signal transduction pathways. Fig. 4 illustrates the top eight enriched pathways. Among the identified KEGG enrichment pathways, we selected only those with a false discovery rate (FDR) < 1.5. The largest number of metabolites was assigned to groups such as linoleic acid metabolism, amino sugar and nucleotide sugar metabolism, sesquiterpenoid and triterpenoid biosynthesis, and cutin, suberine, and wax biosynthesis.

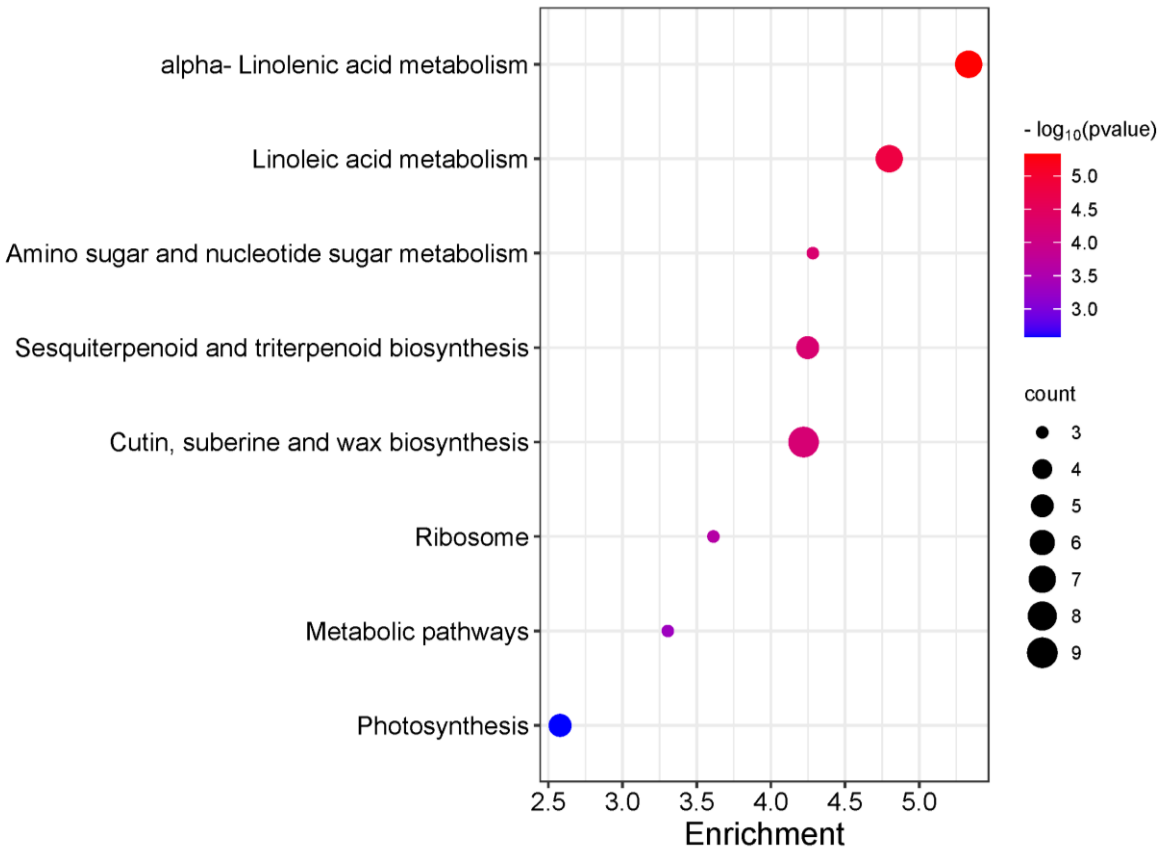

Fig. 4. KEGG enrichment analysis of differentially expressed genes (DEGs) in taproot and lateral roots among rhizotron and container cultivation systems. The degree of significance of the enrichment of DEGs in a pathway is indicated by -log10 (p-value). Circle size represents the number of genes. The color gradient from blue to red indicates low to high enrichment significance.

3.1.2. Gene expression changes within roots between in rhizotron and transplanted comparison

To investigate the potential biological processes involved in and regulating taproot elongation after its earlier inhibition in containers, we harvested regrowing taproots from containerized

seedlings that were transplanted to rhizotrons the following spring. A comparison between rhizotron-grown and transplanted roots revealed a total of 36,297 differentially expressed genes (DEGs), with 20,052 showing decreased expression and 16,245 being up-regulated in the roots of rhizotron seedlings (Fig. 5A). Furthermore, the analysis demonstrated a significantly higher number of DEGs when the taproot was of medium length, regardless of whether it was in the meristematic zone, elongation zone, or harvested lateral roots. The number of specific DEGs in medium-length roots significantly exceeded the number of DEGs in short or long taproots (Fig. 5B-D).

By investigating the activation of specific processes within the roots of transplanted seedlings compared to rhizotron-grown seedlings, we found that differentially expressed genes (DEGs) were notably associated with protein phosphorylation, lignin catabolic process, apoplast, and protein kinase activity (Fig. 6).

In contrast, we found only 3 significantly enriched KEGG pathways, and the highest expression was associated with protein biosynthesis. The top eight enriched pathways are illustrated in Fig. 7. We selected only those pathways with an FDR < 1.5.

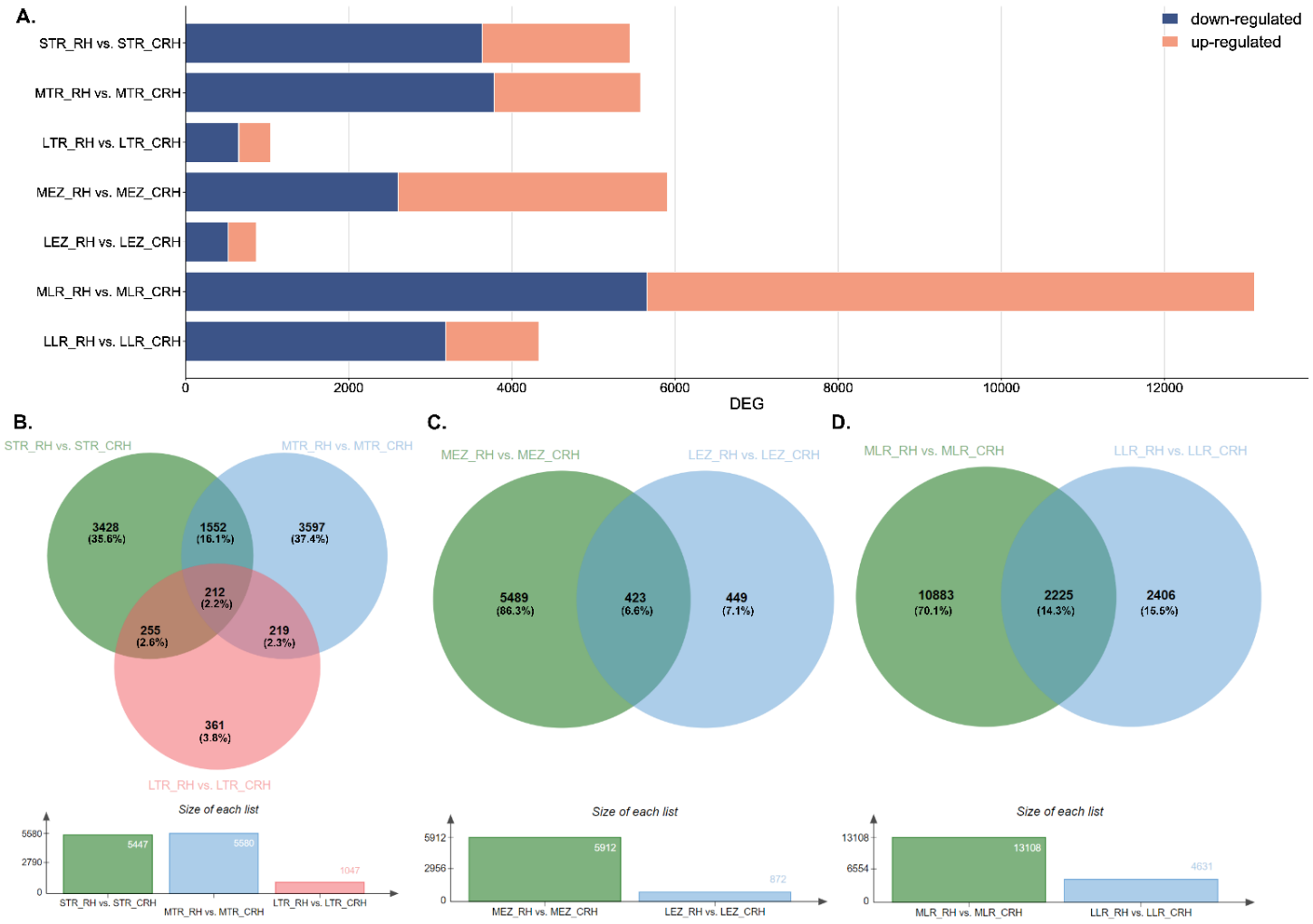

Fig. 5. A) The number of differentially expressed genes (DEGs) in roots between rhizotron and transplanted comparisons. Venn diagram depicting DEGs identified between B) short, medium, and long tips of taproot; C) elongation zone from medium and long taproots; D) and lateral roots harvested from medium or long taproots based on Bardou et al. (2014) [29]. Annotations with log2FC >1.5 were used for the analysis of DEGs.

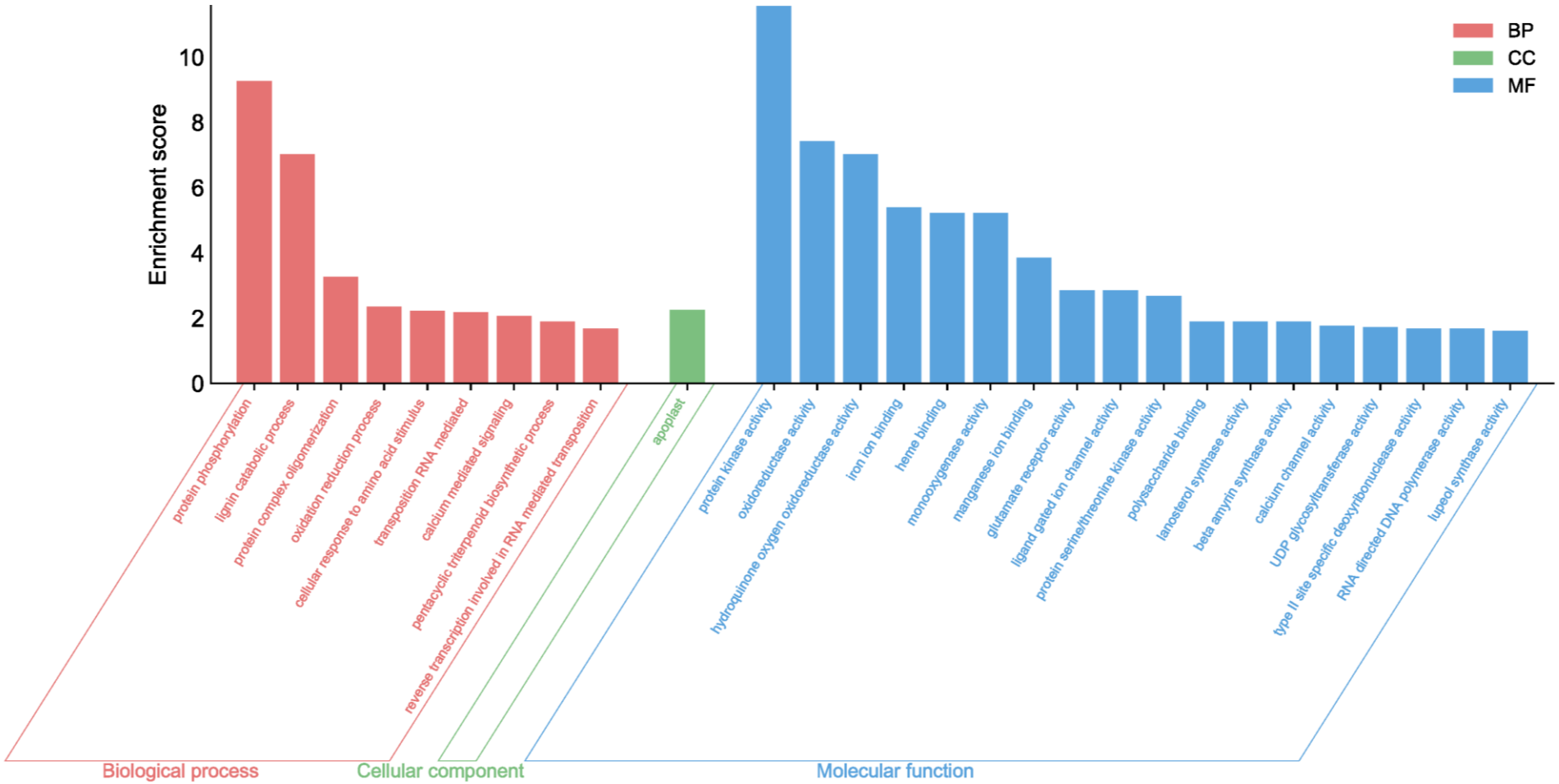

Fig. 6. The GO enrichment analysis for the meristematic and elongation zones of taproots of different lengths, and the meristem zone in lateral roots between rhizotron and transplanted comparisons. The enrichment score is represented as -log10(FDR). Enriched GO terms were selected based on an enrichment score <1.5.

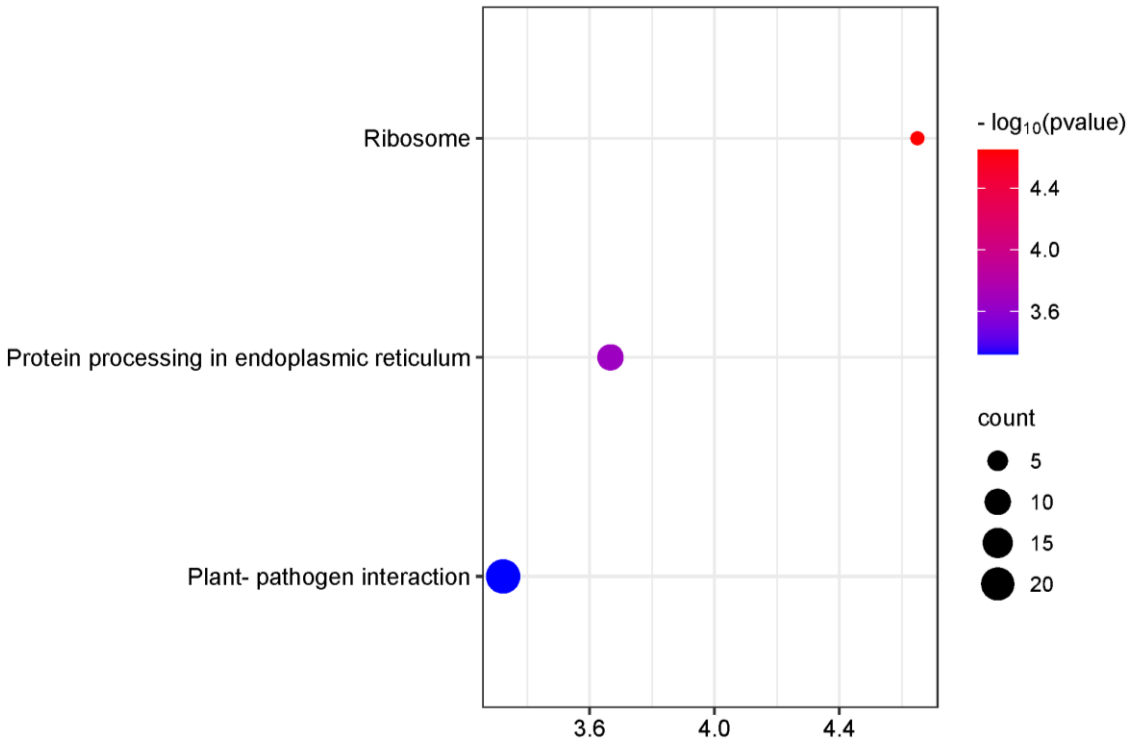

Fig. 7. KEGG enrichment analysis of differentially expressed genes (DEGs) in taproot and lateral roots comparing rhizotron and transplanted cultivation systems. The degree of significance of the enrichment of DEGs in a pathway is indicated by -log10 (p-value). Circle size represents the number of genes. The color gradient from blue to red indicates low to high enrichment significance.

3.1.3. Gene expression changes within roots between in container and transplanted comparison

We also investigated whether the removal of the growth-inhibiting factor in containers, after transplanting seedlings to the rhizotrons, had a distinct effect on gene expression patterns compared to those observed during taproot elongation in containers. The analysis of differentially expressed genes (DEGs) in oak roots growing in both container and transplanted systems revealed a total of 33,754 DEGs, with 16,735 down-regulated and 17,019 up-regulated in roots growing in containers. Notably, the new roots displayed a higher number of up-regulated genes than down-regulated ones in short taproot (Fig. 8A). This suggests that expression changes occurred after transplantation of seedlings from containers to the rhizotrons and influenced the expression pattern, which differed between taproots elongating in containers

and new roots produced after transplantation to rhizotrons. The highest number of DEGs was observed in lateral roots harvested from taproots of medium length, while this number was reduced in long taproots. A similar pattern was observed in the elongation zone of the taproot. Consequently, the induction of DEGs within roots after container seedlings transplantation appeared to be uniform across roots of different lengths, root zones, and types (Fig. 8B-D).

Functional analysis comparing container-grown and transplanted roots showed that differentially expressed genes (DEGs) were involved in processes related to secondary metabolites, such as lignin catabolic processes and suberin biosynthesis. Additionally, the analysis revealed processes related to the extracellular region, cell wall, and monooxygenase activity, which are consistent with the intensification of root formation (Fig. 8).

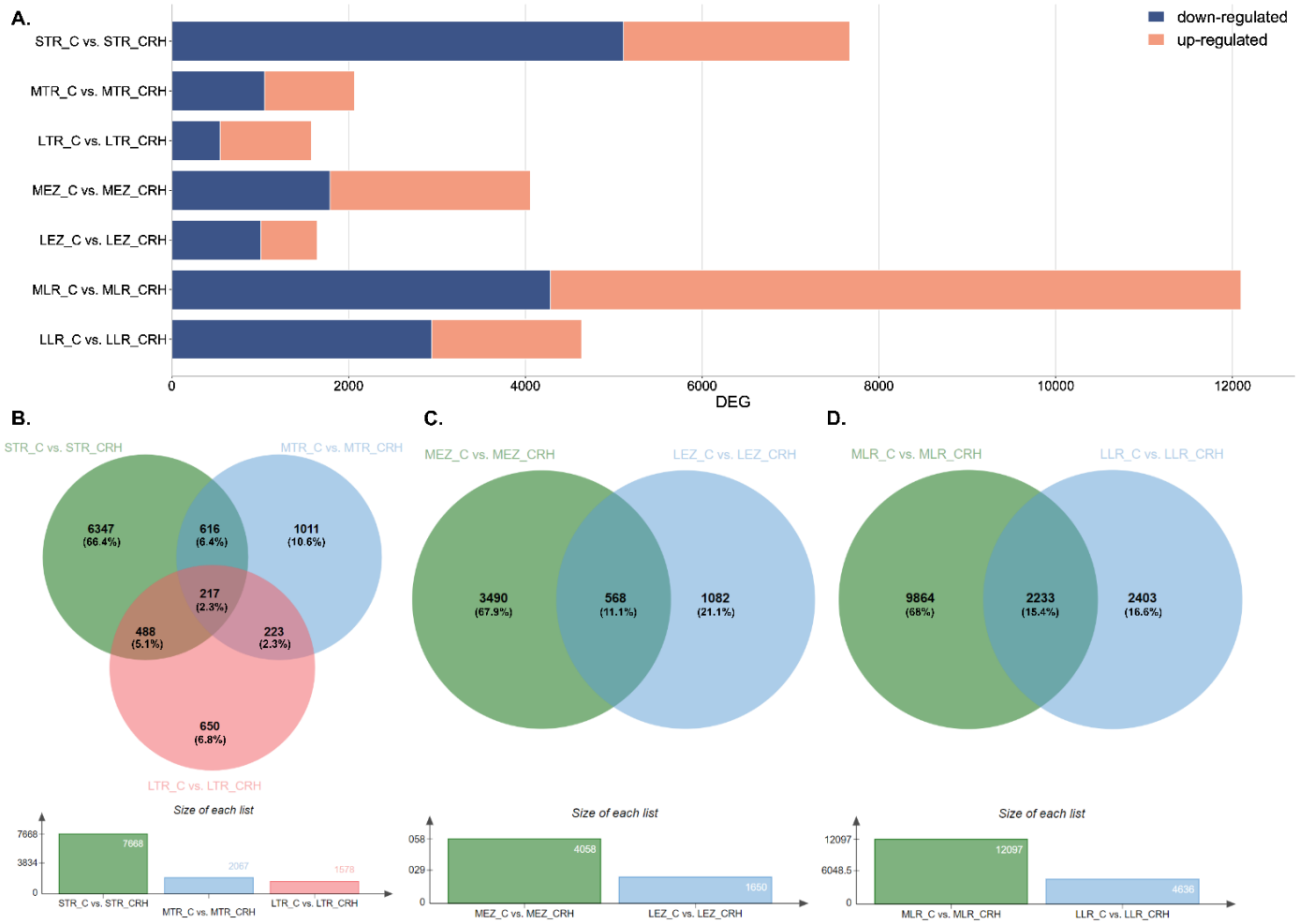

Fig. 8. A) The number of differentially expressed genes (DEGs) in roots within the container and transplanted comparison. Venn diagram of DEGs identified between B) short, medium, and long tips of taproot; C) elongation zone from medium and long taproot; D) and lateral roots harvested from medium and long length taproots based on Bardou et al. (2014). Annotations with log2FC >1.5 were used for the analysis of DEGs.

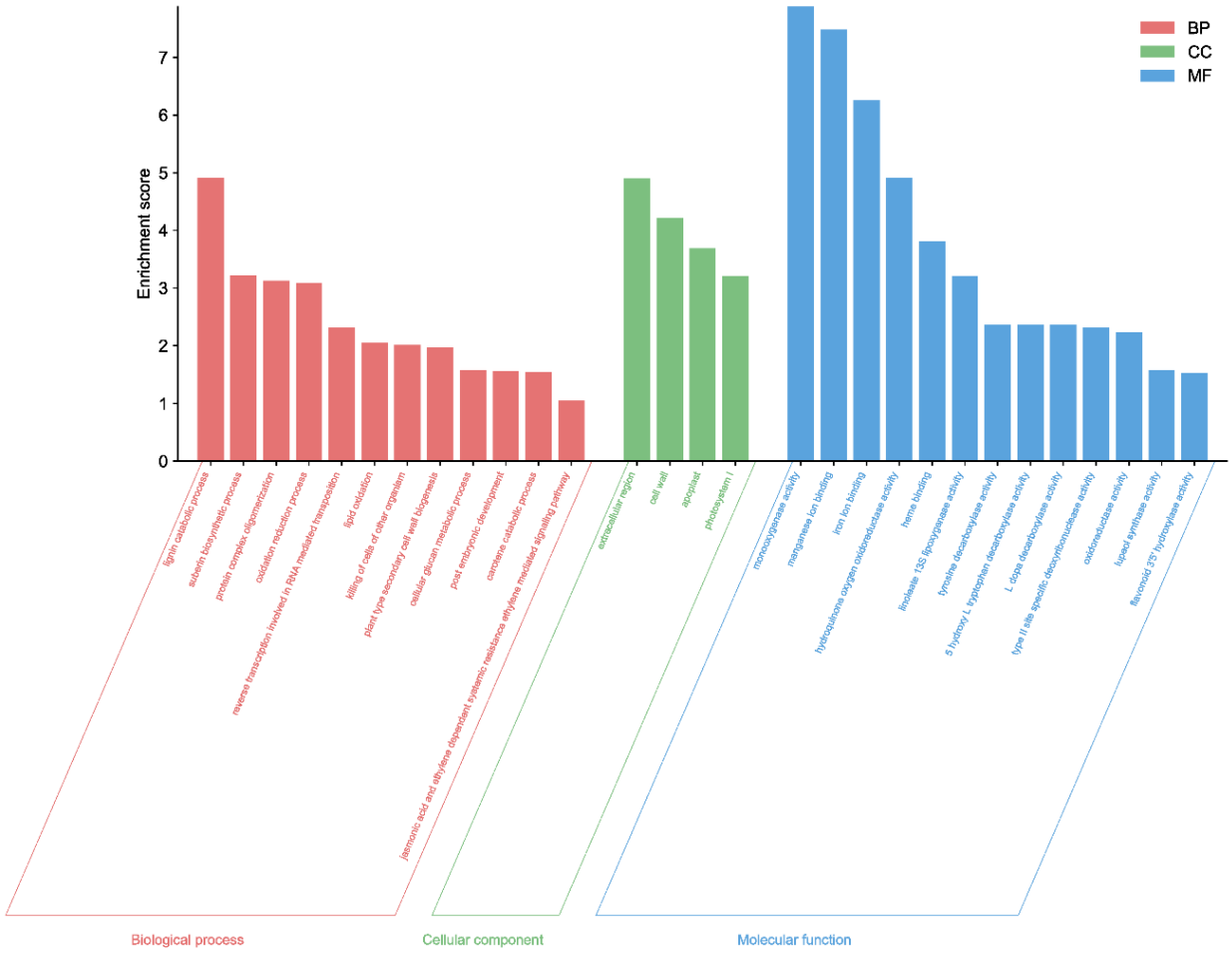

Fig. 9. GO enrichment analysis of differentially expressed genes (DEGs) in the meristematic and elongation zones of taproots of different lengths and the meristem zone in lateral roots, comparing container-grown and transplanted roots. The enrichment score is represented as -log10(FDR). Enriched GO terms were selected based on an enrichment score <1.5.

In this study, KEGG analysis revealed 7 significantly enriched pathways. The top eight enriched pathways were illustrated in Fig. 10, and many of them were related to linolenic acid metabolism and peptide synthesis. Among the identified KEGG enrichment pathways, we focused on those with an FDR < 1.5.

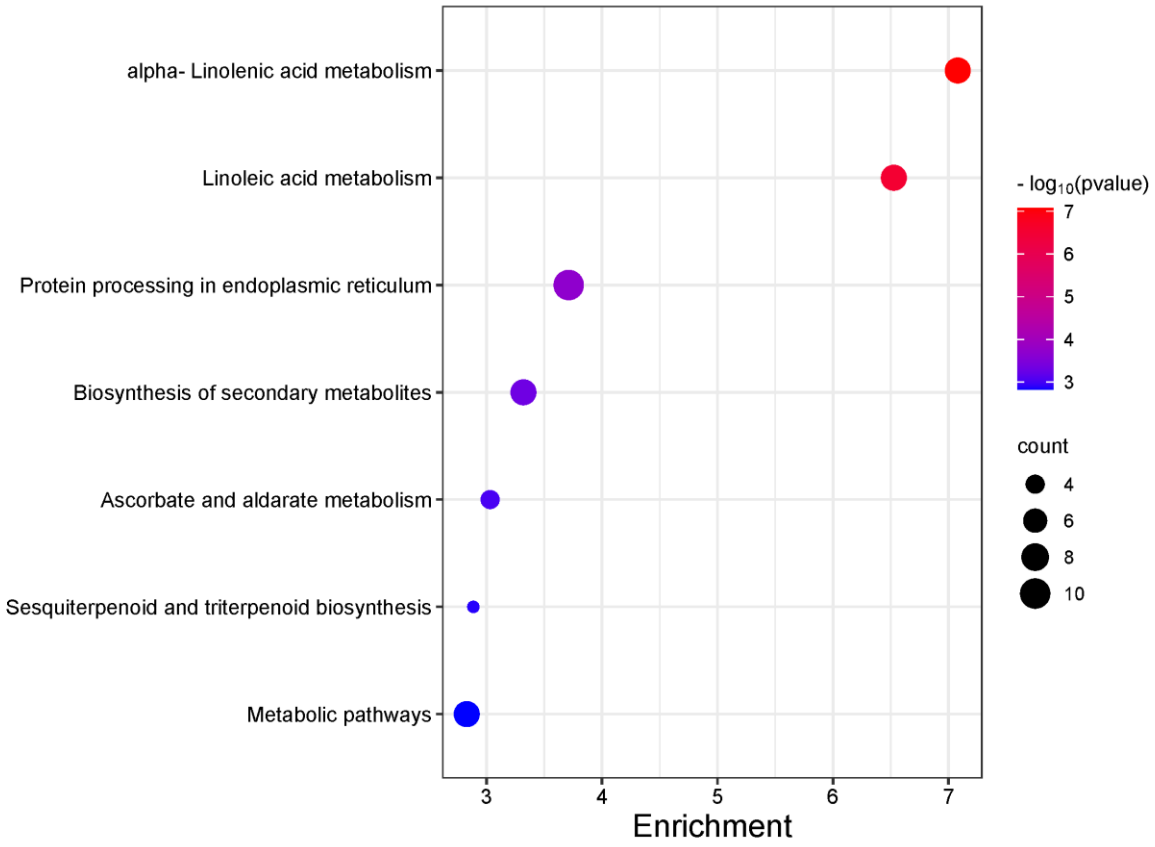

Fig. 10. KEGG enrichment analysis of DEGs in taproot and lateral roots within container and transplanted cultivation systems. The degree of significance of the enrichment of differentially expressed genes (DEGs) in a pathway is indicated by -log10 (p-value). Circle size represents the number of genes. The color gradient from blue to red indicates the level of enrichment significance, from low to high.

3.2.Hormonal analysis

To investigate how cultivation systems influence hormone production during the elongation of taproots and lateral roots, we quantified 17 different endogenous phytohormones in various root zones at different stages of growth under different cultivation conditions.

For the analysis of endogenous auxin levels in root cells, we measured the concentrations of IAA (indole-3-acetic acid) and its conjugates, including indole-3-acetyl-L-alanine (IA-Ala),

indole-3-acetyl-L-leucine (IA-Leu), indole-3-acetyl-L-phenylalanine (IA-Phe) and indole-3-acetyl-L-methionine (IA-Me), and second active form, indole-3-butyric acid (IBA). The concentration of IAA showed a substantial increase in both the meristematic and elongation zones of the transplanted taproots at each stage of elongation. In fact, its concentration was 2-fold or even more than 3-fold higher in the transplanted taproots compared to those of the rhizotron or container-grown seedlings (Fig. 11, Fig. S2). Additionally, in lateral roots harvested from medium-length taproots of transplanted seedlings, IAA and its conjugates exhibited significantly higher concentrations compared to those in the rhizotron and container-grown seedlings (Fig. S6).

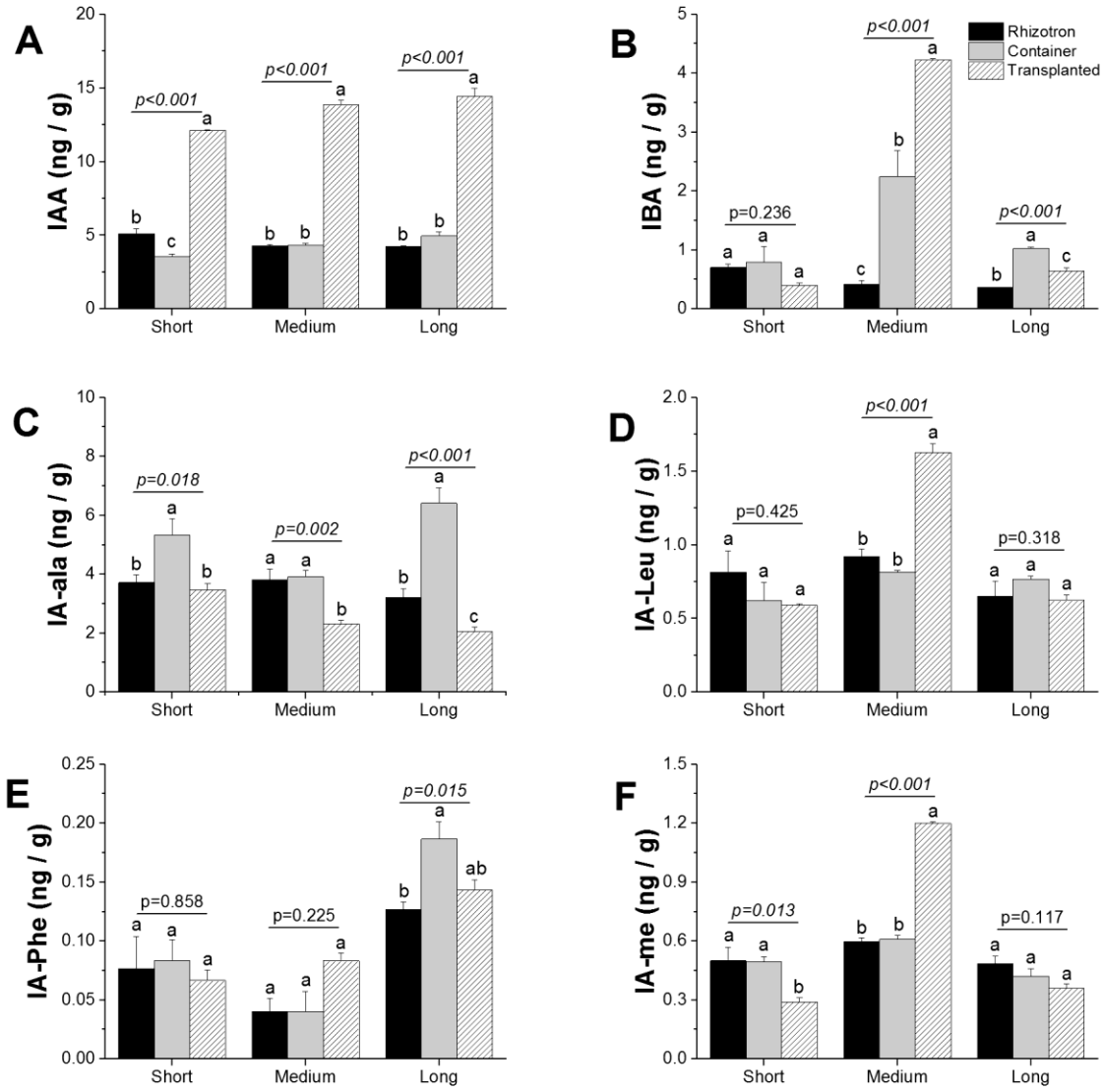

Fig. 11. The impact of cultivation systems: rhizotron (black color), container (grey color), and transplanted (hashed lines) on the concentration of IAA (A), IBA (B), IA-Ala (C), IA-Leu (D),

IA-Phe (E), and IA-Me (F) in the meristematic zone of short, medium, and long taproots of *Q. robur* seedlings. Each data point represents the mean hormone values for each root length class in each cultivation system, incorporating multiple individual roots from each cultivation system. Hormone concentration values were log10-transformed prior to statistical analysis, but the figures present non-transformed data. The significance of variation between cultivation systems within length classes (short, medium, and long) results from an analysis of variance (ANOVA), as indicated for each length class panel. Different lower-case letters indicate significantly different means among different cultivation systems within a given length class at $\alpha = 0.05$, according to Tukey's test. Error bars represent the standard error.

Another hormone we investigated was cytokinins, including trans-Zeatin (tZ) and N6-(2-Isopentenyl)adenine (2iP). Generally, we observed higher levels of endogenous tZ compared to 2iP, across different cultivation systems and root types. Additionally, both hormones exhibited higher concentrations within taproots of rhizotron and container seedlings compared to transplanted seedlings. Notably, there was a visible trend of higher tZ concentration in the medium taproot meristematic zone of rhizotron seedlings compared to container seedlings (Fig. 12). Our analysis indicated no statistically significant differences between the analyzed variants for 2iP in different cultivation systems. However, tZ concentration increased slightly as taproots of rhizotron, container and transplanted seedlings elongated, both in the meristematic and elongation zones of taproot (Fig. 12A, Fig. S2A). Regarding lateral roots, the concentration of both cytokinins was highest when harvested from long-length taproots of transplanted seedlings (Fig. S7). However, a reverse trend was recorded within lateral roots harvested from long taproots.

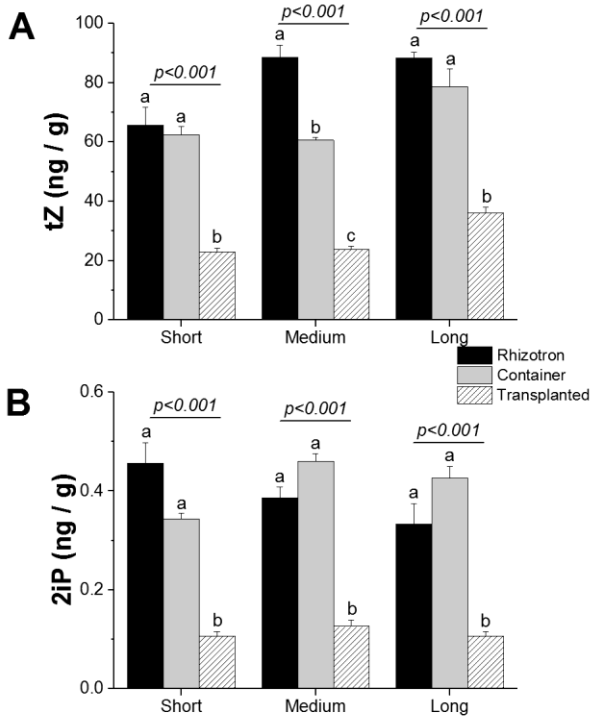

Fig. 12. The impact of cultivation systems: rhizotron (black color), container (grey color), and transplanted (hashed lines) on tZ (A) and 2iP (B) concentrations in the meristematic zone of short, medium, and long taproots of *Q. robur* seedlings. Each point represents the mean hormone values for each root length class in each cultivation system. The data points incorporate multiple individual roots from each cultivation system. Hormone concentration values were log10-transformed before statistical analysis, but figures present non-transformed data. The significance of variation between cultivation systems within length classes, i.e., short, medium, and long, results from an analysis of variance (ANOVA), and the results are presented for each length class panel. Different lowercase letters indicate significantly different means among different cultivation systems within a given length class at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

To understand the interplay between root elongation and ethylene concentration, as well as how different cultivation systems modulate its level, we measured the presence of 1-aminocyclopropane-1-carboxylic acid (ACC), which is the precursor of ethylene, in two zones of taproots and lateral roots. During taproot elongation in the rhizotron, we observed a concomitant increase in ACC in both the meristematic zone (Fig. 13A) and the elongation zone (Fig. S3A) of seedlings. Notably, the elongation zone of taproots growing in the rhizotron showed much higher levels of ACC. In contrast, in the container system, ACC levels peaked

when the roots were medium and decreased in long taproots. Additionally, the cultivation system had an impact on ACC levels, with significantly lower concentrations of ACC in taproots growing in the transplanted system. These roots exhibited only marginal changes in all three length classes, compared to roots growing in the container and in the rhizotron. Moreover, the emergence of lateral roots from medium or long taproots had a strong effect on ACC levels, with its concentration increasing in lateral roots harvested from long taproots in containers and transplanted seedlings, while ACC concentration changed only minimally between lateral roots in the rhizotron system (Fig. S8A).

Subsequently, we determined the level of endogenous abscisic acid (ABA) in oak roots, which is known as a stress hormone but also is engaged in root growth regulation. The highest levels of ABA were found in roots growing in the container system at all stages of development in both the meristematic zone (Fig. 13B) and the elongation zone (Fig. S3B). Another hormone, salicylic acid (SA), also showed significantly higher levels in seedlings growing in the container and rhizotron in every root zone and at every stage of elongation (Fig. 13C, Fig. S3C, Fig. S8C).

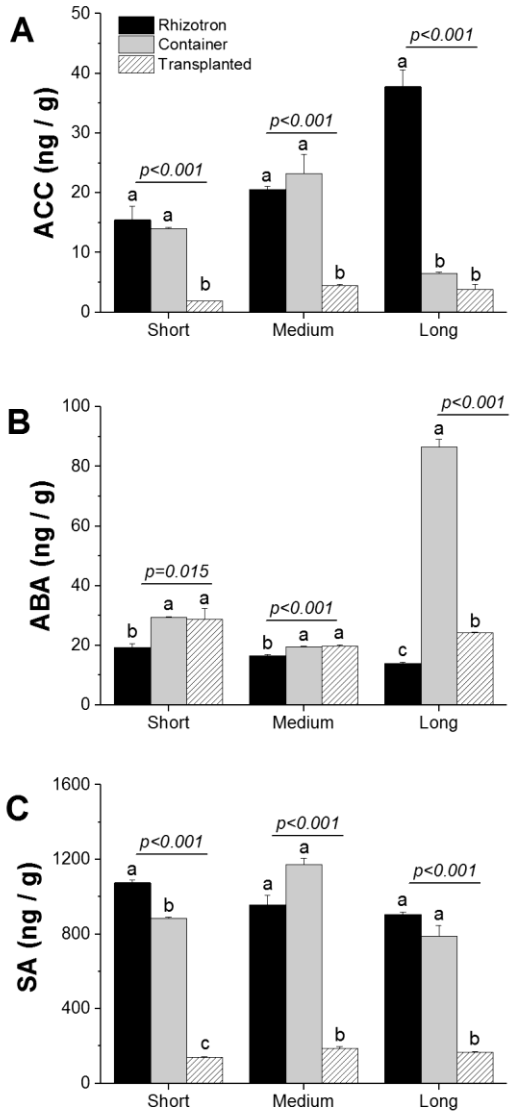

Fig. 13. The effect of cultivation systems: rhizotron (black), container (grey), and transplanted (hatched) on ACC (A), ABA (B), and SA (C) concentration in the meristematic zone of short, medium, and long taproots of *Q. robur* seedlings. Each point represents the mean hormone values for each root length class in each cultivation system. The hormone concentration values were log10-transformed before statistical analysis, but figures present non-transformed data. The significance of variation between cultivation systems within length classes (short, medium, and long) results from an analysis of variance (ANOVA) and is given for each length class panel. Different lowercase letters indicate significantly different means among different cultivation systems within a given length class at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

We also examined the levels of four gibberellins: GA3, GA1, GA7, and GA4. During the elongation of short taproots in all analyzed cultivation systems, GA4 and GA7 concentrations increased, irrespective of the root zone (Fig. 14C-D), except GA7 in the elongation zone (Fig. S4D). There were minor differences in GA4 and GA7 concentrations between the cultivation systems. On the other hand, GA1 and GA3 concentrations varied more across cultivation systems, but their concentration increased during taproot elongation in the meristematic zone of container and transplanted seedlings (Fig. 14). The same trend was observed for GA1 and GA3 in the elongation zone of container seedling taproots (Fig. S4A-B). The length of the taproot was also related to the gibberellins concentration within each cultivation system, where the meristematic zone of short and medium taproots of rhizotron and container seedlings had higher concentrations of gibberellins compared to transplanted seedlings. Conversely, the elongation zone of medium taproots displayed the highest concentration of gibberellins. Within lateral roots, the highest concentration of GA7 was visible in the rhizotron system, regardless of which taproot length point they were harvested (Fig. S9D). Transplanted seedlings produced lateral roots that generally had the lowest concentration of all gibberellin classes in medium and long taproots.

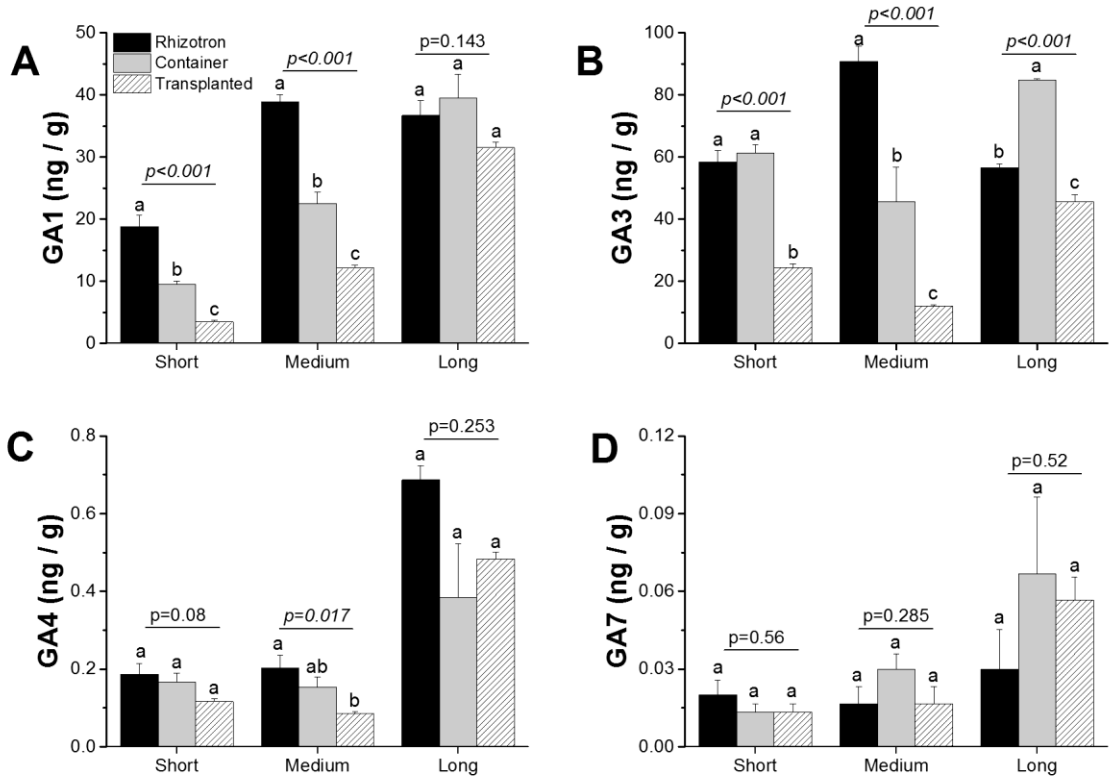

Fig. 14. The effect of cultivation systems: rhizotron (black), container (grey), and transplanted (hatched) on GA1 (A), GA3 (B), GA4 (C), and GA7 (D) concentrations in the meristematic zone of short, medium, and long taproots of *Q. robur* seedlings. Each point represents the mean hormone values for each root length class in each cultivation system. The hormone concentration values were log10-transformed before statistical analysis, but figures present non-transformed data. The significance of variation between cultivation systems within length classes (short, medium, and long) results from an analysis of variance (ANOVA) and is given for each length class panel. Different lowercase letters indicate significantly different means among different cultivation systems within a given length class at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

In addition, we examined the levels of jasmonic acid (JA) and its derivative methyl jasmonate (MeJA). The analysis revealed a significant decrease in both JA and MeJA in roots growing in the transplanted system compared to roots growing in the container and in the rhizotron (Fig. 15, Fig. S5, Fig. S10).

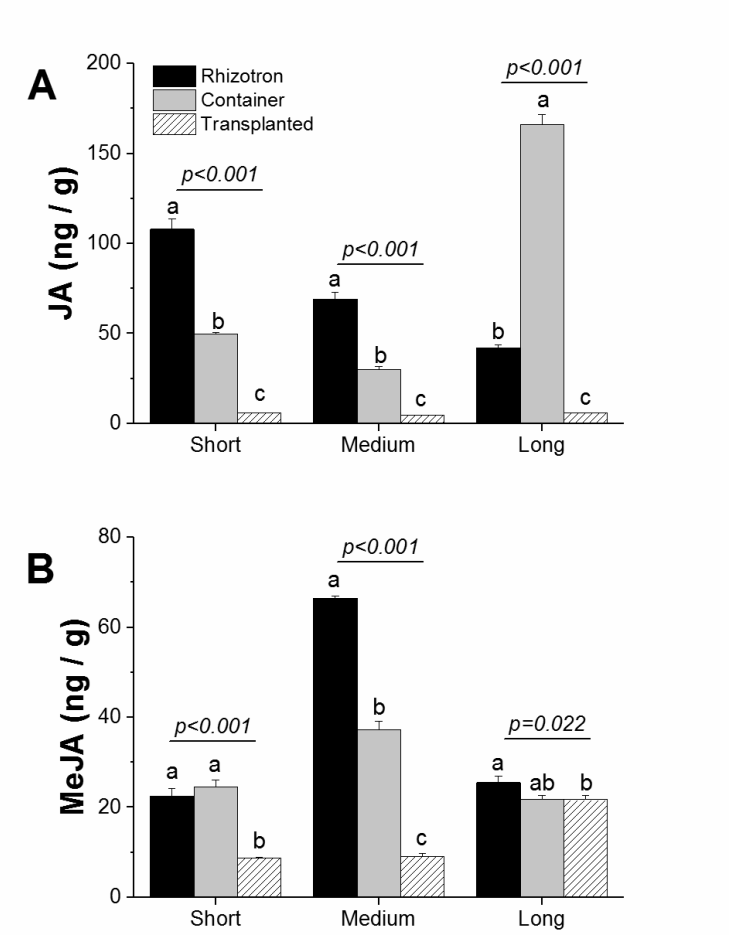

Fig. 15. The impact of cultivation systems (rhizotron - black color, container - grey color, and transplanted - hashed) on JA (A) and MeJA (B) concentrations in the meristematic zone of short, medium, and long taproots of *Q. robur* seedlings. Each data point represents the mean hormone values for each root length class in each cultivation system, incorporating multiple individual roots from each cultivation system. Hormone concentration values were $\log_{10}$-transformed before statistical analysis, but figures present non-transformed data. Significance of variation between cultivation systems within length classes (i.e., short, medium, and long) results from an analysis of variance (ANOVA) and is indicated for each length class panel. Different lowercase letters indicate significantly different means among different cultivation systems within a given length class at $\alpha = 0.05$, as determined by Tukey's test. Error bars represent the standard error.

4. Discussion

Root elongation in trees is regulated by a complex interplay of internal and external factors, mediated through intricate signaling pathways [13, 14, 30, 31]. Understanding the integration

of these internal and external signals in modulating root growth is of particular significance for tree cultivation. Despite substantial research, many essential questions remain unanswered concerning the specific signals and signaling pathways that govern taproot growth. Therefore, our study aims to illustrate and confirm the general pattern of taproot growth and lateral root emergence. However, we have also observed that gene expression and hormone production within the root tip of the taproots play a central role in contributing to growth organization in different cultivation systems and act as regulators of lateral root formation. Through differential gene expression analysis and functional annotations (GO and KEGG), we have identified factors involved in supporting taproot growth, as well as those halting its elongation and delaying lateral root formation. This evidence indicates that signaling arising from taproot tips likely reflects the developmental requirements of the taproot system for different hormones. To the best of our knowledge, this study represents the first report investigating gene expression changes between distinct cultivation systems, encompassing different taproot tissues (meristematic and elongation zones) and various root types (taproot and lateral root) in trees. These findings contribute valuable insights into the regulatory mechanisms of root growth in trees and can have significant implications for tree cultivation and management practices.

4.1. Profiling of differentially expressed genes in roots growing in different cultivation systems

Our transcriptome analysis revealed that as the taproot grows, the number of differentially expressed genes (DEGs) increases when comparing container-grown and rhizotron-grown seedlings (Fig. 2). Interestingly, we observed an increased number of down-regulated DEGs during taproot elongation in the meristematic and elongation zones of rhizotron-grown seedlings, suggesting induced expression of genes in container-grown seedlings. This response may be attributed to container conditions, where taproots sense air at the bottom of the container, resulting in a large increase in DEG expression, likely reflecting signals that hamper root growth. In contrast, undisturbed taproot elongation of rhizotron seedlings is not negatively affected. On the other hand, a significant decrease in the number of genes involved in root growth can be observed in long roots, both in the meristematic and elongation zones, when comparing rhizotron-grown and transplanted seedlings (Fig. 5). The enhanced DEGs expression in transplanted and rhizotron-grown seedlings could be an adaptive response involved in the modulation of root growth extension after germination [32]. Since the ability of trees ability to access water in deeper soil layers is crucial to minimize water stress during periods of drought [5, 6, 10], this potential might enable rapid adjustment of taproot growth to

regulate water absorption under unfavorable conditions, whereas under unaltered growth, fewer genes are involved in root elongation. When comparing root growth between container and transplanted seedlings, the results showed that the ability of trees to restart growth of taproots relies on the enhanced genes expression. Observed down-regulation in container seedlings may have affected their taproot growth cessation earlier, possibly shortly after germination or when reaching a medium length. It appears that sequential events at the level of gene expression are related to taproot growth within container seedlings, with both the apical meristem and elongation zone responding to growth conditions. Conversely, the up-regulation of a series of genes also defines the recovery potential of transplanted seedlings as their replanting from containers to rhizotrons induces rapid changes in gene expression, which gradually decrease with root elongation, reaching expression levels similar to seedlings growing in rhizotrons, especially when roots are longer. This decrease is coincidental with the observed duration of elongation, as the initial phase after germination exhibits the highest growth rate with high cell proliferation [33]. Therefore, it can be inferred that container cultivation of pedunculate oak induces gene expression changes that may influence the further growth of these plants, after transplantation into natural conditions. These findings shed light on the molecular mechanisms underlying root growth regulation in different cultivation systems and provide valuable insights into the adaptability and recovery potential of oak seedlings under changing environmental conditions.

The functional Gene Ontology (GO) analysis revealed that genes associated with "cellular response to amino acid stimulus" exhibited the highest activity in roots growing in rhizotrons compared to containers (Fig. 3). This suggests that transcriptional factors regulating changes in cell state or activity in response to an amino acid stimulus may play a crucial role in promoting taproot rooting in rhizotrons. Considering that the roots in rhizotrons and containers are relatively young (shortly after germination), the enhanced expression of glutamate receptor family genes (*GLR27*, *GLR25*, *GLT24*) may promote taproot elongation, as their expression was reduced to a higher degree in container seedlings. Furthermore, in rhizotron taproots, there was an increase in the expression of genes associated with ion processing, such as "calcium ion transport," "calcium-mediated signaling," "calcium channel activity," and "glutamate receptor activity." These genes are involved in calcium signaling [34], suggesting that this rise in expression is necessary for maintaining continuous root growth. Calcium is involved in processes such as regulating primary root growth through auxin signaling, modulating primary root growth through cytokinin signaling, promoting primary root elongation by interfering with

brassinosteroid signaling, and being involved in abscisic acid-inhibited root growth through ROS signal transduction or influencing ethylene biosynthesis plays a significant role in growth and development [35]. Additionally, calcium facilitates primary root growth by regulating cell wall reformation and is also involved in root development in the absence of sucrose [36]. It also influences key regulators of root growth, *PLETHORA1* and *PLETHORA2*, and positively modulates root meristem size and promotes primary root growth through interaction with the Arabidopsis glutamate receptor-like protein AtGLR3.6 [36]. These results confirm that root growth regulation is determined early, and environmental manipulation affecting calcium-induced gene expression may provide an opportunity to promote specific gene expression-hormone production and thereby affect taproot growth of container seedlings before they reach the bottom of the container and die. The suppressed expression of calcium-related genes in container seedlings supports our assumption that calcium may be a key factor promoting root elongation and growth.

In the comparison between roots growing in the rhizotron and transplanted roots, we observed an enrichment of genes associated with developmental processes such as "protein phosphorylation" and "protein kinase activity." Protein phosphorylation plays a crucial role in metabolism and signaling pathways. Additionally, genes related to "lignin catabolic process" were also observed (Fig. 6). Lignin in cells provides an extracellular barrier to solutes and water and plays a key role in maintaining nutrient homeostasis [37]. The increased activity of genes associated with the "apoplast" may indicate enhanced water transport for the well-developed shoot of transplanted seedlings that is supported by the enhanced expression of *AGT1*, *GL17*, *GP1*, and *EXL7*. Interestingly, our results indicate that genes expressed in the taproot of rhizotron and transplanted seedlings may have similar functions, with growth-promoting processes possibly even higher in the restored taproot of transplanted seedlings (Fig. 6), confirming the existence of recovery potential enabling growth taproots growth that were previously hampered due to environmental factors or cultivation conditions in containers. Especially that in transplanted seedlings, when comparing to containers, we found the enhanced activity of genes associated with lignification and suberization that regulate water and nutrient absorption and enhance root mechanical resistance. [38, 39]

Other genes related to "protein complex oligomerization," "extracellular region," "lipid oxidation," and "linoleate 13S lipoxygenase activity" may indicate the activation of intense developmental processes and tissue specialization, possibly leading to an increased number of genes associated with the "lignin catabolic process" (Fig. 8). The increased metabolic pathway

observed in the KEGG analysis related to fatty acid production (Fig. 9) may indicate enhanced production of jasmonic acid, which participates in the response to pathogen attacks but also may promote root development, acting as a modulator of auxin homeostasis [40, 41]. It appears that transplanted seedlings promote taproot growth after planting in the rhizotron, whereas taproots of seedlings growing in containers promoting vigorous lateral root growth what may be associated with limited space for taproot growth and its inhibition before the root reaches the bottom of the container. However, confirmation of this thesis requires additional research and verification.

4.2. Analysis of plant hormones in roots

The molecules that elicit and regulate root growth and development in plants are known as plant hormones, and they can simultaneously induce root growth initiation as well as root growth inhibition. For example in Arabidopsis, auxin has been shown to act as either a positive or negative regulator of primary root growth, depending on its concentration. High concentrations of auxin (~10^{-6} M) impede primary root elongation, while very low concentrations (~10^{-8} M) promote root elongation, and the effect may be tissue and zone-specific [16, 42]. However, there is limited research pertaining to the impact of hormonal interactions on taproot and lateral root elongation under different nursery cultivation systems of forest trees. Hence, it is crucial to examine hormone levels at different plant growth stages and measure the concentrations of other hormones when analyzing plant hormone effects, especially in long-lived trees. Analyzing different forms of hormones, we revealed that IAA is the dominant form of auxin, and its concentration differs depending on the cultivation system. Roots grown in the transplanted system exhibited a different pattern of auxin levels compared to those grown in containers and rhizotrons, both in the meristematic and elongation zones of the taproot. As the taproot elongated, the level of IAA also increased in taproots of seedlings grown in transplanted system, contrasting with seedlings grown in the rhizotron and container in the meristematic zone. However, a decrease in IAA as taproot elongation occurred was observed in lateral roots of transplanted seedlings. When transplanting seedlings from containers to rhizotrons, we observed the activation of genes involved in auxin biosynthesis in both taproot and lateral roots, as revealed by the analysis of differentially expressed genes (DEGs), in which expression levels of auxin-encoding genes were higher in transplanted seedlings than in rhizotron seedlings (Table S2). Hence, high auxin concentration is required for taproot elongation of transplanted seedlings, while high auxin concentration in taproot tips may operate downstream to regulate lateral root growth by direct interaction with increased

levels of cytokinin as indicated for Arabidopsis by [18], and manifests apical dominance of taproots, which promotes the growth of the primary root while inhibiting lateral root initiation, allowing deeper soil exploration over longer distances [18, 43]. In Arabidopsis, cytokinin can inhibit lateral root growth by reducing the expression of *PIN* genes, which encode auxin efflux carriers in lateral root founder cells [44]. Consequently, cytokinin regulates root architecture by balancing the promoting role of auxin in lateral root development in organisms with a long main root [18, 45]. Our findings of lower cytokinin concentration in the meristematic and elongation zones within taproots and high auxin concentration in lateral roots harvested from medium taproots of transplanted seedlings but higher levels of cytokinin in the meristematic and elongation zones of the taproot observed in rhizotron and container seedlings, support the conclusion that apical dominance within transplanted plants forms later than in latter cultivation systems. The explanation for this contradictory observation is that a lower auxin-to-cytokinin ratio that promote taproot growth in rhizotron but is formed later in transplanted seedlings processes due to time necessary for reestablishment of taproot growth, as indicated by elevated cytokinin concentration in LLR within transplanted seedlings, as the main form of cytokinin, i.e., tZ, slightly increased with root elongation, especially among transplanted seedlings. This, along with the decreasing IAA level, indicates the involvement of an auxin/cytokinin balance in root elongation of transplanted seedlings. The ability to access water from deeper sources is crucial for maintaining tree vitality and services under ongoing and predicted warming. For instance, drought stress can decrease cytokinin synthesis while simultaneously increasing auxin levels, thereby promoting taproot elongation [46].

In addition to the auxin-cytokinin balance, our study also revealed the involvement of gibberellins in promoting taproot growth. This is supported by higher concentrations of dominant gibberellin forms (GA1, GA3) within the meristematic and elongation zone (GA3) of short and medium taproots in both rhizotron and transplanted seedlings. This finding confirms earlier reports of the stimulatory potential of gibberellins on primary root growth [47], especially through their interaction with auxin [48]. Furthermore, the interplay between auxins and gibberellins may modulate taproot elongation in transplanted seedlings. For a visual comparison, please refer to Figure S1 and Figure S4, which show the concentrations of auxins and gibberellins within the elongation zone of transplanted seedlings.

We also observed a concomitant increase in the ethylene precursor ACC in taproots grown in container and rhizotron systems compared with transplanted seedlings. The presence of a high level of ACC in medium taproots of container seedlings, simultaneously with an

enhanced presence of auxin in long taproots of the same cultivation system, suggests that the inhibition process must have taken place before root growth cessation. The clue lies in how the pathway of successive hormone involvement is controlled. High concentrations of ethylene can inhibit primary root growth by suppressing cell proliferation in the apical meristem and the elongation zone [20, 49]. Additionally, the observed sharp decrease in ACC levels in long roots of container seedlings (Fig. 13A), along with higher concentrations of IBA and IA-ala, and a slight increase in tZ at the short and medium taproots, seems to impede their elongation before they reach the bottom of the containers. This effect appears to be due to these factors rather than solely the presence of ethylene itself. In the system with undisturbed growth i.e. rhizotron the enhanced concentration of ACC in long taproots of rhizotron seedlings suggests that its high level in itself is not sufficient for hampering root growth, as continuous taproot growth of rhizotron seedlings is supported by enhanced concentrations of tZ and gibberellins, which are necessary and crucial for continuous growth [50], confirming that the manner by which ethylene controls root inhibition patterning in container seedlings dependent on other hormones Thus, based on the given hormone ratio (lower IAA concentration than CK and predicted higher ET concentration than IAA), it can be presumed how the growth of the main root would be inhibited, especially in container seedlings. The abscisic acid (ABA) synthesis, where low concentrations stimulate primary root growth, while high concentrations have inhibitory effects [51]. In this scenario, growth promotion by ABA at low concentrations is independent of ethylene action and only requires auxin signaling and its transport through auxin efflux carriers, whereas inhibitory effects of ABA at high concentrations would be regulated through auxin and elevated concentration of ethylene [51]. The fact that taproots of rhizotron and container seedlings produced a low amount of ABA, but ABA concentration significantly increased in container seedlings, indicates that this hormone may not promote root elongation but may operate as a factor perpetuating growth inhibition induced earlier by ethylene. The high ABA levels observed simultaneously with only slight changes in GA concentrations in the meristematic or elongation zone of taproots within container seedlings confirm that in oaks, the ABA-Gibberellin complex does not act in a regulatory feedback loop inhibiting elongation of taproot cells and growth inhibition is more likely to be due to the effects of ethylene [52]. Also, other hormones such as jasmonic acid (JA) and its methylated form (MeJA), which are enhanced in concentration in the lateral roots of container seedlings (Fig. S10) and show higher expression of genes involved in jasmonate biosynthesis and fatty acid production (KEGG) – serving as a precursor for JA biosynthesis [40], may be directly involved in the inhibition of taproot growth [53, 54], and should promote lateral root growth in container seedlings.

However, it should be noted that the influence of hormones on root growth is complex and dependent on multiple factors, such as plant species, developmental stage, environmental conditions, and molecular regulatory factors. Nevertheless, our DEG analysis of genes encoding hormone biosynthesis precursors showed a similar pattern to the plant hormone level analysis (Table S2).

5. Conclusion

In summary, our transcriptome analysis provided valuable insights into the gene expression patterns and hormone involvement during taproot growth in different cultivation systems. This container bottom response, triggered by the taproots sensing air in the container, could result in signals that hinder taproot growth in some seedlings. In contrast, rhizotron-grown seedlings exhibited taproot elongation without negative effects on gene expression. Comparing rhizotron-grown and transplanted seedlings, we observed a significant decrease in the number of genes involved in root development in long taproots of rhizotron seedlings. The up-regulation of DEGs in transplanted seedlings is related to taproot growth, indicating a recovery potential for growth in taproots that were hampered when seedlings were previously growing in the container, and the ability of trees to restart growth after transplantation relies on enhanced gene expression, promoting elongation mechanisms This recovery potential may play a crucial role in adjusting taproot growth for water absorption from deeper soil layers under water scarcity. . Functional GO analysis revealed that genes associated with "cellular response to amino acid stimulus" exhibited the highest activity in roots growing in rhizotrons, indicating that transcription factors responding to amino acid stimuli promote taproot rooting in this system. Enhanced expression of glutamate receptor family genes in rhizotron taproots suggests their role in taproot elongation. Additionally, genes associated with ion processing and calcium signaling were up-regulated in rhizotron taproots, highlighting their importance in maintaining continuous root growth. Comparing roots growing in containers and transplanted roots, genes involved in the "suberin biosynthesis process" were most active in container seedlings, reflecting root response to stress within container seedlings. Analyzing the hormone profiles, we found that auxin (IAA) concentration differed among the cultivation systems, with higher levels in taproot of transplanted seedlings. Cytokinin and gibberellin levels were higher in rhizotron, thus promoting continuous taproot growth. ABA showed complex patterns, indicating its involvement in taproot growth inhibition of container seedlings. In conclusion, our study demonstrated that transplanting roots from containers to rhizotrons activates a series of molecular reactions that promote taproot growth, while plants grown in containers may

restrict taproot growth through a complex hormone network. Understanding these molecular mechanisms can help optimize cultivation practices and promote healthy root growth, especially in the early stages of seedling growth and after transplantation into the field. Further research is required to confirm and expand upon these findings and explore the interactions between multiple endogenous factors and their impact on root development, particularly in species other than model plants.

6. Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

The datasets generated and/or analyzed during the current study are available in the NCBI GEO repository, with accession number GSE181860 (https://www.ncbi.nlm.nih.gov/geo/query/acc.cgi?acc=GSE181860). All data generated or analyzed during this study are included in this published article and its supplementary information files.

Competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Author's contributions

PK drafted the manuscript. PK, MZ and PG designing the research. PK and PG conducted the transcriptome analyses. PK and JK conducted the hormone analyses. PK, MZ and JM conducted the statistical analyses. MZ conceived the project and sought funding for it. All authors contributed to the article editing, and approved the submitted version.

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Not applicable

Authors' information

Not applicable

References

1. Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG *et al*: **Global convergence in the vulnerability of forests to drought**. *Nature* 2012, **491**(7426):752-755.
2. Gessler A, Cailleret M, Joseph J, Schönbeck L, Schaub M, Lehmann M, Treydte K, Rigling A, Timofeeva G, Saurer M: **Drought induced tree mortality- a tree-ring isotope based conceptual model to assess mechanisms and predispositions**. *New Phytologist* 2018, **219**(2):485-490.
3. Haavik LJ, Billings SA, Guldin JM, Stephen FM: **Emergent insects, pathogens and drought shape changing patterns in oak decline in North America and Europe**. *Forest Ecology and Management* 2015, **354**:190-205.
4. Rodríguez-Calcerrada J, Sancho-Knapik D, Martin-StPaul NK, Limousin J-M, McDowell NG, Gil-Pelegrín E: **Drought-induced oak decline—factors involved, physiological dysfunctions, and potential attenuation by forestry practices**. In: *Oaks Physiological Ecology Exploring the Functional Diversity of Genus Quercus L.* Edited by Gil-Pelegrín E, Peguero-Pina JJ, Sancho-Knapik D. Cham: Springer International Publishing; 2017: 419-451.
5. Zadworny M, Jagodziński AM, Łakomy P, Ufnalski K, Oleksyn J: **The silent shareholder in deterioration of oak growth: common planting practices affect the long-term response of oaks to periodic drought**. *Forest Ecology and Management* 2014, **318**:133-141.
6. Barbeta A, Peñuelas J: **Increasing carbon discrimination rates and depth of water uptake favor the growth of Mediterranean evergreen trees in the ecotone with temperate deciduous forests**. *Global Change Biology* 2017, **23**(12):5054-5068.
7. Padilla F, Pugnaire F: **Rooting depth and soil moisture control Mediterranean woody seedling survival during drought**. *Functional Ecology* 2007:489-495.
8. Mucha J, Jagodziński AM, Bułaj B, Łakomy P, Talaśka AM, Oleksyn J, Zadworny M: **Functional response of *Quercus robur* L. to taproot pruning: a 5-year case study**. *Annals of Forest Science* 2018, **75**(1):22.

9. Salomón R, Valbuena-Carabaña M, Rodríguez-Calcerrada J, Aubrey D, McGuire M, Teskey R, Gil L, González-Doncel I: **Xylem and soil CO2 fluxes in a *Quercus pyrenaica* Willd. coppice: root respiration increases with clonal size**. *Annals of Forest Science* 2015, **72**(8):1065-1078.
10. Zadworny M, Mucha J, Jagodziński AM, Kościelniak P, Łakomy P, Modrzejewski M, Ufnalski K, Żytkowiak R, Comas LH, Rodríguez-Calcerrada J: **Seedling regeneration techniques affect root systems and the response of *Quercus robur* seedlings to water shortages**. *Forest Ecology and Management* 2021, **479**:11.
11. Grossnickle SC, Ivetić V: **Root system development and field establishment: effect of seedling quality**. *New Forests* 2022, **53**(6):1021-1067.
12. Pemán J, Chirino E, Espelta JM, Jacobs DF, Martín-Gómez P, Navarro-Cerrillo R, Oliet JA, Vilagrosa A, Villar-Salvador P, Gil-Pelegrín E: **Physiological keys for natural and artificial regeneration of oaks**. *Oaks Physiological Ecology Exploring the Functional Diversity of Genus Quercus L* 2017:453-511.
13. Kościelniak P, Glazińska P, Kęsy J, Zadworny M: **Formation and development of taproots in deciduous tree species**. *Frontiers in Plant Science* 2021, **12:772567**
14. Mitsis T, Efthimiadou A, Bacopoulou F, Vlachakis D, Chrousos GP, Eliopoulos E: **Transcription factors and evolution: An integral part of gene expression (Review)**. *World Academy of Sciences Journal* 2020, **2**(1):3-8.
15. Slovak R, Ogura T, Satbhai SB, Ristova D, Busch W: **Genetic control of root growth: from genes to networks**. *Annals of Botany* 2016, **117**(1):9-24.
16. Overvoorde P, Fukaki H, Beeckman T: **Auxin control of root development**. *Cold Spring Harbor Perspectives in Biology* 2010, **2**(6):a001537.
17. Zolman BK, Yoder A, Bartel B: **Genetic analysis of indole-3-butyric acid responses in Arabidopsis thaliana reveals four mutant classes**. *Genetics* 2000, **156**(3):1323-1337.
18. Aloni R, Aloni E, Langhans M, Ullrich CI: **Role of cytokinin and auxin in shaping root architecture: regulating vascular differentiation, lateral root initiation, root apical dominance and root gravitropism**. *Annals of Botany* 2006, **97**(5):883-893.
19. Qin H, He L, Huang R: **The coordination of ethylene and other hormones in primary root development**. *Frontiers in Plant Science* 2019, **10**:874.
20. Růzicka K, Ljung K, Vanneste S, Podhorská R, Beeckman T, Friml J, Benková E: **Ethylene regulates root growth through effects on auxin biosynthesis and transport-dependent auxin distribution**. *Plant Cell* 2007, **19**(7):2197-2212.
21. Casson SA, Lindsey K: **Genes and signalling in root development**. *New Phytologist* 2003, **158**(1):11-38.
22. Abeles FB, Morgan PW, Saltveit Jr ME: **Ethylene in plant biology**: Academic press; 2012.
23. Ristova D, Metesch K, Busch W: **Natural genetic variation shapes root system responses to phytohormones in *Arabidopsis***. *bioRxiv* 2017:155184.
24. Pacheco-Villalobos D, Sankar M, Ljung K, Hardtke CS: **Disturbed local auxin homeostasis enhances cellular anisotropy and reveals alternative wiring of auxin-ethylene crosstalk in *Brachypodium distachyon* seminal roots**. *PLoS Genetics* 2013, **9**(6):e1003564.
25. Kościelniak P, Glazińska P, Zadworny M: **OakRootRNADB—a consolidated RNA-seq database for coding and noncoding RNA in roots of pedunculate oak (*Quercus robur*)**. *Database: The Journal of Biological Databases and Curation* 2022, **baac097**
26. Love MI, Huber W, Anders S: **Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2**. *Genome Biology* 2014, **15**(12):550.
27. González-Curbelo MÁ, Socas-Rodríguez B, Herrera-Herrera AV, González-Sálamo J, Hernández-Borges J, Rodríguez-Delgado MÁ: **Evolution and applications of the QuEChERS method**. *Trends in Analytical Chemistry* 2015, **71**:169-185.
28. Pu CH, Lin SK, Chuang WC, Shyu TH: **Modified QuEChERS method for 24 plant growth regulators in grapes using LC-MS/MS**. *Journal of Food and Drug Analysis* 2018, **26**(2):637-648.
29. Bardou P, Mariette J, Escudié F, Djemiel C, Klopp C: **jvenn: an interactive Venn diagram viewer**. *BMC Bioinformatics* 2014, **15**(1):293.

30. Lynch J, Marschner P, Rengel Z: **Effect of internal and external factors on root growth and development**. San Diego: Elsevier Academic Press Inc; 2012.
31. Petricka JJ, Winter CM, Benfey PN: **Control of *Arabidopsis* root development**. *Annual Review of Plant Biology* 2012, **63**:563-590.
32. Freschet GT, Pagès L, Iversen CM, Comas LH, Rewald B, Roumet C, Klimešová J, Zadworny M, Poorter H, Postma JA *et al*: **A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements**. *New Phytologist* 2021, **232**(3):973-1122.
33. Svolacchia N, Salvi E, Sabatini S: **Arabidopsis primary root growth: let it grow, can't hold it back anymore!** *Current Opinion in Plant Biology* 2020, **57**:133-141.
34. Qiu X-M, Sun Y-Y, Ye X-Y, Li Z-G: **Signaling role of glutamate in plants**. *Frontiers in Plant Science* 2020, **10:1743**.
35. Lv B, Tian H, Zhang F, Liu J, Lu S, Bai M, Li C, Ding Z: **Brassinosteroids regulate root growth by controlling reactive oxygen species homeostasis and dual effect on ethylene synthesis in Arabidopsis**. *PLoS Genetics* 2018, **14**(1):e1007144.
36. Zhang XP, Ma CX, Sun LR, Hao FS: **Roles and mechanisms of Ca(2+) in regulating primary root growth of plants**. *Plant Signaling & Behavior* 2020, **15**(5):1748283.
37. Reyt G, Ramakrishna P, Salas-González I, Fujita S, Love A, Tiemessen D, Lapierre C, Morreel K, Calvo-Polanco M, Flis P *et al*: **Two chemically distinct root lignin barriers control solute and water balance**. *Nature Communications* 2021, **12**(1):2320.
38. Degenhardt B, Gimmler H: **Cell wall adaptations to multiple environmental stresses in maize roots**. *Journal of Experimental Botany* 2000, **51**(344):595-603.
39. Enstone DE, Peterson CA, Ma F: **Root endodermis and exodermis: structure, function, and responses to the environment**. *Journal of Plant Growth Regulation* 2002, **21**(4):335-351.
40. Wasternack C, Song S: **Jasmonates: biosynthesis, metabolism, and signaling by proteins activating and repressing transcription**. *Journal of Experimental Botany* 2016, **68**(6):1303-1321.
41. Gutierrez L, Mongelard G, Floková K, Păcurar DI, Novák O, Staswick P, Kowalczyk M, Păcurar M, Demailly H, Geiss G *et al*: **Auxin controls *Arabidopsis* adventitious root initiation by regulating jasmonic acid homeostasis**. *The Plant Cell* 2012, **24**(6):2515-2527.
42. Tillberg E, Eliasson L: **Indoleacetic acid enhancement of the inhibition of Lemna growth caused by abscisic acid**. *Planta* 1976, **130**:53-55.
43. Zhang N, Hasenstein KH: **Initiation and elongation of lateral roots in *Lactuca sativa***. *International Journal of Plant Sciences* 1999, **160**(3):511-519.
44. Laplaze L, Benková E, Casimiro I, Maes L, Vanneste S, Swarup R, Weijers D, Calvo V, Parizot B, Herrera-Rodriguez MB *et al*: **Cytokinins act directly on lateral root founder cells to inhibit root initiation**. *Plant Cell* 2007, **19**(12):3889-3900.
45. Aloni R, Langhans M, Aloni E, Ullrich CI: **Role of cytokinin in the regulation of root gravitropism**. *Planta* 2004, **220**:177-182.
46. Hai NN, Chuong NN, Tu NHC, Kisiala A, Hoang XLT, Thao NP: **Role and regulation of cytokinins in plant response to drought stress**. *Plants (Basel)* 2020, **9**(4).
47. Ubeda-Tomás S, Federici F, Casimiro I, Beemster GTS, Bhalerao R, Swarup R, Doerner P, Haseloff J, Bennett MJ: **Gibberellin signaling in the endodermis controls *Arabidopsis* root meristem size**. *Current Biology* 2009, **19**(14):1194-1199.
48. Fu X, Harberd NP: **Auxin promotes *Arabidopsis* root growth by modulating gibberellin response**. *Nature* 2003, **421**(6924):740-743.
49. Street IH, Aman S, Zubo Y, Ramzan A, Wang X, Shakeel SN, Kieber JJ, Schaller GE: **Ethylene inhibits cell proliferation of the *Arabidopsis* root meristem**. *Plant Physiology* 2015, **169**(1):338-350.
50. Achard P, Vriezen WH, Van Der Straeten D, Harberd NP: **Ethylene regulates *Arabidopsis* development via the modulation of DELLA protein growth repressor function**. *The Plant Cell* 2003, **15**(12):2816-2825.

51. Li X, Chen L, Forde BG, Davies WJ: **The biphasic root growth response to abscisic acid in *Arabidopsis* involves interaction with ethylene and auxin signalling pathways**. *Frontiers in plant science* 2017, **8**:1493.
52. Achard P, Cheng H, De Grauwe L, Decat J, Schoutteten H, Moritz T, Van Der Straeten D, Peng J, Harberd NP: **Integration of plant responses to environmentally activated phytohormonal signals**. *Science* 2006, **311**(5757):91-94.
53. Chen Q, Sun J, Zhai Q, Zhou W, Qi L, Xu L, Wang B, Chen R, Jiang H, Qi J: **The basic helix-loop-helix transcription factor MYC2 directly represses *PLETHORA* expression during jasmonate-mediated modulation of the root stem cell niche in *Arabidopsis***. *The Plant Cell* 2011, **23**(9):3335-3352.
54. Cai X-T, Xu P, Zhao P-X, Liu R, Yu L-H, Xiang C-B: ***Arabidopsis* ERF109 mediates cross-talk between jasmonic acid and auxin biosynthesis during lateral root formation**. *Nature Communications* 2014, **5**(1):5833.

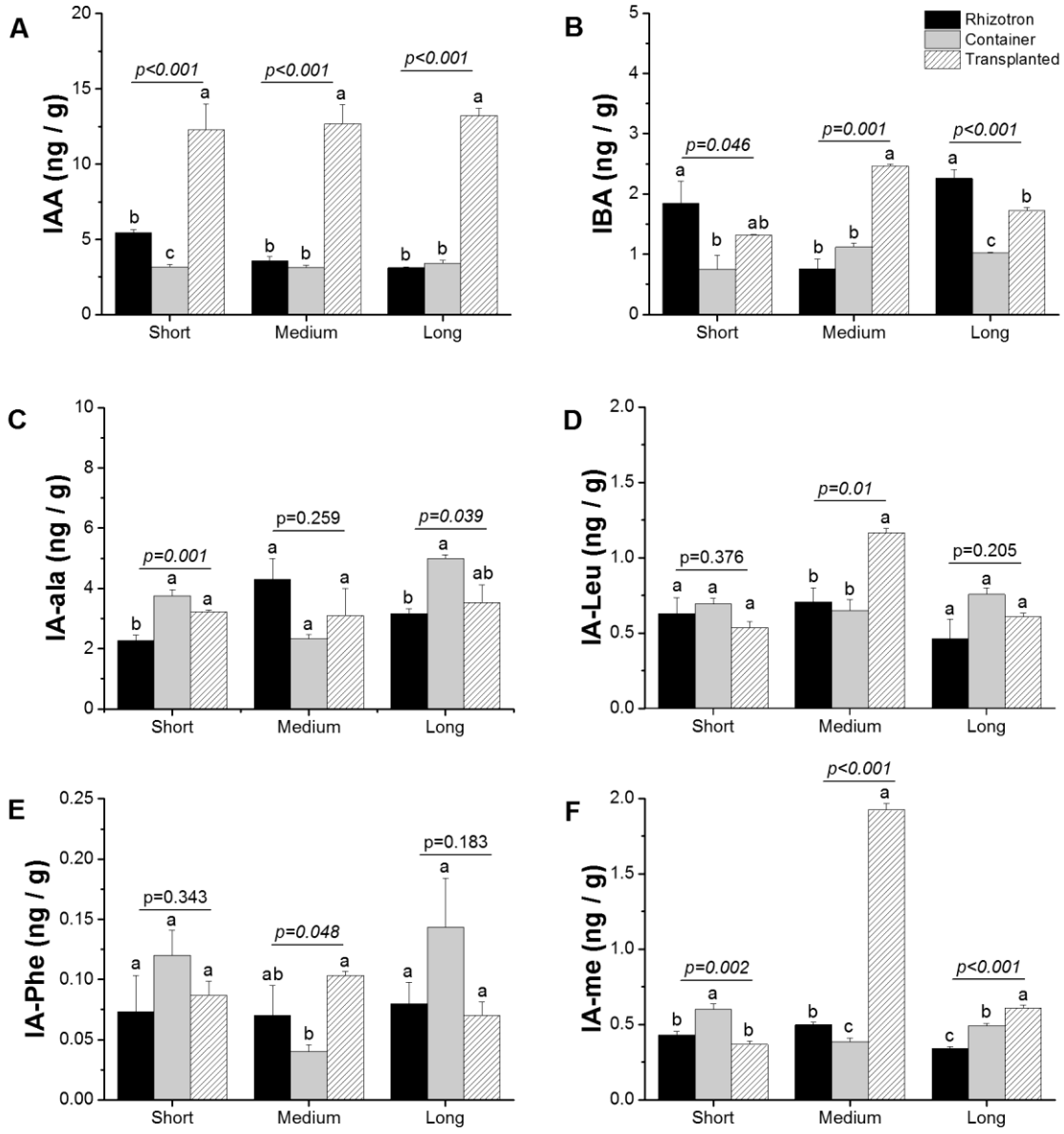

Fig. S1. The effect of cultivation systems: rhizotron (black color), container (grey color) and transplanted (hacked) on IAA (A), IBA (B), IA-Ala (C), IA-Leu (D), IA-Phe (E), IA-Me (F) concentration in elongation zone of short, medium and long taproots of *Q. robur* seedlings. Each point represents the mean hormone values for each root length classes in each cultivation system. Each point represents the mean incorporating multiple individual roots from each cultivation systems. Hormones concentration values were $\log_{10}$-transformed before statistical analysis, but figures present non-transformed data. Significance of variation between cultivation systems within length classes i.e. short, medium and long results from an analysis of variance (ANOVA) are given for each length classes panel. Different lower-case letters indicate significantly different means among different cultivation systems within a given length classes at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

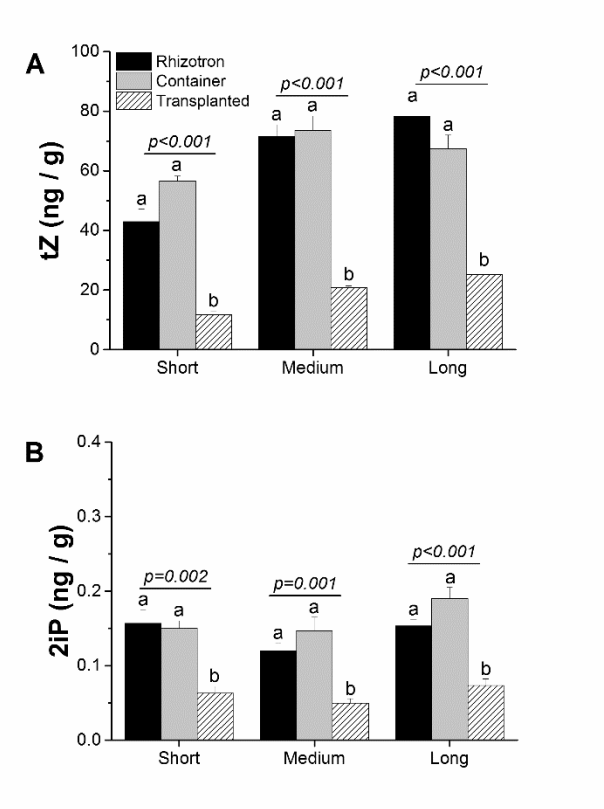

Fig. S2. The effect of cultivation systems: rhizotron (black color), container (grey color) and transplanted (hacked) on tZ (A), 2iP (B) concentration in elongation zone of short, medium and long taproots of *Q. robur* seedlings. Each point represents the mean hormone values for each root length classes in each cultivation system. Each point represents the mean incorporating multiple individual roots from each cultivation systems. Hormones concentration values were $\log_{10}$-transformed before statistical analysis, but figures present non-transformed data. Significance of variation between cultivation systems within length classes i.e. short, medium and long results from an analysis of variance (ANOVA) are given for each length classes panel. Different lower-case letters indicate significantly different means among different cultivation systems within a given length classes at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

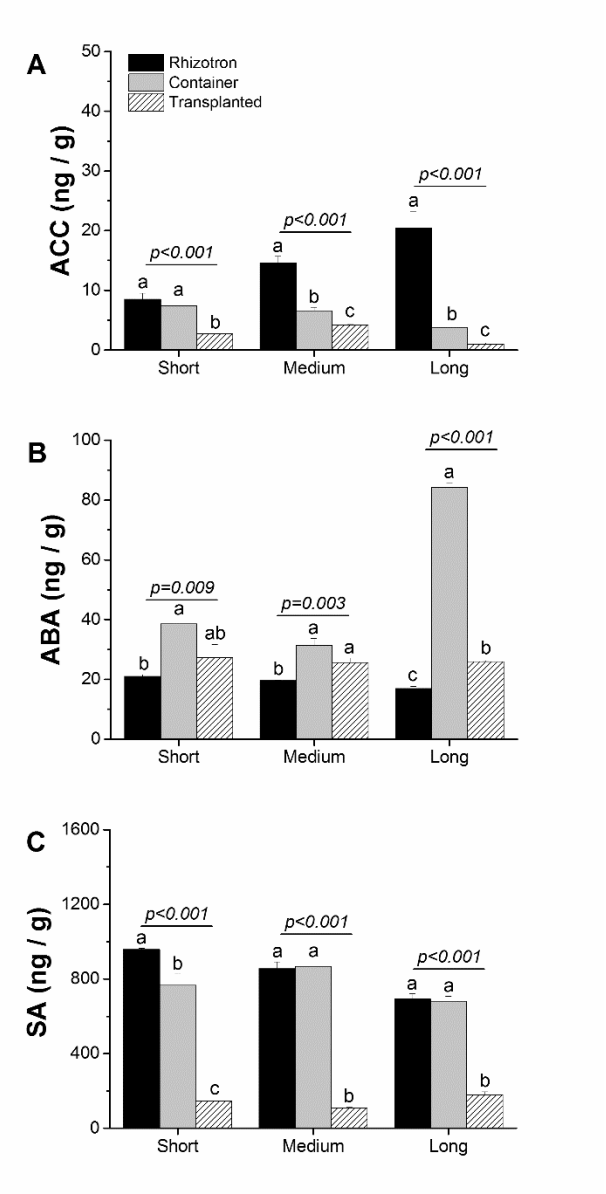

Fig. S3. The effect of cultivation systems: rhizotron (black color), container (grey color) and transplanted (hacked) on ACC (A), ABA (B), SA (C) concentration in elongation zone of short, medium and long taproots of *Q. robur* seedlings. Each point represents the mean hormone values for each root length classes in each cultivation system. Each point represents the mean incorporating multiple individual roots from each cultivation systems. Hormones concentration values were $\log_{10}$-transformed before statistical analysis, but figures present non-transformed data. Significance of variation between cultivation systems within length classes i.e. short, medium and long results from an analysis of variance (ANOVA) are given for each length classes panel. Different lower-case letters indicate significantly different means among different cultivation systems within a given length classes at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

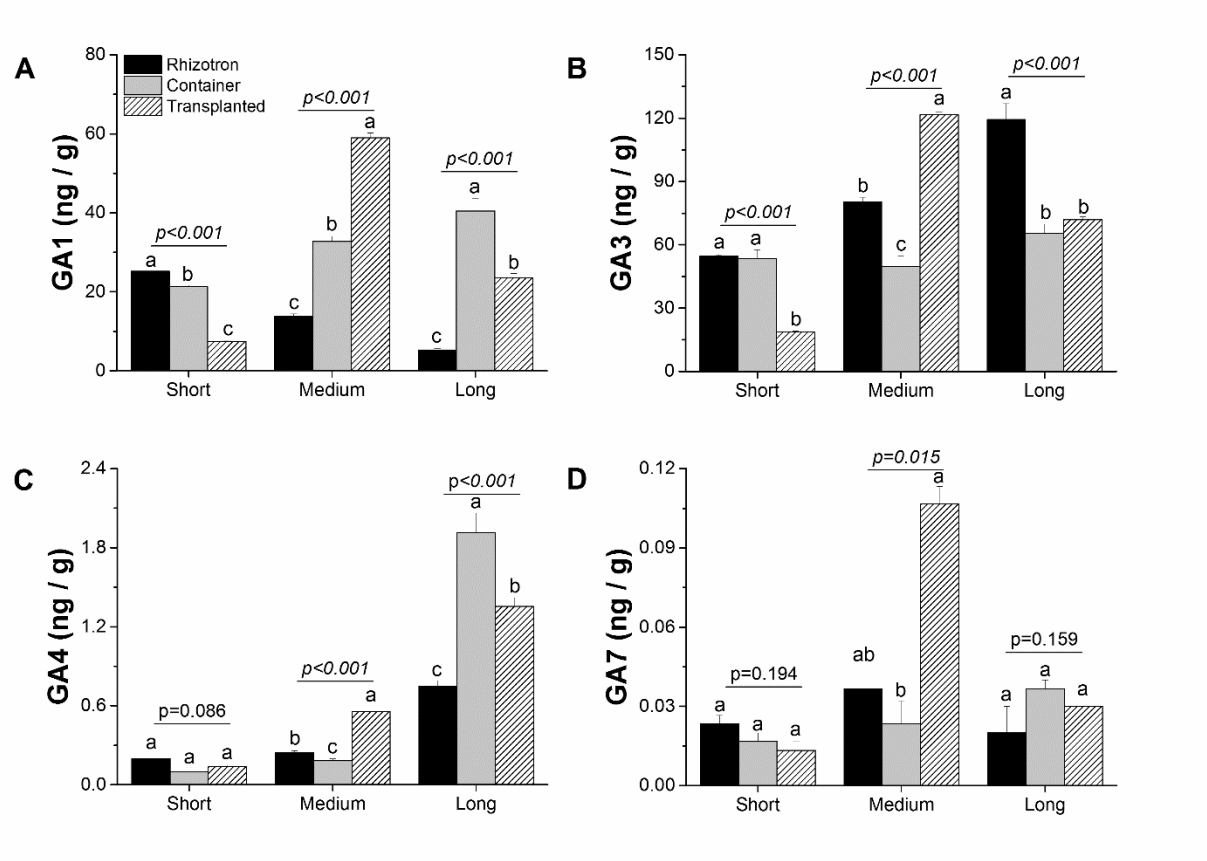

Fig. S4. The effect of cultivation systems: rhizotron (black color), container (grey color) and transplanted (hacked) on GA1 (A), GA3 (B), GA4 (C) GA7 (D) concentration in elongation zone of short, medium and long taproots of *Q. robur* seedlings. Each point represents the mean hormone values for each root length classes in each cultivation system. Each point represents the mean incorporating multiple individual roots from each cultivation systems. Hormones concentration values were $\log_{10}$-transformed before statistical analysis, but figures present non-transformed data. Significance of variation between cultivation systems within length classes i.e. short, medium and long results from an analysis of variance (ANOVA) are given for each length classes panel. Different lower-case letters indicate significantly different means among different cultivation systems within a given length classes at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

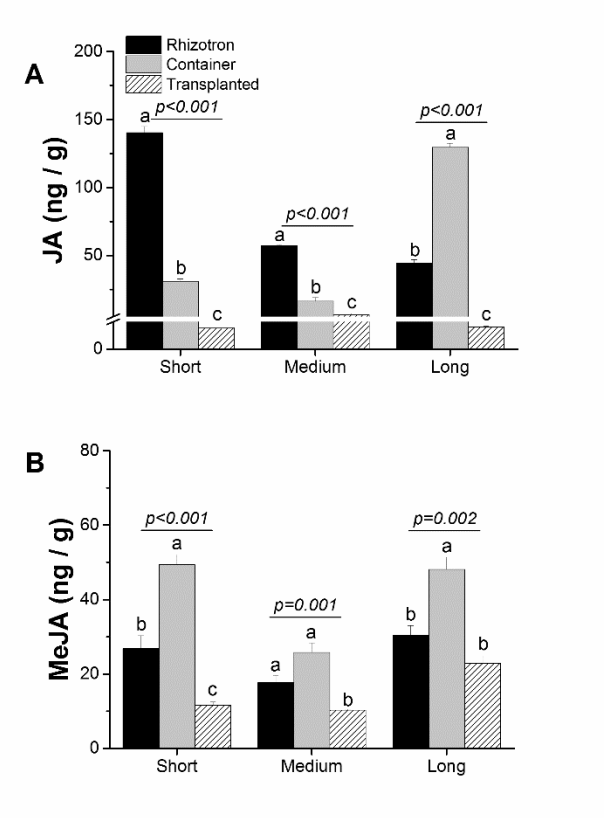

Fig. S5. The effect of cultivation systems: rhizotron (black color), container (grey color) and transplanted (hacked) on JA (A), MeJA (B) concentration in elongation zone of short, medium and long taproots of *Q. robur* seedlings. Each point represents the mean hormone values for each root length classes in each cultivation system. Each point represents the mean incorporating multiple individual roots from each cultivation systems. Hormones concentration values were $\log_{10}$-transformed before statistical analysis, but figures present non-transformed data. Significance of variation between cultivation systems within length classes i.e. short, medium and long results from an analysis of variance (ANOVA) are given for each length classes panel. Different lower-case letters indicate significantly different means among different cultivation systems within a given length classes at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

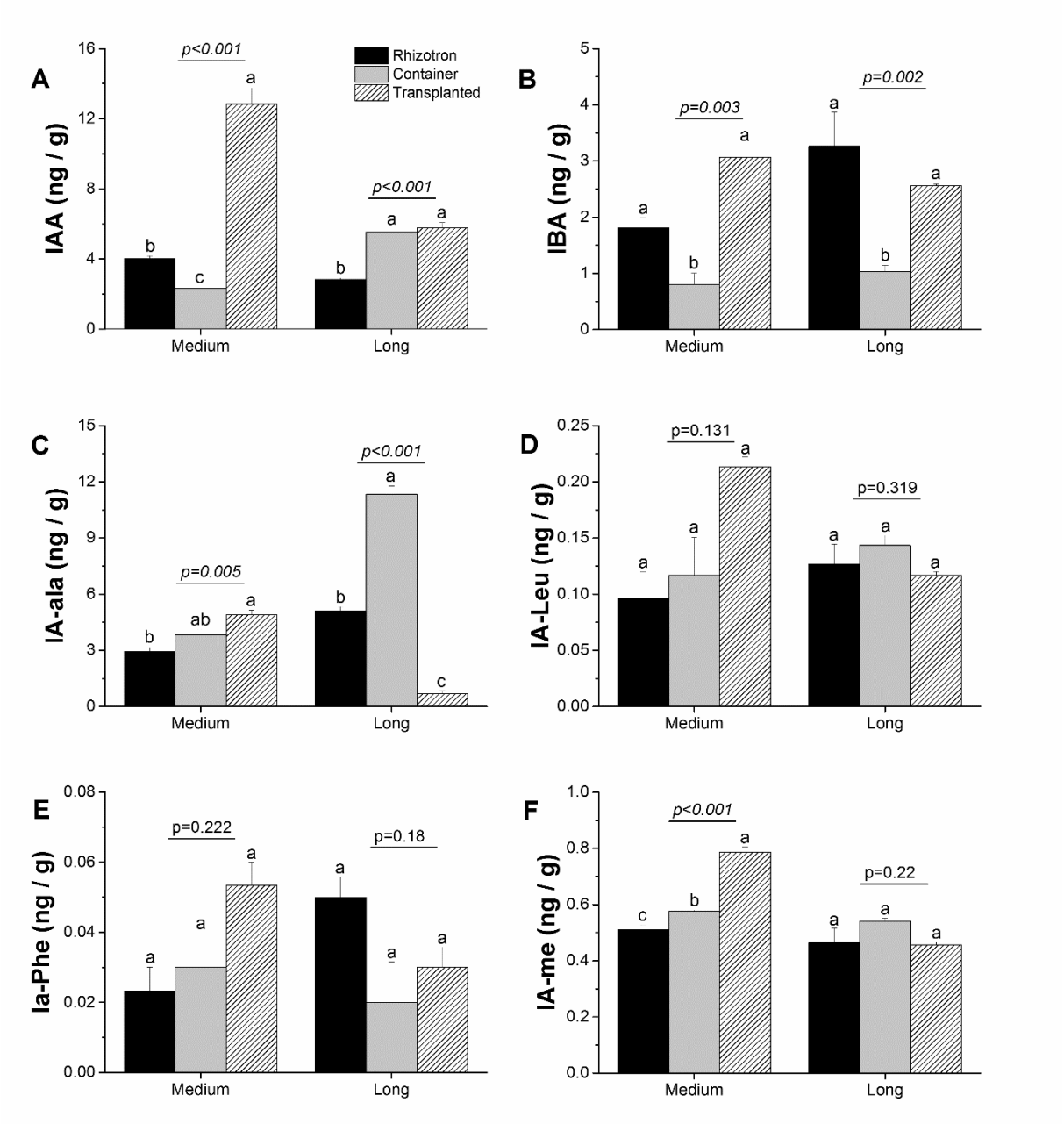

Fig. S6. The effect of cultivation systems: rhizotron (black color), container (grey color) and transplanted (hacked) on IAA (A), IBA (B), IA-Ala (C), IA-Leu (D), IA-Phe (E), IA-Me (F) concentration in meristematic zone of medium and long lateral roots of *Q. robur* seedlings. Each point represents the mean hormone values for each root length classes in each cultivation system. Each point represents the mean incorporating multiple individual roots from each cultivation systems. Hormones concentration values were $\log_{10}$-transformed before statistical analysis, but figures present non-transformed data. Significance of variation between cultivation systems within length classes i.e. short, medium and long results from an analysis of variance (ANOVA) are given for each length classes panel. Different lower-case letters indicate significantly different means among different cultivation systems within a given length classes at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

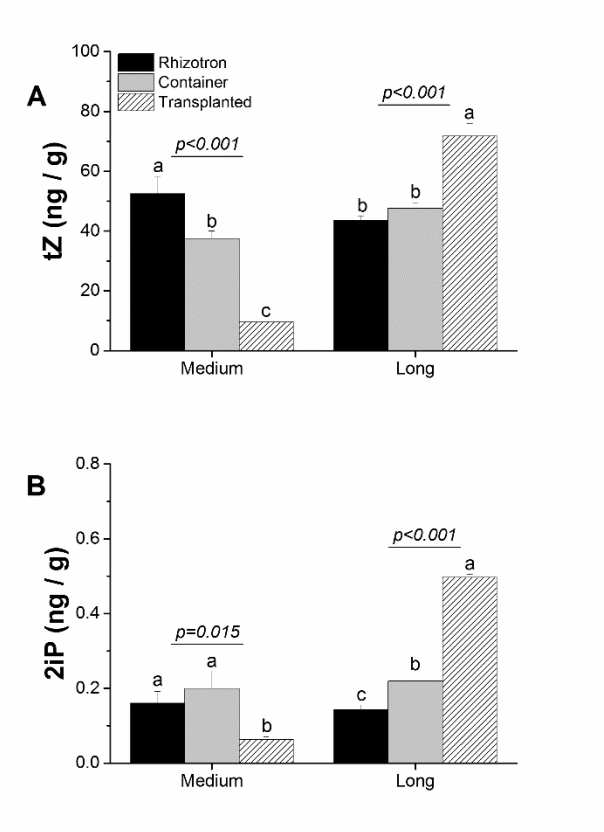

Fig. S7. The effect of cultivation systems: rhizotron (black color), container (grey color) and transplanted (hacked) on tZ (A), 2iP (B) concentration in meristematic zone of medium and long lateral root of *Q. robur* seedlings. Each point represents the mean hormone values for each root length classes in each cultivation system. Each point represents the mean incorporating multiple individual roots from each cultivation systems. Hormones concentration values were $\log_{10}$-transformed before statistical analysis, but figures present non-transformed data. Significance of variation between cultivation systems within length classes i.e. short, medium and long results from an analysis of variance (ANOVA) are given for each length classes panel. Different lower-case letters indicate significantly different means among different cultivation systems within a given length classes at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

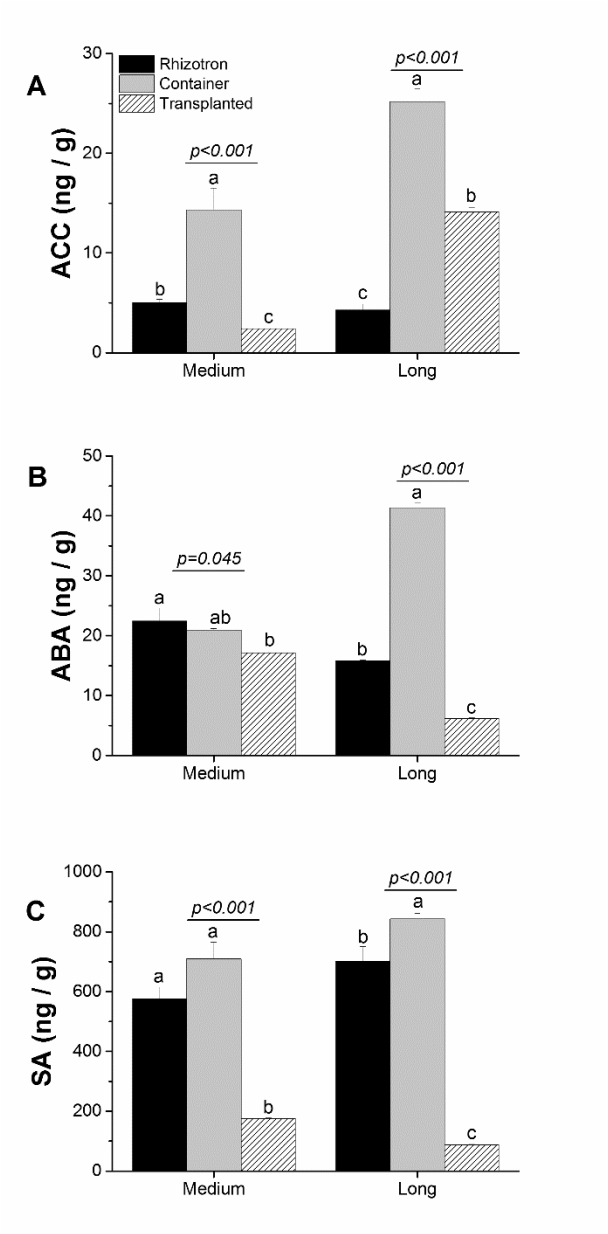

Fig. S8. The effect of cultivation systems: rhizotron (black color), container (grey color) and transplanted (hacked) on ACC (A), ABA (B), SA (C) concentration in meristematic zone of medium and long lateral roots of *Q. robur* seedlings. Each point represents the mean hormone values for each root length classes in each cultivation system. Each point represents the mean incorporating multiple individual roots from each cultivation systems. Hormones concentration values were $\log_{10}$-transformed before statistical analysis, but figures present non-transformed data. Significance of variation between cultivation systems within length classes i.e. short, medium and long results from an analysis of variance (ANOVA) are given for each length classes panel. Different lower-case letters indicate significantly different means among different cultivation systems within a given length classes at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

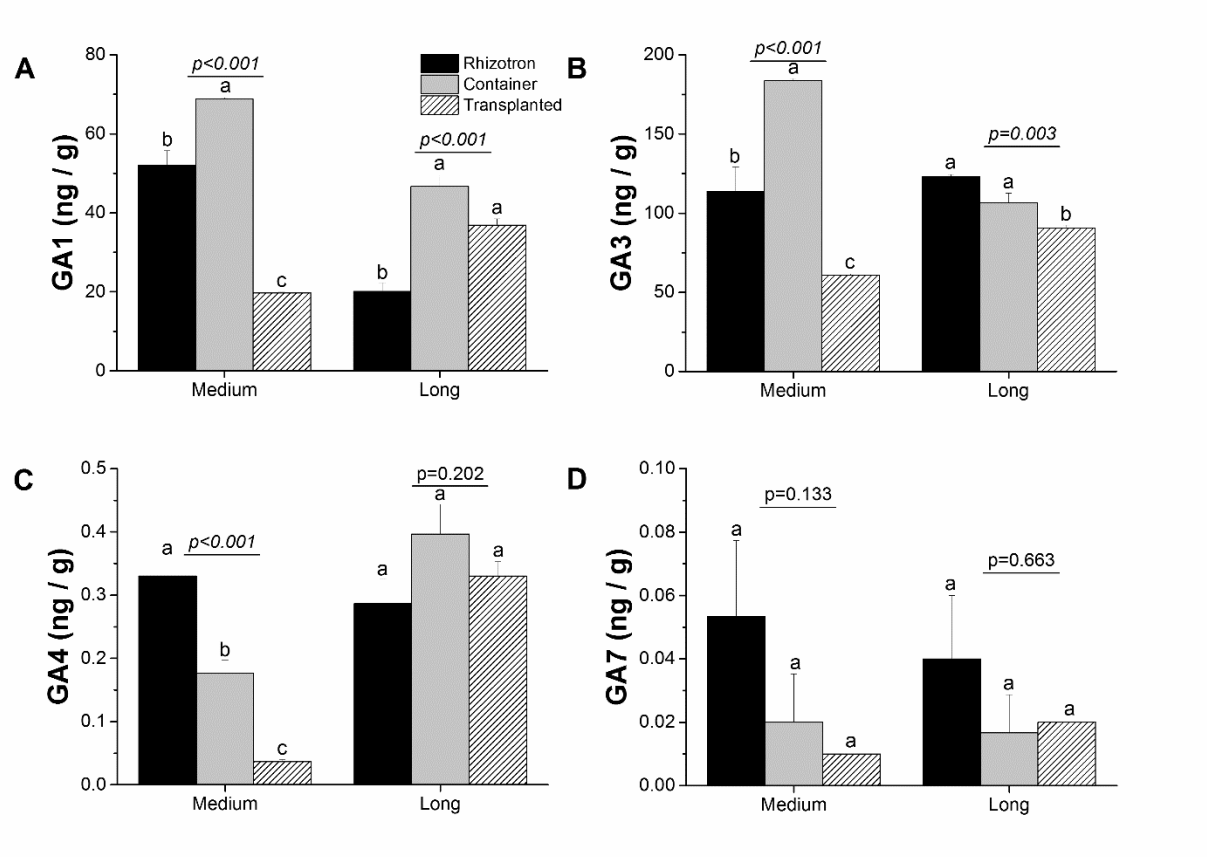

Fig. S9. The effect of cultivation systems: rhizotron (black color), container (grey color) and transplanted (hacked) on GA1 (A), GA3 (B), GA4 (C) GA7 (D) concentration in meristematic zone of medium and long lateral roots of *Q. robur* seedlings. Each point represents the mean hormone values for each root length classes in each cultivation system. Each point represents the mean incorporating multiple individual roots from each cultivation systems. Hormones concentration values were $\log_{10}$-transformed before statistical analysis, but figures present non-transformed data. Significance of variation between cultivation systems within length classes i.e. short, medium and long results from an analysis of variance (ANOVA) are given for each length classes panel. Different lower-case letters indicate significantly different means among different cultivation systems within a given length classes at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

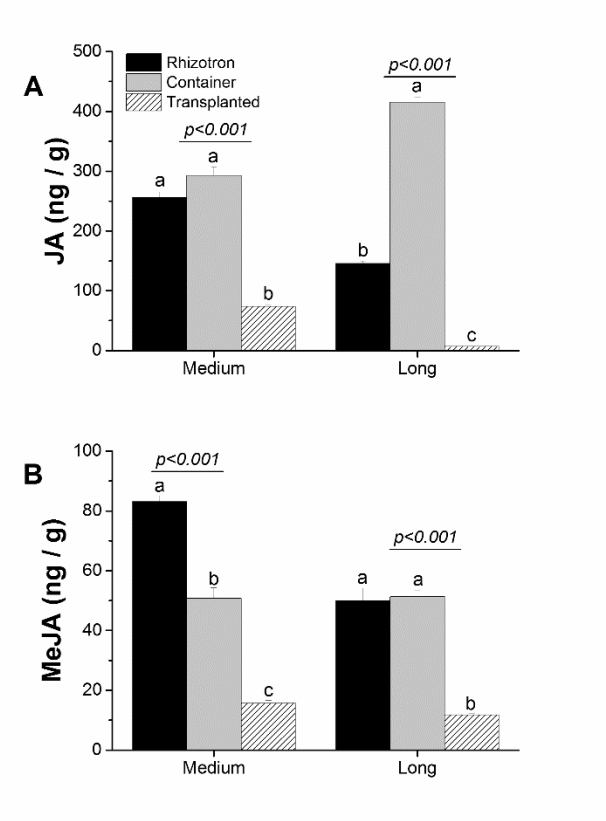

Fig. S10. The effect of cultivation systems: rhizotron (black color), container (grey color) and transplanted (hacked) on JA (A), MeJA (B) concentration in meristematic zone of medium and long lateral roots of *Q. robur* seedlings. Each point represents the mean hormone values for each root length classes in each cultivation system. Each point represents the mean incorporating multiple individual roots from each cultivation systems. Hormones concentration values were $\log_{10}$-transformed before statistical analysis, but figures present non-transformed data. Significance of variation between cultivation systems within length classes i.e. short, medium and long results from an analysis of variance (ANOVA) are given for each length classes panel. Different lower-case letters indicate significantly different means among different cultivation systems within a given length classes at $\alpha = 0.05$ according to Tukey's test. Error bars represent the standard error.

Table S1. MRM values and positive (+) and negative (-) ionization used in the analysis of phytohormones and deuterated standards.

Hormone	Full name	MRM values and ionization	
		endogenous phytohormone	deuterated standard
IAA	indole-3-acetic acid	IAA(+) 176→130	d2-IAA(+) 178→132
IA-Ala	Indole-3-acetyl-L-alanine	IA-Ala(+) 247→130	d5,15N-IA-Ala(+) 252→134
IA-Leu	indole-3-acetyl-L-leucine	IA-Leu(+) 294→134	d2-IA-Leu(+) 294→134
IA-Phe	indole-3-acetyl-L-phenylalanine	IA-Phe(+) 362→130	d2-IA-Phe(+) 328→134
IA-Me	indole-3-acetyl-L-methionine	IAMe(+) 190→130	d5-IAMe(+) 194→134
IBA	indole-3-butyric acid	IBA(+) 204→130	d2-IBA(+) 206→131
tZ	trans-Zeatin	tZ(+) 220→202	d5-tZ(+) 225→137
2iP	N6-(2-Isopentenyl)adenine	2iP(+) 204→148	d5-2iP(+) 210→137
ACC	1-aminocyclopropane-1-carboxylic acid	ACC(+) 102→58	d2-ACC(+) 106→60
ABA	abscisic acid	ABA(-) 263→153	d5-ABA(-) 269→159
SA	salicylic acid	SA(-) 137→93	d4-SA (-) 141→97
GA3	gibberellins 3	GA3(-) 345→239	d2-GA3(-) 347→241
GA1	gibberellins 1	GA1(-) 347→259	d2-GA1(-) 349→261
GA7	gibberellins 7	GA7(-) 329→223	d2GA7(-) 331→225
GA4	gibberellins 4	GA4(-) 331→287	d2-GA4(-) 333→259
JA	jasmonic acid	JA(+) 211→133	d5-JA(+) 214→134
MeJA	methyl jasmonate	MeJA(+) 225→151	d2-JAMe(+) 227→153

Table S2. Differential expression patterns of plant hormone biosynthesis related genes in library comparison between roots in different cultivation systems.

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Transplanted**	**RPKM Container**	**Function**
STR_C vs. STR_CRH	IAA	MSTRG.11988.1	MSTRG.11988	-2,2732	TAA1	L-tryptophan--pyruvate aminotransferase 1	77,67	13,67	auxin biosynthesis
MTR_C vs. MTR_CRH	IAA	MSTRG.9561.1	MSTRG.9561	-2,9936	TAA1	L-tryptophan--pyruvate aminotransferase 1	60,33	7,67	auxin biosynthesis
LTR_C vs. LTR_CRH	IAA	MSTRG.11988.1	MSTRG.11988	-1,899	TAA1	L-tryptophan--pyruvate aminotransferase 1	126,33	38,67	auxin biosynthesis
MEZ_C vs. MEZ_CRH	IAA	MSTRG.11988.1	MSTRG.11988	-3,4452	TAA1	L-tryptophan--pyruvate aminotransferase 1	7,00	0,67	auxin biosynthesis
MLR_C vs. MLR_CRH	IAA	MSTRG.30679.1	MSTRG.30679	-1,8779	YUC6	Indole-3-pyruvate monooxygenase YUCCA6	542,33	162,00	auxin biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Transplanted**	**RPKM Rhizotron**	**Function**
MTR_RH vs. MTR_CRH	IAA	MSTRG.9561.1	MSTRG.9561	-2,6868	TAA1	L-tryptophan--pyruvate aminotransferase 1	60,33	9,33	auxin biosynthesis
LTR_RH vs. LTR_CRH	IAA	MSTRG.9561.1	MSTRG.9561	-2,8859	TAA1	L-tryptophan--pyruvate aminotransferase 1	45,33	6,00	auxin biosynthesis
MEZ_RH vs. MEZ_CRH	IAA	MSTRG.34007.1	MSTRG.34007	-1,9869	YUC8	Probable indole-3-pyruvate monooxygenase YUCCA8	20,00	5,00	auxin biosynthesis
MEZ_RH vs. MEZ_CRH	IAA	MSTRG.11988.1	MSTRG.11988	-3,4025	TAA1	L-tryptophan--pyruvate aminotransferase 1	7,00	0,67	auxin biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	RPKM Transplanted	RPKM Container	**Function**
MLR_C vs. MLR_CRH	CK	MSTRG.19148.1	MSTRG.19148	2,34	LOG7	Cytokinin riboside 5'-monophosphate	7,67	43,00	cytokinin biosynthesis

						phosphoribohydrolase LOG7			
MLR_C vs. MLR_CRH	CK	MSTRG.23760.1	MSTRG.23760	3,0556	C7351	Cytokinin hydroxylase	1,33	12,33	cytokinin biosynthesis
LLR_C vs. LLR_CRH	CK	MSTRG.17298.3	MSTRG.17298	-1,6816	ZOG	Zeatin O-glucosyltransferase	2649,33	942,67	cytokinin biosynthesis
LLR_C vs. LLR_CRH	CK	MSTRG.1370.1	MSTRG.1370	-1,6328	LOG1	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG1	36,67	13,33	cytokinin biosynthesis
STR_C vs. STR_CRH	CK	MSTRG.23763.1	MSTRG.23763	3,3415	C7351	Cytokinin hydroxylase	3,00	28,00	cytokinin biosynthesis
LTR_C vs. LTR_CRH	CK	MSTRG.3451.1	MSTRG.3451	1,9203	LOG3	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG3	43,00	194,67	cytokinin biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	RPKM Transplanted	RPKM Rhizotron	Function
MLR_RH vs. MLR_CRH	CK	MSTRG.3451.1	MSTRG.3451	1,5668	LOG3	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG3	90,00	267,33	cytokinin biosynthesis
MLR_RH vs. MLR_CRH	CK	MSTRG.19148.1	MSTRG.19148	1,9355	LOG7	Cytokinin riboside 5'-monophosphate phosphoribohydrolase LOG7	7,67	29,67	cytokinin biosynthesis
MLR_RH vs. MLR_CRH	CK	MSTRG.32112.1	MSTRG.32112	1,7977	IPT	Adenylate isopentenyltransferase	4,67	16,33	cytokinin biosynthesis
LLR_RH vs. LLR_CRH	CK	MSTRG.17298.1	MSTRG.17298	-1,9515	ZOG	Zeatin O-glucosyltransferase	2649,33	798,67	cytokinin biosynthesis
MEZ_RH vs. MEZ_CRH	CK	MSTRG.23763.1	MSTRG.23763	1,7632	C7351	Cytokinin hydroxylase	5,67	19,67	cytokinin biosynthesis
STR_RH vs. STR_CRH	CK	MSTRG.23763.1	MSTRG.23763	2,7732	C7351	Cytokinin hydroxylase	3,00	19,00	cytokinin biosynthesis

STR_RH vs. STR_CRH	CK	MSTRG.17298.1	MSTRG.17298	2,3155	ZOG	Zeatin O-glucosyltransferase	522,33	2465,00	cytokinin biosynthesis
MTR_RH vs. MTR_CRH	CK	MSTRG.17298.1	MSTRG.17298	1,7026	ZOG	Zeatin O-glucosyltransferase	469,67	1527,33	cytokinin biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Container**	**RPKM Rhizotron**	**Function**
LEZ_RH vs. LEZ_C	CK	MSTRG.5409.1	MSTRG.5409	1,5832	C7351	Cytokinin hydroxylase	41,33	113,00	cytokinin biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Transplanted**	**RPKM Container**	**Function**
MLR_C vs. MLR_CRH	ET	MSTRG.8808.1	MSTRG.8808	1,7462	ACCH3	1-aminocyclopropane-1-carboxylate oxidase homolog	8,33	30,67	ethylene biosynthesis
MLR_C vs. MLR_CRH	ET	MSTRG.17225.1	MSTRG.17225	2,0719	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	201,67	939,00	ethylene biosynthesis
MLR_C vs. MLR_CRH	ET	MSTRG.25190.1	MSTRG.25190	2,0875	1A12	1-aminocyclopropane-1-carboxylate synthase CMA101	8,00	37,67	ethylene biosynthesis
MLR_C vs. MLR_CRH	ET	MSTRG.17222.1	MSTRG.17222	2,3439	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	267,00	1494,00	ethylene biosynthesis
MLR_C vs. MLR_CRH	ET	MSTRG.17222.10	MSTRG.17222	2,3439	ACCH6	1-aminocyclopropane-1-carboxylate oxidase homolog 6	267,00	1494,00	ethylene biosynthesis
MLR_C vs. MLR_CRH	ET	MSTRG.32014.1	MSTRG.32014	2,4175	1A1C	1-aminocyclopropane-1-carboxylate synthase	36,33	214,00	ethylene biosynthesis
MLR_C vs. MLR_CRH	ET	MSTRG.14291.1	MSTRG.14291	2,6614	1A1C	1-aminocyclopropane-1-carboxylate synthase	18,33	128,33	ethylene biosynthesis
MLR_C vs. MLR_CRH	ET	MSTRG.14325.1	MSTRG.14325	3,1908	1A1C	1-aminocyclopropane-1-carboxylate synthase	1,00	10,00	ethylene biosynthesis

MLR_C vs. MLR_CRH	ET	MSTRG.15402.1	MSTRG.15402	4,6245	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	0,00	5,00	ethylene biosynthesis
MLR_C vs. MLR_CRH	ET	MSTRG.17223.1	MSTRG.17223	4,8928	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	0,00	6,00	ethylene biosynthesis
MLR_C vs. MLR_CRH	ET	MSTRG.13653.1	MSTRG.13653	5,8341	ACCO5	1-aminocyclopropane-1-carboxylate oxidase 5	49,00	3100,33	ethylene biosynthesis
MLR_C vs. MLR_CRH	ET	MSTRG.15403.1	MSTRG.15403	7,589	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	0,67	140,33	ethylene biosynthesis
LLR_C vs. LLR_CRH	ET	MSTRG.5697.1	MSTRG.5697	1,6026	ACCO1	1-aminocyclopropane-1-carboxylate oxidase 1	115,67	404,33	ethylene biosynthesis
LLR_C vs. LLR_CRH	ET	MSTRG.14325.1	MSTRG.14325	1,7203	1A1C	1-aminocyclopropane-1-carboxylate synthase	8,00	30,67	ethylene biosynthesis
MEZ_C vs. MEZ_CRH	ET	MSTRG.14325.1	MSTRG.14325	1,6454	1A1C	1-aminocyclopropane-1-carboxylate synthase	16,00	52,00	ethylene biosynthesis
MEZ_C vs. MEZ_CRH	ET	MSTRG.24860.1	MSTRG.24860	2,1829	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	9,33	44,00	ethylene biosynthesis
MEZ_C vs. MEZ_CRH	ET	MSTRG.13653.1	MSTRG.13653	3,1066	ACCO5	1-aminocyclopropane-1-carboxylate oxidase 5	59,33	546,33	ethylene biosynthesis
STR_C vs. STR_CRH	ET	MSTRG.15408.1	MSTRG.15408	1,7855	ACCH3	1-aminocyclopropane-1-carboxylate oxidase homolog	6,33	19,67	ethylene biosynthesis
STR_C vs. STR_CRH	ET	MSTRG.11166.1	MSTRG.11166	1,9514	1A11	1-aminocyclopropane-1-carboxylate synthase 1	27,00	94,00	ethylene biosynthesis
STR_C vs. STR_CRH	ET	MSTRG.14325.1	MSTRG.14325	2,4896	1A1C	1-aminocyclopropane-1-carboxylate synthase	15,00	77,67	ethylene biosynthesis
STR_C vs. STR_CRH	ET	MSTRG.15402.1	MSTRG.15402	3,4001	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	5,67	53,33	ethylene biosynthesis

MTR_C vs. MTR_CRH	ET	MSTRG.13876.1	MSTRG.13876	1,5208	ACCO	1-aminocyclopropane-1-carboxylate oxidase	188,00	559,00	ethylene biosynthesis
MTR_C vs. MTR_CRH	ET	MSTRG.15404.1	MSTRG.15404	2,3528	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	16,00	85,33	ethylene biosynthesis
LTR_C vs. LTR_CRH	ET	MSTRG.14325.1	MSTRG.14325	1,5945	1A1C	1-aminocyclopropane-1-carboxylate synthase	22,67	82,67	ethylene biosynthesis
LTR_C vs. LTR_CRH	ET	MSTRG.11166.1	MSTRG.11166	1,9149	1A11	1-aminocyclopropane-1-carboxylate synthase 1	34,33	154,67	ethylene biosynthesis
LTR_C vs. LTR_CRH	ET	MSTRG.17227.1	MSTRG.17227	2,1644	ACH11	1-aminocyclopropane-1-carboxylate oxidase homolog 11	9,33	51,67	ethylene biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Transplanted**	**RPKM Rhizotron**	**Function**
MLR_RH vs. MLR_CRH	ET	MSTRG.5763.1	MSTRG.5763	1,5732	1A17	1-aminocyclopropane-1-carboxylate synthase 7	81,00	242,33	ethylene biosynthesis
MLR_RH vs. MLR_CRH	ET	MSTRG.14291.1	MSTRG.14291	1,8214	1A1C	1-aminocyclopropane-1-carboxylate synthase	18,33	65,00	ethylene biosynthesis
MLR_RH vs. MLR_CRH	ET	MSTRG.8809.1	MSTRG.8809	1,9822	ACCH4	1-aminocyclopropane-1-carboxylate oxidase homolog 4	105,33	417,00	ethylene biosynthesis
MLR_RH vs. MLR_CRH	ET	MSTRG.24860.1	MSTRG.24860	2,0684	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	61,00	257,00	ethylene biosynthesis
MLR_RH vs. MLR_CRH	ET	MSTRG.13876.1	MSTRG.13876	2,1981	ACCO	1-aminocyclopropane-1-carboxylate oxidase	250,67	1153,00	ethylene biosynthesis
MLR_RH vs. MLR_CRH	ET	MSTRG.8808.1	MSTRG.8808	2,703	ACCH3	1-aminocyclopropane-1-carboxylate oxidase homolog	8,33	55,00	ethylene biosynthesis
MLR_RH vs. MLR_CRH	ET	MSTRG.8814.1	MSTRG.8814	2,7361	ACCH3	1-aminocyclopropane-1-carboxylate oxidase homolog 3	1,00	6,67	ethylene biosynthesis

MLR_RH vs. MLR_CRH	ET	MSTRG.14325.1	MSTRG.14325	3,7382	1A1C	1-aminocyclopropane-1-carboxylate synthase	1,00	13,33	ethylene biosynthesis
MLR_RH vs. MLR_CRH	ET	MSTRG.17223.1	MSTRG.17223	4,0255	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	0,00	3,00	ethylene biosynthesis
MLR_RH vs. MLR_CRH	ET	MSTRG.13653.1	MSTRG.13653	5,8244	ACCO5	1-aminocyclopropane-1-carboxylate oxidase 5	49,00	2789,00	ethylene biosynthesis
MLR_RH vs. MLR_CRH	ET	MSTRG.15403.1	MSTRG.15403	7,968	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	0,67	167,00	ethylene biosynthesis
MEZ_RH vs. MEZ_CRH	ET	MSTRG.32014.1	MSTRG.32014	1,5757	1A1C	1-aminocyclopropane-1-carboxylate synthase	181,00	549,33	ethylene biosynthesis
MEZ_RH vs. MEZ_CRH	ET	MSTRG.24860.1	MSTRG.24860	2,7359	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	9,33	62,67	ethylene biosynthesis
MEZ_RH vs. MEZ_CRH	ET	MSTRG.13653.1	MSTRG.13653	3,3332	ACCO5	1-aminocyclopropane-1-carboxylate oxidase 5	59,33	607,33	ethylene biosynthesis
STR_RH vs. STR_CRH	ET	MSTRG.11166.1	MSTRG.11166	1,8609	1A11	1-aminocyclopropane-1-carboxylate synthase 1	27,00	94,00	ethylene biosynthesis
STR_RH vs. STR_CRH	ET	MSTRG.5697.1	MSTRG.5697	1,9471	ACCO1	1-aminocyclopropane-1-carboxylate oxidase 1	495,00	1820,67	ethylene biosynthesis
STR_RH vs. STR_CRH	ET	MSTRG.14325.1	MSTRG.14325	2,1543	1A1C	1-aminocyclopropane-1-carboxylate synthase	15,00	63,67	ethylene biosynthesis
STR_RH vs. STR_CRH	ET	MSTRG.15402.1	MSTRG.15402	2,1695	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	5,67	24,00	ethylene biosynthesis
MTR_RH vs. MTR_CRH	ET	MSTRG.15404.1	MSTRG.15404	2,7644	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	16,00	109,00	ethylene biosynthesis
LTR_RH vs. LTR_CRH	ET	MSTRG.15400.1	MSTRG.15400	1,7854	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	65,00	227,33	ethylene biosynthesis

Comparison	Hormone	Trasncript ID	Gene ID	log2FoldChange	Symbol	Gene description	RPKM Container	RPKM Rhizotron	Function
MLR_RH vs. MLR_C	ET	MSTRG.15402.1	MSTRG.15402	-4,6209	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	5,00	0,00	ethylene biosynthesis
MLR_RH vs. MLR_C	ET	MSTRG.5769.1	MSTRG.5769	-3,0655	1A17	1-aminocyclopropane-1-carboxylate synthase 7	9,33	1,00	ethylene biosynthesis
MLR_RH vs. MLR_C	ET	MSTRG.17225.1	MSTRG.17225	-2,7369	ACCH1	1-aminocyclopropane-1-carboxylate oxidase homolog 1	939,00	127,00	ethylene biosynthesis
MLR_RH vs. MLR_C	ET	MSTRG.17227.1	MSTRG.17227	-1,8917	ACH11	1-aminocyclopropane-1-carboxylate oxidase homolog 11	16,33	4,00	ethylene biosynthesis
MLR_RH vs. MLR_C	ET	MSTRG.32014.1	MSTRG.32014	-1,6316	1A1C	1-aminocyclopropane-1-carboxylate synthase	214,00	62,00	ethylene biosynthesis
MLR_RH vs. MLR_C	ET	MSTRG.11166.1	MSTRG.11166	-1,5633	1A11	1-aminocyclopropane-1-carboxylate synthase 1	63,00	19,67	ethylene biosynthesis
LLR_RH vs. LLR_C	ET	MSTRG.17227.1	MSTRG.17227	-4,2357	ACH11	1-aminocyclopropane-1-carboxylate oxidase homolog 11	6,67	0,33	ethylene biosynthesis
LEZ_RH vs. LEZ_C	ET	MSTRG.6777.1	MSTRG.6777	1,595	ACCO	1-aminocyclopropane-1-carboxylate oxidase	20,67	57,67	ethylene biosynthesis
LEZ_RH vs. LEZ_C	ET	MSTRG.14291.1	MSTRG.14291	2,1246	1A1C	1-aminocyclopropane-1-carboxylate synthase	157,00	596,67	ethylene biosynthesis
LEZ_RH vs. LEZ_C	ET	MSTRG.32014.1	MSTRG.32014	2,3005	1A1C	1-aminocyclopropane-1-carboxylate synthase	202,33	875,67	ethylene biosynthesis
STR_RH vs. STR_C	ET	MSTRG.25190.1	MSTRG.25190	1,5638	1A12	1-aminocyclopropane-1-carboxylate synthase CMA101	29,00	95,00	ethylene biosynthesis
MTR_RH vs. MTR_C	ET	MSTRG.14291.1	MSTRG.14291	-2,0497	1A1C	1-aminocyclopropane-1-carboxylate synthase	360,67	83,33	ethylene biosynthesis
MTR_RH vs. MTR_C	ET	MSTRG.11166.1	MSTRG.11166	-1,8753	1A11	1-aminocyclopropane-1-carboxylate synthase 1	56,67	15,33	ethylene biosynthesis

MTR_RH vs. MTR_C	ET	MSTRG.32014.1	MSTRG.32014	-1,8003	1A1C	1-aminocyclopropane-1-carboxylate synthase	362,67	99,33	ethylene biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Transplanted**	**RPKM Rhizotron**	**Function**
MEZ_RH vs. MEZ_CRH	ABA	MSTRG.13453.1	MSTRG.13453	-2,4408	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	2309,00	432,33	abscisc acid biosynthesis
MEZ_RH vs. MEZ_CRH	ABA	MSTRG.32782.1	MSTRG.32782	-2,2765	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	120,67	25,33	abscisc acid biosynthesis
LEZ_RH vs. LEZ_CRH	ABA	MSTRG.32782.1	MSTRG.32782	-2,5658	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	348,33	62,33	abscisc acid biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Container**	**RPKM Rhizotron**	**Function**
LLR_RH vs. LLR_C	ABA	MSTRG.32782.1	MSTRG.32782	-2,2745	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	405,67	84,67	abscisc acid biosynthesis
LLR_RH vs. LLR_C	ABA	MSTRG.13453.1	MSTRG.13453	-2,0892	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	2557,00	609,33	abscisc acid biosynthesis
LEZ_RH vs. LEZ_C	ABA	MSTRG.13453.1	MSTRG.13453	-2,1878	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	4296,00	890,67	abscisc acid biosynthesis
LTR_RH vs. LTR_C	ABA	MSTRG.13453.1	MSTRG.13453	-2,4219	NCED1	9-cis-epoxycarotenoid dioxygenase NCED1	1796,67	278,67	abscisc acid biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Transplanted**	**RPKM Container**	**Function**
MLR_C vs. MLR_CRH	GA	MSTRG.33954.1	MSTRG.33954	2,2458	G2OX2	Gibberellin 2-beta-dioxygenase 2	42,33	219,33	gibberellin biosynthesis
MLR_C vs. MLR_CRH	GA	MSTRG.23935.1	MSTRG.23935	2,3816	GAOX2	Gibberellin 20 oxidase 2	24,33	140,67	gibberellin biosynthesis
MLR_C vs. MLR_CRH	GA	MSTRG.13536.1	MSTRG.13536	5,0469	GAOX2	Gibberellin 20 oxidase 2	0,67	24,33	gibberellin biosynthesis
LLR_C vs. LLR_CRH	GA	MSTRG.22681.1	MSTRG.22681	2,0065	G3OX	Gibberellin 3-beta-dioxygenase 1	6,67	31,00	gibberellin biosynthesis

LEZ_C vs. LEZ_CRH	GA	MSTRG.31144.1	MSTRG.31144	-1,9939	G3OX	Gibberellin 3-beta-dioxygenase 1	142,00	39,00	gibberellin biosynthesis
LEZ_C vs. LEZ_CRH	GA	MSTRG.9123.1	MSTRG.9123	-1,696	G2OX6	Gibberellin 2-beta-dioxygenase 6	38,33	13,33	gibberellin biosynthesis
STR_C vs. STR_CRH	GA	MSTRG.22681.1	MSTRG.22681	3,9855	G3OX	Gibberellin 3-beta-dioxygenase 1	23,33	306,33	gibberellin biosynthesis
MTR_C vs. MTR_CRH	GA	MSTRG.22681.1	MSTRG.22681	2,4425	G3OX	Gibberellin 3-beta-dioxygenase 1	39,33	220,00	gibberellin biosynthesis
MTR_C vs. MTR_CRH	GA	MSTRG.32735.1	MSTRG.32735	-1,9282	KO1	Ent-kaurene oxidase	219,00	60,00	gibberellin biosynthesis
LTR_C vs. LTR_CRH	GA	MSTRG.33954.1	MSTRG.33954	1,9776	G2OX2	Gibberellin 2-beta-dioxygenase 2	74,33	341,67	gibberellin biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Transplanted**	**RPKM Rhizotron**	**Function**
MLR_RH vs. MLR_CRH	GA	MSTRG.31144.1	MSTRG.31144	1,6723	G3OX	Gibberellin 3-beta-dioxygenase 1	134,33	430,33	gibberellin biosynthesis
MLR_RH vs. MLR_CRH	GA	MSTRG.13439.1	MSTRG.13439	1,9892	G2OX1	Gibberellin 2-beta-dioxygenase 1	271,33	1080,00	gibberellin biosynthesis
MLR_RH vs. MLR_CRH	GA	MSTRG.33954.1	MSTRG.33954	2,4759	G2OX2	Gibberellin 2-beta-dioxygenase 2	42,33	237,00	gibberellin biosynthesis
LLR_RH vs. LLR_CRH	GA	MSTRG.32736.1	MSTRG.32736	1,8664	KO1	Ent-kaurene oxidase	27,67	118,00	gibberellin biosynthesis
LLR_RH vs. LLR_CRH	GA	MSTRG.22681.1	MSTRG.22681	1,995	G3OX	Gibberellin 3-beta-dioxygenase 1	6,67	31,33	gibberellin biosynthesis
MEZ_RH vs. MEZ_CRH	GA	MSTRG.15029.1	MSTRG.15029	-2,6083	G2OX2	Gibberellin 2-beta-dioxygenase 2	74,00	12,33	gibberellin biosynthesis
MEZ_RH vs. MEZ_CRH	GA	MSTRG.9123.1	MSTRG.9123	-1,6949	G2OX6	Gibberellin 2-beta-dioxygenase 6	52,33	16,33	gibberellin biosynthesis
STR_RH vs. STR_CRH	GA	MSTRG.20624.1	MSTRG.20624	1,6516	GAOXL	Gibberellin 20-oxidase-like protein	63,33	187,33	gibberellin biosynthesis
STR_RH vs. STR_CRH	GA	MSTRG.22681.1	MSTRG.22681	3,3931	G3OX	Gibberellin 3-beta-dioxygenase 1	23,33	233,33	gibberellin biosynthesis
MTR_RH vs. MTR_CRH	GA	MSTRG.22681.1	MSTRG.22681	2,6425	G3OX	Gibberellin 3-beta-dioxygenase 1	39,33	243,67	gibberellin biosynthesis

LTR_RH vs. LTR_CRH	GA	MSTRG.22681.1	MSTRG.22681	2,1804	G3OX	Gibberellin 3-beta-dioxygenase 1	25,67	120,67	gibberellin biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Container**	**RPKM Rhizotron**	**Function**
MLR_RH vs. MLR_C	GA	MSTRG.13536.1	MSTRG.13536	-5,0455	GAOX2	Gibberellin 20 oxidase 2	24,33	0,67	gibberellin biosynthesis
LTR_RH vs. LTR_C	GA	MSTRG.15029.1	MSTRG.15029	-2,4024	G2OX2	Gibberellin 2-beta-dioxygenase 2	23,00	3,67	gibberellin biosynthesis
LTR_RH vs. LTR_C	GA	MSTRG.33954.1	MSTRG.33954	-2,1981	G2OX2	Gibberellin 2-beta-dioxygenase 2	341,67	62,33	gibberellin biosynthesis
LTR_RH vs. LTR_C	GA	MSTRG.9123.1	MSTRG.9123	-2,0415	G2OX6	Gibberellin 2-beta-dioxygenase 6	81,00	16,67	gibberellin biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Transplanted**	**RPKM Container**	**Function**
MLR_C vs. MLR_CRH	JA	MSTRG.424.1	MSTRG.424	5,0547	LOX21	Linoleate 13S-lipoxygenase 2-1	1,33	49,67	jasmonate biosynthesis
MLR_C vs. MLR_CRH	JA	MSTRG.34848.1	MSTRG.34848	6,176	LOX21	Linoleate 13S-lipoxygenase 2-1	0,00	14,33	jasmonate biosynthesis
MLR_C vs. MLR_CRH	JA	MSTRG.572.1	MSTRG.572	6,3809	LOX21	Linoleate 13S-lipoxygenase 2-1	0,00	16,67	jasmonate biosynthesis
MLR_C vs. MLR_CRH	JA	MSTRG.575.1	MSTRG.575	7,1496	LOX21	Linoleate 13S-lipoxygenase 2-1	0,00	28,33	jasmonate biosynthesis
MLR_C vs. MLR_CRH	JA	MSTRG.34849.1	MSTRG.34849	8,2276	LOX21	Linoleate 13S-lipoxygenase 2-1	0,00	59,67	jasmonate biosynthesis
MLR_C vs. MLR_CRH	JA	MSTRG.3282.1	MSTRG.3282	5,9236	OPR1	12-oxophytodienoate reductase 1	0,00	12,33	jasmonate biosynthesis
LLR_C vs. LLR_CRH	JA	MSTRG.424.1	MSTRG.424	1,5328	LOX21	Linoleate 13S-lipoxygenase 2-1	25,33	84,33	jasmonate biosynthesis
LLR_C vs. LLR_CRH	JA	MSTRG.34849.1	MSTRG.34849	1,9076	LOX21	Linoleate 13S-lipoxygenase 2-1	21,67	90,33	jasmonate biosynthesis
LLR_C vs. LLR_CRH	JA	MSTRG.570.1	MSTRG.570	2,0014	LOX21	Linoleate 13S-lipoxygenase 2-1	20,33	93,00	jasmonate biosynthesis

LLR_C vs. LLR_CRH	JA	MSTRG.28842.1	MSTRG.28842	2,1471	AOS3	Allene oxide synthase 3	4,67	23,33	jasmonate biosynthesis
MEZ_C vs. MEZ_CRH	JA	MSTRG.424.1	MSTRG.424	6,2907	LOX21	Linoleate 13S-lipoxygenase 2-1	5,00	400,67	jasmonate biosynthesis
LEZ_C vs. LEZ_CRH	JA	MSTRG.34851.1	MSTRG.34851	1,8815	LOX21	Linoleate 13S-lipoxygenase 2-1	80,00	336,33	jasmonate biosynthesis
LEZ_C vs. LEZ_CRH	JA	MSTRG.424.1	MSTRG.424	2,1204	LOX21	Linoleate 13S-lipoxygenase 2-1	151,67	733,00	jasmonate biosynthesis
LEZ_C vs. LEZ_CRH	JA	MSTRG.34849.1	MSTRG.34849	4,0821	LOX21	Linoleate 13S-lipoxygenase 2-1	3,33	64,33	jasmonate biosynthesis
LEZ_C vs. LEZ_CRH	JA	MSTRG.570.1	MSTRG.570	4,3374	LOX21	Linoleate 13S-lipoxygenase 2-1	2,00	45,33	jasmonate biosynthesis
LEZ_C vs. LEZ_CRH	JA	MSTRG.34848.1	MSTRG.34848	4,5201	LOX21	Linoleate 13S-lipoxygenase 2-1	0,67	17,67	jasmonate biosynthesis
LEZ_C vs. LEZ_CRH	JA	MSTRG.572.1	MSTRG.572	4,6844	LOX21	Linoleate 13S-lipoxygenase 2-1	0,67	19,00	jasmonate biosynthesis
LEZ_C vs. LEZ_CRH	JA	MSTRG.575.1	MSTRG.575	5,8275	LOX21	Linoleate 13S-lipoxygenase 2-1	0,33	23,00	jasmonate biosynthesis
STR_C vs. STR_CRH	JA	MSTRG.24102.1	MSTRG.24102	1,9919	OPR2	12-oxophytodienoate reductase 2	70,00	255,33	jasmonate biosynthesis
MTR_C vs. MTR_CRH	JA	MSTRG.24102.1	MSTRG.24102	1,9166	OPR2	12-oxophytodienoate reductase 2	68,00	268,00	jasmonate biosynthesis
LTR_C vs. LTR_CRH	JA	MSTRG.570.1	MSTRG.570	5,3367	LOX21	Linoleate 13S-lipoxygenase 2-1	0,00	9,00	jasmonate biosynthesis
LTR_C vs. LTR_CRH	JA	MSTRG.7230.1	MSTRG.7230	1,769	OPR2	12-oxophytodienoate reductase 2	85,33	362,33	jasmonate biosynthesis
LTR_C vs. LTR_CRH	JA	MSTRG.24084.1	MSTRG.24084	2,3973	OPR2	12-oxophytodienoate reductase 2	230,67	1456,00	jasmonate biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Transplanted**	**RPKM Rhizotron**	**Function**
MLR_RH vs. MLR_CRH	JA	MSTRG.28846.1	MSTRG.28846	2,2599	AOS3	Allene oxide synthase 3	2,00	9,67	jasmonate biosynthesis
MLR_RH vs. MLR_CRH	JA	MSTRG.28845.1	MSTRG.28845	2,5742	AOS3	Allene oxide synthase 3	1150,33	6870,33	jasmonate biosynthesis

MLR_RH vs. MLR_CRH	JA	MSTRG.9496.1	MSTRG.9496	2,8	AOS3	Allene oxide synthase 3	120,33	840,33	jasmonate biosynthesis
MLR_RH vs. MLR_CRH	JA	MSTRG.424.1	MSTRG.424	4,5847	LOX21	Linoleate 13S-lipoxygenase 2-1	1,33	32,33	jasmonate biosynthesis
MLR_RH vs. MLR_CRH	JA	MSTRG.570.1	MSTRG.570	6,2556	LOX21	Linoleate 13S-lipoxygenase 2-1	0,33	27,67	jasmonate biosynthesis
MLR_RH vs. MLR_CRH	JA	MSTRG.34848.1	MSTRG.34848	6,2793	LOX21	Linoleate 13S-lipoxygenase 2-1	0,00	14,33	jasmonate biosynthesis
MLR_RH vs. MLR_CRH	JA	MSTRG.572.1	MSTRG.572	6,3596	LOX21	Linoleate 13S-lipoxygenase 2-1	0,00	15,00	jasmonate biosynthesis
MLR_RH vs. MLR_CRH	JA	MSTRG.575.1	MSTRG.575	6,8587	LOX21	Linoleate 13S-lipoxygenase 2-1	0,00	21,33	jasmonate biosynthesis
MLR_RH vs. MLR_CRH	JA	MSTRG.34849.1	MSTRG.34849	8,0917	LOX21	Linoleate 13S-lipoxygenase 2-1	0,00	50,67	jasmonate biosynthesis
LLR_RH vs. LLR_CRH	JA	MSTRG.28842.1	MSTRG.28842	1,9528	AOS3	Allene oxide synthase 3	4,67	21,00	jasmonate biosynthesis
MEZ_RH vs. MEZ_CRH	JA	MSTRG.34849.1	MSTRG.34849	4,3383	LOX21	Linoleate 13S-lipoxygenase 2-1	1,33	27,00	jasmonate biosynthesis
MEZ_RH vs. MEZ_CRH	JA	MSTRG.424.1	MSTRG.424	4,9347	LOX21	Linoleate 13S-lipoxygenase 2-1	5,00	154,67	jasmonate biosynthesis
MEZ_RH vs. MEZ_CRH	JA	MSTRG.575.1	MSTRG.575	5,05	LOX21	Linoleate 13S-lipoxygenase 2-1	0,00	6,33	jasmonate biosynthesis
STR_RH vs. STR_CRH	JA	MSTRG.34851.1	MSTRG.34851	2,5359	LOX21	Linoleate 13S-lipoxygenase 2-1	20,33	113,00	jasmonate biosynthesis
STR_RH vs. STR_CRH	JA	MSTRG.24102.1	MSTRG.24102	2,0691	OPR2	12-oxophytodienoate reductase 2	70,00	278,33	jasmonate biosynthesis
MTR_RH vs. MTR_CRH	JA	MSTRG.34849.1	MSTRG.34849	3,7277	LOX21	Linoleate 13S-lipoxygenase 2-1	0,33	4,67	jasmonate biosynthesis
MTR_RH vs. MTR_CRH	JA	MSTRG.424.1	MSTRG.424	3,929	LOX21	Linoleate 13S-lipoxygenase 2-1	36,67	559,67	jasmonate biosynthesis
MTR_RH vs. MTR_CRH	JA	MSTRG.24102.1	MSTRG.24102	1,8333	OPR2	12-oxophytodienoate reductase 2	68,00	241,00	jasmonate biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	RPKM Container	RPKM Rhizotron	Function
MLR_RH vs. MLR_C	JA	MSTRG.24102.1	MSTRG.24102	-2,0239	OPR2	12-oxophytodienoate reductase 2	1067,67	240,00	jasmonate biosynthesis
LLR_RH vs. LLR_C	JA	MSTRG.424.1	MSTRG.424	-1,7244	LOX21	Linoleate 13S-lipoxygenase 2-1	84,33	26,00	jasmonate biosynthesis
LLR_RH vs. LLR_C	JA	MSTRG.7230.1	MSTRG.7230	-2,1301	OPR2	12-oxophytodienoate reductase 2	39,67	9,33	jasmonate biosynthesis
MEZ_RH vs. MEZ_C	JA	MSTRG.34849.1	MSTRG.34849	4,8177	LOX21	Linoleate 13S-lipoxygenase 2-1	1,00	27,00	jasmonate biosynthesis
LEZ_RH vs. LEZ_C	JA	MSTRG.575.1	MSTRG.575	-4,979	LOX21	Linoleate 13S-lipoxygenase 2-1	23,00	0,67	jasmonate biosynthesis
LEZ_RH vs. LEZ_C	JA	MSTRG.34849.1	MSTRG.34849	-4,6594	LOX21	Linoleate 13S-lipoxygenase 2-1	64,33	2,33	jasmonate biosynthesis
LEZ_RH vs. LEZ_C	JA	MSTRG.34848.1	MSTRG.34848	-4,599	LOX21	Linoleate 13S-lipoxygenase 2-1	17,67	0,67	jasmonate biosynthesis
LEZ_RH vs. LEZ_C	JA	MSTRG.570.1	MSTRG.570	-4,3795	LOX21	Linoleate 13S-lipoxygenase 2-1	45,33	2,00	jasmonate biosynthesis
LEZ_RH vs. LEZ_C	JA	MSTRG.572.1	MSTRG.572	-3,7326	LOX21	Linoleate 13S-lipoxygenase 2-1	19,00	1,33	jasmonate biosynthesis
LEZ_RH vs. LEZ_C	JA	MSTRG.34851.1	MSTRG.34851	-2,7888	LOX21	Linoleate 13S-lipoxygenase 2-1	336,33	45,33	jasmonate biosynthesis
LEZ_RH vs. LEZ_C	JA	MSTRG.424.1	MSTRG.424	-2,0554	LOX21	Linoleate 13S-lipoxygenase 2-1	733,00	165,00	jasmonate biosynthesis
STR_RH vs. STR_C	JA	MSTRG.9496.1	MSTRG.9496	1,9554	AOS3	Allene oxide synthase 3	55,00	224,67	jasmonate biosynthesis
STR_RH vs. STR_C	JA	MSTRG.28842.1	MSTRG.28842	2,3178	AOS3	Allene oxide synthase 3	24,67	132,67	jasmonate biosynthesis
LTR_RH vs. LTR_C	JA	MSTRG.570.1	MSTRG.570	-5,3356	LOX21	Linoleate 13S-lipoxygenase 2-1	9,00	0,00	jasmonate biosynthesis
LTR_RH vs. LTR_C	JA	MSTRG.34849.1	MSTRG.34849	-4,6275	LOX21	Linoleate 13S-lipoxygenase 2-1	10,67	0,33	jasmonate biosynthesis
LTR_RH vs. LTR_C	JA	MSTRG.575.1	MSTRG.575	-4,4007	LOX21	Linoleate 13S-lipoxygenase 2-1	4,67	0,00	jasmonate biosynthesis

Comparison	Hormone	Trasncript ID	Gene ID	log2FoldChange	Symbol	Gene description	RPKM Transplanted	RPKM Container	Function
MLR_C vs. MLR_CRH	SA	MSTRG.11572.1	MSTRG.11572	1,6568	EPS1	Protein ENHANCED PSEUDOMONAS SUSCEPTIBILITY 1	226,00	787,00	salicylic acid biosynthesis
MLR_C vs. MLR_CRH	SA	MSTRG.32865.2	MSTRG.32865	2,4552	EPS1	Protein ENHANCED PSEUDOMONAS SUSCEPTIBILITY 1	48,33	290,33	salicylic acid biosynthesis
MLR_C vs. MLR_CRH	SA	MSTRG.16782.2	MSTRG.16782	1,9309	SABP2	Salicylic acid-binding protein 2	384,67	1612,67	salicylic acid biosynthesis
MLR_C vs. MLR_CRH	SA	MSTRG.6567.1	MSTRG.6567	2,0693	SABP2	Salicylic acid-binding protein 2	10,67	49,67	salicylic acid biosynthesis
MLR_C vs. MLR_CRH	SA	MSTRG.16784.1	MSTRG.16784	2,1565	SABP2	Salicylic acid-binding protein 2	30,67	150,00	salicylic acid biosynthesis
MLR_C vs. MLR_CRH	SA	MSTRG.34341.1	MSTRG.34341	2,5333	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	54,00	342,33	salicylic acid biosynthesis
MLR_C vs. MLR_CRH	SA	MSTRG.10608.2	MSTRG.10608	3,0625	BSMT3	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 3	4,67	43,33	salicylic acid biosynthesis
MLR_C vs. MLR_CRH	SA	MSTRG.28611.1	MSTRG.28611	3,3071	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	3,67	39,67	salicylic acid biosynthesis
LLR_C vs. LLR_CRH	SA	MSTRG.32865.2	MSTRG.32865	1,8702	EPS1	Protein ENHANCED PSEUDOMONAS SUSCEPTIBILITY 1	76,67	321,00	salicylic acid biosynthesis
LLR_C vs. LLR_CRH	SA	MSTRG.18629.1	MSTRG.18629	2,3134	BSMT1	S-adenosyl-L-methionine:benzoic acid/salicylic acid	61,00	344,67	salicylic acid biosynthesis

						carboxyl methyltransferase 1			
LLR_C vs. LLR_CRH	SA	MSTRG.28611.2	MSTRG.28611	3,6715	BSMT3	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 3	10,67	156,33	salicylic acid biosynthesis
LLR_C vs. LLR_CRH	SA	MSTRG.16250.1	MSTRG.16250	5,3258	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	1,33	61,67	salicylic acid biosynthesis
MEZ_C vs. MEZ_CRH	SA	MSTRG.32865.2	MSTRG.32865	1,8432	EPS1	Protein ENHANCED PSEUDOMONAS SUSCEPTIBILITY 1	711,67	2663,67	salicylic acid biosynthesis
STR_C vs. STR_CRH	SA	MSTRG.18629.1	MSTRG.18629	3,3665	BSMT1	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 1	6,33	50,67	salicylic acid biosynthesis
STR_C vs. STR_CRH	SA	MSTRG.28611.1	MSTRG.28611	3,5283	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	102,00	1117,67	salicylic acid biosynthesis
MTR_C vs. MTR_CRH	SA	MSTRG.18629.1	MSTRG.18629	2,767	BSMT1	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 1	9,00	66,67	salicylic acid biosynthesis
LTR_C vs. LTR_CRH	SA	MSTRG.10608.2	MSTRG.10608	2,2952	BSMT3	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 3	10,67	66,00	salicylic acid biosynthesis

Comparison	Hormone	Trasncript ID	Gene ID	log2FoldChange	Symbol	Gene description	RPKM Transplanted	RPKM Rhizotron	Function
MLR_RH vs. MLR_CRH	SA	MSTRG.16790.2	MSTRG.16790	2,0967	SABP2	Salicylic acid-binding protein 2	381,33	1636,33	salicylic acid biosynthesis
MLR_RH vs. MLR_CRH	SA	MSTRG.16782.2	MSTRG.16782	2,1955	SABP2	Salicylic acid-binding protein 2	384,67	1769,67	salicylic acid biosynthesis
MLR_RH vs. MLR_CRH	SA	MSTRG.16784.1	MSTRG.16784	2,3985	SABP2	Salicylic acid-binding protein 2	30,67	161,67	salicylic acid biosynthesis
MLR_RH vs. MLR_CRH	SA	MSTRG.6567.1	MSTRG.6567	2,4592	SABP2	Salicylic acid-binding protein 2	10,67	59,33	salicylic acid biosynthesis
MLR_RH vs. MLR_CRH	SA	MSTRG.34341.1	MSTRG.34341	3,544	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	54,00	631,33	salicylic acid biosynthesis
MLR_RH vs. MLR_CRH	SA	MSTRG.28611.2	MSTRG.28611	3,6765	BSMT3	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 3	3,67	46,33	salicylic acid biosynthesis
MLR_RH vs. MLR_CRH	SA	MSTRG.10608.2	MSTRG.10608	3,8565	BSMT3	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 3	4,67	68,33	salicylic acid biosynthesis
LEZ_RH vs. LEZ_CRH	SA	MSTRG.18629.1	MSTRG.18629	3,117	BSMT1	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 1	61,67	529,00	salicylic acid biosynthesis
STR_RH vs. STR_CRH	SA	MSTRG.28611.1	MSTRG.28611	2,6592	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	102,00	613,33	salicylic acid biosynthesis

STR_RH vs. STR_CRH	SA	MSTRG.18629.1	MSTRG.18629	3,7462	BSMT1	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 1	6,33	80,67	salicylic acid biosynthesis
STR_RH vs. STR_CRH	SA	MSTRG.32865.2	MSTRG.32865	2,0331	EPS1	Protein ENHANCED PSEUDOMONAS SUSCEPTIBILITY 1	570,67	2230,67	salicylic acid biosynthesis
MTR_RH vs. MTR_CRH	SA	MSTRG.32865.2	MSTRG.32865	1,8283	EPS1	Protein ENHANCED PSEUDOMONAS SUSCEPTIBILITY 1	721,67	2557,00	salicylic acid biosynthesis
MTR_RH vs. MTR_CRH	SA	MSTRG.18629.1	MSTRG.18629	1,5689	BSMT1	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 1	9,00	27,00	salicylic acid biosynthesis
MTR_RH vs. MTR_CRH	SA	MSTRG.28611.1	MSTRG.28611	1,574	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	113,67	337,33	salicylic acid biosynthesis
LTR_RH vs. LTR_CRH	SA	MSTRG.16250.1	MSTRG.16250	2,0643	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	70,00	279,33	salicylic acid biosynthesis

Comparison	**Hormone**	**Trasncript ID**	**Gene ID**	**log2FoldChange**	**Symbol**	**Gene description**	**RPKM Container**	**RPKM Rhizotron**	**Function**
LLR_RH vs. LLR_C	SA	MSTRG.16250.1	MSTRG.16250	-5,9687	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	61,67	1,00	salicylic acid biosynthesis

LLR_RH vs. LLR_C	SA	MSTRG.29136.1	MSTRG.29136	-4,3004	BSMT3	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 3	7,00	0,33	salicylic acid biosynthesis
LLR_RH vs. LLR_C	SA	MSTRG.28611.1	MSTRG.28611	-2,8483	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	156,33	22,00	salicylic acid biosynthesis
MTR_RH vs. MTR_C	SA	MSTRG.16250.1	MSTRG.16250	-4,9345	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	31,67	1,00	salicylic acid biosynthesis
MTR_RH vs. MTR_C	SA	MSTRG.34341.1	MSTRG.34341	-4,1376	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	75,67	4,33	salicylic acid biosynthesis
MTR_RH vs. MTR_C	SA	MSTRG.6568.3	MSTRG.6568	-1,9195	SABP2	Salicylic acid-binding protein 2	11793,00	2992,33	salicylic acid biosynthesis
LTR_RH vs. LTR_C	SA	MSTRG.18629.1	MSTRG.18629	3,4702	BSMT1	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 1	21,00	194,00	salicylic acid biosynthesis
LTR_RH vs. LTR_C	SA	MSTRG.16250.1	MSTRG.16250	6,8106	BSMT2	S-adenosyl-L-methionine:benzoic acid/salicylic acid carboxyl methyltransferase 2	3,00	279,33	salicylic acid biosynthesis

OŚWIADCZENIA WSPÓŁAUTORÓW

ARTYKUŁ 1

Kościelniak P., Glazińska P., Kęsy J., Zadworny M. (2021) Formation and development of taproots in deciduous tree species. *Frontiers in Plant Science* 12:772567.

Poznań, 22.08.2023 rok

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OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak, P., Glazińska, P., Kęsy, J., Zadworny, M. (2021) Formation and development of taproots in deciduous tree species. Frontiers in Plant Science 12:772567

mój udział polegał na:

- Opracowaniu koncepcji,
- Przygotowaniu wszystkich rozdziałów pracy,
- Przygotowaniu schematów,
- Odpowiedzi na uwagi recenzentów,
- Przygotowaniu publikacji do druku.

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OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak, P., Glazińska, P., Kęsy, J., Zadworny, M. (2021) Formation and Development of Taproots in Deciduous Tree Species Frontiers in Plant Science 12:772567 mój udział polegał na: redagowaniu i recenzji rozdziału „Genetic factors involved in root development".

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OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak, P., Glazińska, P., Kęsy, J., Zadworny, M. (2021) Formation and Development of Taproots in Deciduous Tree Species Frontiers in Plant Science 12:772567 mój udział polegał na: redagowaniu i recenzji rozdziału „Effect of Phytohormones on Root Growth".

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Poznań, 22.08.2023 rok

OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak, P., Glazińska, P., Kęsy, J., Zadworny, M. (2021). Formation and development of taproots in deciduous tree species opublikowanej w Frontiers in Plant Science 12:772567 mój udział polegał na: pomyśle projektu badawczego, udziale w dyskusji koncepcji pracy oraz udziale w przygotowaniu publikacji do druku.

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ARTYKUŁ 2

Kościelniak P., Glazińska P., Zadworny M. (2022) OakRootRNADB—a consolidated RNA-seq database for coding and noncoding RNA in roots of pedunculate oak (*Quercus robur*).
Database: *The Journal of Biological Databases and Curation* baac097.

Poznań, 22.08.2023 rok

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OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak, P., Glazińska, P., Zadworny, M. (2022) OakRootRNADB—a consolidated RNA-seq database for coding and noncoding RNA in roots of pedunculate oak (*Quercus robur*) Database: The Journal of Biological Databases and Curation, Volume 2022, baac097

mój udział polegał na:

- Wysiewie i uprawie dębu szypułkowego w systemie kontenerowym i w ryzotronach,
- Zbiorze materiału,
- Optymalizacji warunków izolacji RNA, reakcji odwrotnej transkrypcji oraz łańcuchowej reakcji polimerazy w czasie rzeczywistym dla korzeni palowych i bocznych dębu szypułkowego,
- Przygotowaniu materiału do sekwencjonowania NGS (analizie ilościowej i jakościowej),
- Walidacji wyników po sekwencjonowaniu NGS (przeprowadzenie reakcji odwrotnej transkrypcji i real-time PCR),
- Interpretacji wyników,
- Analizie bioinformatycznej,
- Analizie statystycznej,
- Przygotowaniu koncepcji bazy danych,
- Przygotowaniu wszystkich rozdziałów manuskryptu,
- Przygotowaniu schematów, figur i tabel,
- Redagowaniu manuskryptu,
- Przygotowaniu odpowiedzi na uwagi recenzentów,
- Przygotowaniu końcowej wersji pracy.

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OŚWIADCZENIE

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- udziale w opracowaniu koncepcji i założeń pracy,
- optymalizacji warunków izolacji RNA, reakcji odwrotnej transkrypcji oraz łańcuchowej reakcji polimerazy w czasie rzeczywistym w korzeniach palowych i bocznych dębu,
- opiece merytorycznej podczas wykonania analiz,
- konsultacji naukowej,
- wsparciu w analizie i interpretacji wyników,
- redakcji manuskryptu

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Poznań, 22.08.2023 rok

OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak, P., Glazińska, P., Zadworny, M. (2022). OakRootRNADB—a consolidated RNA-seq database for coding and noncoding RNA in roots of pedunculate oak (*Quercus robur*). Database: The Journal of Biological Databases and Curation, Volume 2022, baac097 mój udział polegał na: pomyśle projektu badawczego, udziale w dyskusji koncepcji pracy oraz udziale w przygotowaniu publikacji do druku.

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ARTYKUŁ 3

Kościelniak P., Glazińska P., Zadworny M. (2023) Early stages in the formation of *Quercus robur* root system: variation in gene expression is linked to the functional type of roots.

Poznań, 22.08.2023 rok

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OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak P., Glazińska P., Zadworny M. (2023) Early stages in the formation of *Quercus robur* root system: variation in gene expression is linked to the functional type of roots.

mój udział polegał na:

- Opracowaniu koncepcji i planu badań,
- Wysiewie i uprawie dębu szypułkowego w ryzotronach,
- Klasyfikacji korzeni według długości i morfologii,
- Zbiorze materiału,
- Optymalizacji warunków izolacji RNA, reakcji odwrotnej transkrypcji oraz łańcuchowej reakcji polimerazy w czasie rzeczywistym dla korzeni palowych i bocznych dębu szypułkowego,
- Przygotowaniu materiału do sekwencjonowania NGS (analizie ilościowej i jakościowej),
- Walidacji wyników po sekwencjonowaniu NGS (przeprowadzenie reakcji odwrotnej transkrypcji i real-time PCR),
- Interpretacji wyników,
- Analizie bioinformatycznej (w tym opracowaniu wyników dla DEG, GO, KEGG, Heat-mapy),
- Analizie statystycznej,
- Przygotowaniu manuskryptu,
- Przygotowaniu schematów, figur i tabel,
- Redagowaniu manuskryptu,
- Przygotowaniu końcowej wersji pracy.

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OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak P., Glazińska P., Zadworny M. (2023) Early stages in the formation of *Quercus robur* root system: variation in gene expression is linked to the functional type of roots udział polegał na:
- udziale w opracowaniu koncepcji i założeń pracy,
- nadzorze nad wykonanymi analizami bioinformatycznymi (DEG, GO, KEGG),
- opiece merytorycznej podczas wykonania analiz,
- wsparciu w interpretacji wyników,
- konsultacji naukowej,
- przygotowaniu i redakcji manuskryptu

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OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak P., Glazińska P., Zadworny M. (2023) Early stages in the formation of Quercus robur root system: variation in gene expression is linked to the functional type of roots udział polegał na: pomyśle projektu badawczego, udziale w opracowaniu i dyskusji koncepcji pracy, udziale w przygotowaniu preparatów anatomicznych, oraz udziale w przygotowaniu publikacji.

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ARTYKUŁ 4

Kościelniak P., Glazińska P., Kęsy J., Mucha J., Zadworny M. (2023) Identification of genetics and hormonal factors involved in *Quercus robur* root growth regulation in different cultivation system.

Poznań, 22.08.2023 rok

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OŚWIADCZENIE

Oświadczam, że w pracy Identification of genetics and hormonal factors involved in *Quercus robur* root growth regulation in different cultivation

mój udział polegał na:

- Opracowaniu koncepcji i planu badań,
- Wysiewie i uprawie dębu szypułkowego w systemie kontenerowym i w ryzotronach,
- Klasyfikacji korzeni według długości i morfologii,
- Zbiorze materiału,
- Optymalizacji warunków izolacji RNA, reakcji odwrotnej transkrypcji oraz łańcuchowej reakcji polimerazy w czasie rzeczywistym dla korzeni palowych i bocznych dębu szypułkowego,
- Przygotowaniu materiału do sekwencjonowania NGS (analizie ilościowej i jakościowej),
- Walidacji wyników po sekwencjonowaniu NGS (przeprowadzenie reakcji odwrotnej transkrypcji i real-time PCR),
- Analizie bioinformatycznej (w tym opracowaniu wyników dla DEG, GO, KEGG),
- Optymalizacji warunków izolacji i ilościowej analizy hormonów roślinnych w korzeniach palowych i bocznych dębu szypułkowego,
- Wykonaniu analiz ilościowych badanych fitohormonów,
- Interpretacji wyników,
- Analizie statystycznej,
- Przygotowaniu manuskryptu,
- Przygotowaniu schematów, figur i tabel,
- Redagowaniu manuskryptu,
- Przygotowaniu końcowej wersji pracy.

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OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak P., Glazińska P., Kęsy J., Mucha J., Zadworny M. (2023) Identification of genetics and hormonal factors involved in *Quercus robur* root growth regulation in different cultivation system udział polegał na:
- udziale w opracowaniu koncepcji i założeń pracy,
- opiece merytorycznej podczas wykonywania analiz bioinformatycznych (DEG, GO, KEGG),
- wsparciu w interpretacji wyników,
- konsultacji naukowej,
- redakcji manuskryptu

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OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak P., Glazińska P., Kęsy J., Mucha J., Zadworny M. (2023) Identification of genetics and hormonal factors involved in *Quercus robur* root growth regulation in different cultivation system mój udział polegał na:
- optymalizacji warunków izolacji i ilościowej analizy hormonów roślinnych w korzeniach palowych i bocznych
- opiece merytorycznej podczas wykonywania analiz poziomu hormonów roślinnych
- wsparciu w interpretacji wyników,
- konsultacji naukowej,
- redakcji manuskryptu

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OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak P., Glazińska P., Kęsy J., Mucha J., Zadworny M. (2023) Identification of genetics and hormonal factors involved in *Quercus robur* root growth regulation in different cultivation system udział polegał na: udziale w przeprowadzeniu analizy statystycznej i przygotowaniu manuskryptu.

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OŚWIADCZENIE

Oświadczam, że w pracy Kościelniak P., Glazińska P., Kęsy J., Mucha J., Zadworny M. (2023) Identification of genetics and hormonal factors involved in *Quercus robur* root growth regulation in different cultivation system udział polegał na: pomyśle projektu badawczego, udziale w opracowaniu i dyskusji koncepcji pracy oraz udziale w przygotowaniu publikacji.

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