**Instytut Dendrologii Polskiej Akademii Nauk**

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# Dynamika stanu biomasy runa i jej rozkładu w lesie grądowym *Galio sylvatici-Carpinetum* (R.Tx. 1937) Oberd. 1957

Dynamics of the understory biomass and its decomposition in the *Galio sylvatici-Carpinetum* (R.Tx. 1937) Oberd. 1957 oak-hornbeam forest

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**Lista publikacji stanowiących rozprawę doktorską**

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**Abstract**

Production and decomposition are crucial biogeochemical cycles in nature. Despite numerous studies on these processes in forest ecosystems, little attention has been given to the herbaceous layer. This study aimed to fill this knowledge gap by investigating the dynamics of biomass production and decomposition rates of herbaceous plant species in oak-hornbeam forests. The following research hypotheses were formulated: (H1) the biomass of the herbaceous layer would undergo seasonal changes, with the highest biomass recorded in May, (H2) the contribution of the herbaceous layer to the annual net primary production (ANPP) would not exceed 5%, (H3) the decomposition rate of herbaceous plant litter would be higher than that of trees leaf litter from oak-hornbeam forests and would not exceed one year, (H4) spring ephemerals biomass would decompose the fastest, while summer-green plants biomass would decompose the slowest, (H5) the decomposition and nutrient release rates of herbaceous leaf litter would be significantly faster than those of stem litter. The study was conducted during four years (2012-2015) in an oak-hornbeam forest located in the Czmoń Forest District (W Poland).

During the study, it was found that the seasonal dynamics of herbaceous layer biomass showed a single-peak pattern, starting in spring and extending into early autumn, contradicting previous studies that suggested a bimodal biomass dynamics (H1). Additionally, the contribution of herbaceous biomass to the annual litterfall production was 9.23% of the total litterfall and 13.86% of the labile fraction during the three growing seasons studied, which was higher than previously described in the literature (H2). The decomposition rate of summer-greens was similar to that of leaf- litter from trees (H3). Complete decomposition of herbaceous plant-litter did not always occur within a year, challenging previous findings that suggested all herbaceous-litter belonged to the labile fraction of litter. The decomposition and nutrient release rates were highest for spring ephemerals (H4), and the decomposition rate and N and C release from *Alliaria petiolata* leaves biomass were approximately six times faster than those from *A. petiolata* stems biomass (H5).

The obtained results highlight the importance of the herbaceous layer in forest ecosystems, emphasizing the need for its protection. They also indicate a lack of comprehensive knowledge about its functioning, debunking some previously held

assumptions. Therefore, further research and dissemination of knowledge regarding the ecological significance of herbaceous layers in forests are encouraged.

**Streszczenie**

Produkcja oraz rozkład materii organicznej to kluczowe procesy biogeochemiczne odpowiadające za obieg pierwiastków w przyrodzie. Pomimo wielu prac poświęconych tym procesom w ekosystemach leśnych, niewiele z nich dotyczyło warstwy zielnej lasów. W niniejszych badaniach podjęto próbę wypełnienia tej luki. Celem badań było określenie dynamiki produkcji oraz tempa dekompozycji biomasy roślin naczyniowych runa lasów grądowych. Przyjęto następujące hipotezy badawcze: (H1) stan biomasy runa leśnego podlegać będzie sezonowym zmianom, przy czym najwyższe stany odnotowane zostaną w maju, (H2) udział warstwy zielnej w rocznej produkcji pierwotnej lasu nie będzie wyższy niż 5%, (H3) czas niezbędny do rozkładu nekromasy roślin zielnych runa lasu grądowego będzie krótszy niż potrzebny do rozkładu liści drzew gatunków grądowych i nie przekroczy roku, (H4) najszybciej rozkładać się będzie nekromasa geofitów wiosennych, najwolniej zaś nekromasa roślin pełni lata, (H5) tempo rozkładu oraz uwalniania azotu i węgla z nekromasy liści roślin zielnych będzie znacznie szybsze niż z nekromasy ich łodyg. Badania prowadzono przez cztery lata (2012-2015) w kompleksie lasów grądowych zlokalizowanych w Leśnictwie Czmoń.

W toku realizacji badań stwierdzono, iż sezonowa dynamika biomasy warstwy zielnej wykazała jeden wyraźny szczyt, rozpoczynający się wiosną i trwający do wczesnej jesieni, a nie jak wskazywały wcześniejsze badania dwa szczyty stanu biomasy (H1). Ponadto udział produkcji biomasy warstwy zielnej w rocznej produkcji opadu roślinnego wynosił 9,23% całkowitej ilości opadu roślinnego i 13,86% udziału frakcji łatwo rozkładającej się w trzech badanych sezonach wegetacyjnych, co stanowiło wartość wyższą od dotychczas opisywanych w literaturze (H2). Tempo rozkładu biomasy niektórych roślin pełni lata było zbliżone do tempa rozkładu biomasy liści drzew (H3). Pełny rozkład nekromasy roślin zielnych nie zawsze zachodził w ciągu roku – nie cały opad roślin zielnych należy do labilnej frakcji opadu, jak sugerowały wyniki wcześniejszych badań. Tempo rozkładu oraz tempo uwalniania azotu (N) i węgla (C) jest najszybsze w przypadku geofitów wiosennych (H4), a tempo rozkładu nekromasy oraz uwalniania azotu i węgla z liści *Alliaria petiolata* było około sześciu razy szybsze niż w przypadku nekromasy łodyg tego gatunku (H5).

Uzyskane wyniki podkreślają ogromne znaczenie warstwy runa leśnego w ekosystemie, wskazując konieczność większego zainteresowania oraz ochrony tej

warstwy lasu. Wskazują również na brak gruntownej wiedzy dotyczącej jej funkcjonowania, obalając część obowiązujących do tej pory stwierdzeń na ten temat. Tym samym zachęcają również do dalszego zgłębiania oraz popularyzacji wiedzy na temat ekologicznego znaczenia warstwy zielnej lasów.

## 1. Wstęp

Warstwa zielna lasów, w porównaniu z warstwą drzew, jest słabo widoczna w krajobrazie leśnym. Również jej znaczenie ekonomiczne jest relatywnie niskie, jednak istnieje wiele powodów, dla których należy poznać i docenić tę warstwę. Zestawienia wyników badań warstwy zielnej potwierdzają jej ogromne znaczenie ekologiczne (Gilliam 2007; Landuyt i in. 2019, 2020). Warstwa zielna runa ma znaczący wkład w różnorodność gatunkową lasów, stanowiąc nawet 80% gatunków roślin naczyniowych w lesie (Gilliam 2007). Ponadto, rzadkie gatunki roślin z warstwy zielnej, dzięki swoim wąskim wymaganiom ekologicznym, są dobrymi wskaźnikami jakości siedlisk leśnych, żyzności gleby czy przeszłości gospodarczej lasów (Ellenberg 1988; Dyderski i in. 2017). Rośliny zielne w lasach konkurują o zasoby środowiskowe z młodymi drzewami, co ma wpływ na skład gatunkowy warstw lasu (Baraloto i in. 2005). Warstwa zielna pełni również funkcję siedliska i źródła pożywienia dla zwierząt (Gill i Beardall 2001; Boch i in. 2013; Smolko i in. 2018). Obecność roślin zielnych oraz ich skład gatunkowy wpływa na właściwości fizykochemiczne gleby (Stefanowicz i in. 2023) oraz na występowanie i różnorodność arbuskularnych grzybów mykoryzowych i innych mikroorganizmów glebowych (Zubek i in. 2022).

Nieliczne dotychczasowe badania podkreślają, iż gatunki zielne mają istotne znaczenie dla retencji składników odżywczych w lesie (Bormann 1953; Muller i Bormann 1976; Muller 2014). Warstwa zielna może stanowić nawet 16% rocznego opadu ściółki w lasach (Gilliam 2007; Muller 2014). W lasach liściastych w klimacie umiarkowanym gatunki zielne dostarczają opadu ściółki równomiernie przez cały sezon wegetacyjny, a nie tylko w jesiennej fali, jak ma to miejsce w przypadku opadu liści drzew (Wise i Shaefer 1994). Dodatkowo, koncentracje niektórych składników odżywczych (takich jak azot, fosfor, potas czy magnez) w liściach roślin zielnych są wyższe niż w przypadku drzew (Gilliam 2007), a także przyjmuje się, iż nekromasa roślin zielnych rozkłada się w czasie krótszym niż 1 rok (Muller 2014). Ponadto jedna z grup roślin zielnych (geofity wiosenne), jak mówi teoria „wiosennej tamy", może stanowić barierę chroniącą pierwiastki przed wymywaniem do głębszych warstw gleby. W okresie wczesnej wiosny, gdy drzewa nie są jeszcze ulistnione i nie pobierają pierwiastków z gleby, korzystają z nich geofity, wbudowując je we własną biomasę. Następnie szybko zamierają i w procesie mineralizacji uwalniają pierwiastki, z których korzystają ulistnione już w tym okresie roku drzewa (Muller 2014).

Produkcja i dekompozycja masy organicznej są kluczowymi procesami biologicznymi na Ziemi, a w kontekście zdolności do retencji węgla nabierają one coraz większego znaczenia w badaniach ekosystemów leśnych (Berg i McClaugherty 2014). Warstwa zielna lasów często jest pomijana w badaniach dotyczących produkcji i dekompozycji materii organicznej, ponieważ stanowi stosunkowo niewielki udział (około 1-2%) w biomasie ekosystemów leśnych. Badania dotyczące produkcji biomasy nadziemnej w lasach często skupiają się głównie na warstwie drzew (Jagodziński i in. 2019; Tuan i in. 2022; Viet i in. 2022), a dotyczące procesu dekompozycji w ekosystemach leśnych na liściach gatunków drzewiastych (np. Dziadowiec 1987, 1990; Hobbie i in. 2006; Jackson i in. 2013; Horodecki i Jagodziński 2017, 2019; Jurkšienė i in. 2017; Horodecki i in. 2019) oraz drewnie (np. Bantle i in. 2014; Harmon i in. 2000).

Najnowsze zestawienia badań przeprowadzonych w lasach liściastych klimatu umiarkowanego wskazują, że biomasa warstwy zielnej, która zwykle wynosi od 0 do 500 g $m^{-2}$ (Landuyt i in. 2020; Rawlik i Jagodziński 2022), może być porównywalna z biomasą opadu liści drzew (100 do 900 g $m^{-2}$; Sayer 2006). To podkreśla znaczący wkład warstwy zielnej w labilną frakcję ściółki, która w znacznej części ulega rozkładowi w pierwszym roku dekompozycji. Jednakże badania produkcji warstwy zielnej runa oraz opadu z górnych warstw drzewostanu w tym samym obiekcie są niezwykle rzadkie (Landuyt i in. 2019), a nieliczne prowadzone były w ciągu jednego lub dwóch sezonów wegetacyjnych.

Produkcja pierwotna netto (PPN) to różnica między produkcją pierwotną brutto (całkowitą fotosyntezą) a całkowitym oddychaniem roślin w lesie i może być zmierzona jako całkowita ilość nowej materii organicznej wyprodukowanej w określonym przedziale czasu (Clark i in. 2001). Najczęściej stosowaną metodą szacowania rocznej PPN w lasach jest pomiar ilości biomasy stojącej wytworzonej w ciągu roku (Clark i in. 2001). W przypadku warstwy zielnej w lasach liściastych klimatu umiarkowanego najprostszą metodą jest uznawanie PPN za równą najwyższej obserwowanej wartości biomasy w ciągu roku (Rawlik i Jagodziński 2022). Jednak stosowanie tej metody prowadzi do niedoszacowania PPN, zwłaszcza w przypadku lasów liściastych, gdzie różne grupy roślin zielnych osiągają szczyt biomasy w różnym czasie i szybko obumierają po osiągnięciu tego szczytu (Rawlik i Jagodziński 2020). Występujące w runie lasów liściastych strefy umiarkowanej rośliny zielne wykorzystują różne

strategie przystosowania do życia w środowisku o ograniczonym dostępie światła, które można ogólnie opisać jako unikanie cienia (geofity wiosenne), tolerowanie cienia (rośliny pełni lata) lub wykorzystywanie okresu zimowego do fotosyntezy (zimujące, wiecznie zielone; Uemura 1994; Neufeld i Young 2014; Jagodziński i in. 2016). Rośliny z tych grup rosną i osiągają maksymalną biomasę w różnych porach roku, dlatego rezultaty wcześniejszych badań, które skupiały się na jednym zbiorze biomasy w momencie osiągnięcia maksymalnej wartości, są niewystarczająca do dokładnego opisania dynamiki biomasy (Rawlik i Jagodziński 2022). Dotychczasowe badania opisały dwa szczyty biomasy w sezonowej dynamice: pierwszy wiosną, związany z dominacją wiosennych geofitów w biomasie, a drugi pod koniec lata lub na początku jesieni, związany z dominacją roślin pełni lata (np. Jagodziński i in. 2013; Czapiewska i in. 2019; Rawlik i Jagodziński 2022). Jednak wcześniejsze badania pomijały okres zimowy, zakładając brak jakichkolwiek zmian w biomasie poza sezonem wegetacyjnym, oraz opisywały tylko sumaryczną masę roślinności zielnej (bez podziału na gatunki). Według Rawlika i Jagodzińskiego (2022), którzy porównali dotychczas stosowane metody szacowania PPN roślin runa, te najczęściej stosowane metody prowadzą do blisko dwuipółkrotnego niedoszacowania rocznej nadziemnej produkcji netto. Wzorce sezonowej zmienności biomasy warstwy zielnej są ściśle związane z ilościowymi relacjami między grupami roślin tworzącymi tę warstwę. Sezonowe wzorce produkcji warstwy zielnej można przewidzieć na podstawie składu gatunkowego lub informacji na temat grup funkcjonalnych. Dotychczas uzyskane informacje na temat pełnej sezonowej dynamiki biomasy roślin zielnych runa (włączając okres zimowy) w lasach grądowych umiarkowanej strefy klimatycznej są zdecydowanie niepełne.

Wyniki dotychczasowych badań dotyczących rozkładu materii organicznej w lasach liściastych skupiały się na tempie rozkładu opadłych liści drzew (Hobbie i in. 2006; Horodecki i Jagodziński 2017, 2019; Horodecki i in. 2019), jedynie nieliczne badania dotyczyły rozkładu nekromasy roślin zielnych (Wise i Shaefer 1994; Mayer 2008; Rodgers i in. 2008; Halabuk i Gerhátová 2011) oraz interakcji z organizmami glebowymi (Wise i Shaefer 1994). Większość tych badań wskazuje, że nekromasa roślin zielnych w lasach liściastych strefy umiarkowanej ulega całkowitemu rozkładowi w ciągu sześciu miesięcy po opadnięciu (obumarciu; Mayer 2008; Rodgers i in. 2008; Halabuk i Gerhátová 2011; Muller 2014). Jedynie martwa biomasa roślin zielnych,

w której dominowały turzyce, krzewinki i mchy (Hobbie 1996) lub paprocie i krzewinki (MacLean i Wein 1978), potrzebowała ponad roku, aby ulec całkowitemu rozkładowi.

Związek między strategią adaptacyjną gatunków roślin a podatnością na rozkład pochodzącego z nich materiału ma kluczowe znaczenie dla zrozumienia oddziaływań między roślinnością a glebą. Istnieje ogólna koncepcja, że cechy funkcjonalne liści (LES = Leaf Economic Spectrum; Wright i in. 2005) wpływają na rozkład opadłej ściółki i uwalnianie składników odżywczych (Cornelissen i Thompson 1997; Zukswert i Prescott 2017). Według tej koncepcji gatunki roślin o konserwatywnych strategiach życiowych (oszczędzające zasoby środowiskowe), które charakteryzują się takimi cechami jak: wysoka zawartość suchej masy liścia (leaf dry matter content=LDMC), niska koncentracja składników odżywczych i niska specyficzna powierzchnia liścia (specific leaf area=SLA), rozkładają się wolniej niż gatunki szybko rosnące, o efektywnej strategii pozyskiwania zasobów środowiskowych (Wright i in. 2005; Freschet i in. 2010, 2012; Díaz i in. 2016). Badania, które umieszczają tempo rozkładu w kontekście kompromisu między obroną a produkcją fotosyntetyczną, często prowadzone były na liściach drzew (Melillo i in. 1982; Makkonen i in. 2012; Zukswert i Prescott 2017) lub gatunkach zielnych zbiorowisk trawiastych (Cornelissen i Thompson 1997; Cornwell i in. 2008). Dotychczasowe badania wskazują, że geofity wiosenne wytwarzają krótkowieczne liście, o cechach typowych dla roślin rosnących w pełnym świetle. Liście te wykazują największą aktywność metaboliczną, najwyższe tempo fotosyntezy i największą koncentrację azotu spośród wszystkich fenologicznych grup roślin zielnych runa (Rothstein i Zak 2001; Muller 2014). Ogólnie, koncentracja składników odżywczych w liściach roślin zielnych jest wyższa niż u gatunków tworzących piętro drzew. W wielu wcześniejszych badaniach stwierdzono, że tempo rozkładu silnie koreluje dodatnio z koncentracją azotu w liściach i ujemnie z długością życia liścia (Wright i in. 2005; Cornwell i in. 2008; Bakker i in. 2011). Jak dotąd nie ma informacji na temat różnic w tempie rozkładu między gatunkami reprezentującymi różne strategie życiowe wśród roślin runa lasu grądowego.

Chemiczne cechy liści, takie jak zawartość azotu (N), fosforu (P) i wapnia (Ca) (Aerts 1997), pH (Cornelissen i in. 2006) oraz stosunki koncentracji składników odżywczych (np. C:N, N:P) są istotnymi predyktorami tempa rozkładu obumarłych liści (Freschet i in. 2012; Patoine i in. 2020). Wpływ cech funkcjonalnych na rozkład opadłych (obumarłych) liści jest dobrze udokumentowany, podczas gdy dla innych

organów takie wyraźne wzorce nie zostały jeszcze znalezione (Tuo i in. 2021). Dlatego wpływ cech innych organów lub cech związanych z alokacją biomasy na tempo rozkładu pozostają niezbadane. Różnice w cechach strukturalnych i fizjologicznych między organami, związane z różnymi funkcjami biologicznymi, mogą wpływać na różną podatność na dekompozycję, a tym samym w rezultacie na właściwości gleby i relacje biogeochemiczne całego ekosystemu (Freschet i in. 2012). Bumb i in. (2018) wykazali, że nie ma znaczących różnic w tempie rozkładu liści i pędów 16 gatunków roślin zielnych z obszaru śródziemnomorskich pastwisk. Natomiast Zuo i in. (2018) stwierdzili, że liście zazwyczaj rozkładają się szybciej niż gałęzie i pędy, a gałęzie zazwyczaj rozkładają się szybciej niż konary w przypadku jedenastu gatunków drzewiastych z obszaru klimatu umiarkowanego. Pietsch i in. (2014) oszacowali, że tempo rozkładu drewna jest ogólnie niższe niż tempo rozkładu liści, jednak Zanne i in. (2015) stwierdzili słabe korelacje między tempem rozkładu różnych organów (liść, gałąź i drewno) u 21 gatunków drzewiastych w klimacie umiarkowanym lasu dębowo-orzechowego w USA.

Tempo rozkładu ma wpływ na istotne procesy ekosystemowe, takie jak bilans wymiany węgla, magazynowanie węgla i krążenie składników odżywczych, dlatego modele procesu dekompozycji, opracowane w badaniach empirycznych, są bezpośrednio wykorzystywane w globalnych modelach obiegu węgla (Brovkin i in. 2012). Mimo istnienia wielu różnych modeli procesów rozkładu, najczęściej stosowanym jest pojedynczy model wykładniczy, zaproponowany przez Olsona (Olson 1963; Berg i McClaugherty 2014). Ten model jest stosunkowo prosty i dobrze sprawdza się w modelowaniu wczesnych stadiów rozkładu, zakładając stałe tempo rozkładu i całkowite rozłożenie materii (Gholz i in. 2000). Metoda ta wielokrotnie była krytykowana jako adekwatna tylko dla homogenicznego materiału składającego się z frakcji o jednakowej rozkładalności (Wieder i Lang 1982; Cheshire i in. 1988; Prescott 2005; Adair i in. 2008). Model oparty na założeniu, że opadłe liście są mieszanką materiałów składających się z frakcji o różnym tempie rozkładu, to podwójny model wykładniczy (Berg i McClaugherty 2014). Obumarłe rośliny zielne są mieszanym materiałem, składającym się z łatwo rozkładających się liści i trudniejszych do rozłożenia łodyg, dlatego podwójny model wykładniczy powinien lepiej opisać proces ich rozkładu (Berg i McClaugherty 2014). Ponadto, pojedynczy model wykładniczy sprawdza się tylko we wczesnych stadiach rozkładu, gdy pozostaje

około 20% początkowej masy, podczas gdy podwójny model wykładniczy lepiej opisuje cały proces rozkładu (Berg i McClaugherty 2014). Dynamika rozkładu jest najlepiej opisana dla igliwia i innych liści drzew (Berg i McClaugherty 2014), dlatego ważne jest sprawdzenie, czy obumarłe rośliny zielne odzwierciedlają ogólne wzorce.

## 2. Cele i hipotezy

Celem rozprawy doktorskiej jest określenie udziału roślin zielnych runa leśnego w rocznej nadziemnej produkcji pierwotnej, a także określenie tempa dekompozycji roślin zielnych runa leśnego w lesie grądowym. W badaniach przyjęto następujące hipotezy:

(1) stan biomasy runa leśnego podlegać będzie sezonowym zmianom, przy czym najwyższe stany odnotowane zostaną w maju (w okresie rozpoczęcia listnienia drzew).

Uzasadnienie: Dynamika sezonowa zmian biomasy warstwy zielnej jest ściśle związana z ilościowymi relacjami pomiędzy grupami ekologicznymi roślin tworzących tę warstwę leśną (geofity wiosenne, rośliny pełni lata, zimozielone), więc może być prognozowana na podstawie składu gatunkowego i składu grup ekologicznych roślin tworzących tę warstwę leśną (Rawlik i Jagodziński 2022). Wcześniejsze badania w podobnych zbiorowiskach roślinnych (np. Jagodziński i in. 2013; Czapiewska i in. 2019; Rawlik i Jagodziński 2022) wykazały, że dynamika biomasy warstwy zielnej wykazuje dwa szczyty: większy, występujący na wiosnę, związany z dominacją geofitów wiosennych, i drugi, występujący pod koniec lata lub na początku jesieni, związany z dominacją roślin letnich.

(2) udział warstwy zielnej w rocznej produkcji pierwotnej lasu nie będzie wyższy niż 5%.

Uzasadnienie: Wcześniejsze badania wykazały, że udział warstwy zielnej w PPN w różnych rodzajach lasów zazwyczaj mieści się w zakresie od 0,5% do 16%, ale może być wyższy (aż do 41%) w bardziej otwartych zbiorowiskach leśnych (Gilliam 2007; Muller 2014; Landuyt i in. 2019). W lasach liściastych umiarkowanej strefy klimatycznej zazwyczaj jest to mniej niż 5% (DeAngelis i in. 1981; Welch i in. 2007).

(3) czas niezbędny do rozkładu nekromasy roślin zielnych runa lasu grądowego będzie krótszy niż potrzebny do rozkładu liści drzew gatunków grądowych i w przypadku roślin zielnych nie przekroczy roku.

Uzasadnienie: Wyniki dotychczasowych badań wskazują, że nekromasa gatunków zielnych w lasach liściastych strefy umiarkowanej ulega całkowitemu rozkładowi w ciągu sześciu miesięcy po opadnięciu (Mayer 2008; Rodgers i in. 2008; Halabuk i Gerhátová 2011; Muller 2014). Tylko ściółka z dominacją biomasy gatunków takich jak turzyce, krzewy i mchy (Hobbie 1996) lub paprocie i krzewy (MacLean i Wein 1978) wymagała więcej niż jednego roku, aby ulec całkowitej dekompozycji.

(4) najszybciej rozkładać się będzie nekromasa roślin aspektu wiosennego (geofity), najwolniej natomiast nekromasa roślin pełni lata.

Uzasadnienie: Korelacje tempa dekompozycji ze strategią życiową i cechami funkcjonalnymi zostały opisane dla roślin drzewiastych (Berg i McClaugherty 2014) lub roślin zielnych łąk (Scherer-Lorenzen 2008). Na podstawie wyników tych badań zakładamy, że nekromasa geofitów wiosennych, produkujących szybko krótkowieczne organy, będzie ulegała rozkładowi szybciej niż nekromasa roślin pełni lata, które produkują organy wolniej, inwestując więcej w związki obronne.

(5) tempo rozkładu oraz uwalniania azotu i węgla z nekromasy liści będzie znacznie szybsze niż z nekromasy łodyg.

Uzasadnienie: Cechy strukturalne oraz fizjologiczne różnych organów roślinnych, związane z pełnionymi przez nie funkcjami biologicznymi, mogą powodować różne tempo rozkładu ich biomasy (Freschet i in. 2012). Wyniki wcześniejszych badań tempa rozkładu różnych organów roślinnych nie są jednoznaczne, jednak pozwalają przypuszczać, iż tempo rozkładu liści będzie szybsze niż łodyg u roślin zielnych runa lasu grądowego (Pietsch i in. 2014; Zanne i in. 2015).

Ze względu na złożoność układu doświadczalnego, w każdej z opublikowanych prac przyjęto dodatkowe hipotezy, odnoszące się bezpośrednio do zakresu wyników w nich prezentowanych.

## 3. Materiał i metody

### 3.1. Teren badań

Powierzchnie badawcze zostały założone w obrębie dużego, zwartego kompleksu lasów grądowych, niedaleko miejscowości Czmoń, w środkowej Wielkopolsce (Leśnictwo Czmoń, Nadleśnictwo Babki). Średnia roczna temperatura w tym obszarze wynosiła 8,7°C, a średnioroczne opady wynosiły odpowiednio 514 mm w latach 1971–2010 oraz 9,2°C i 535 mm w latach 2001–2010 (Mały Rocznik Statystyczny Polski 2020). Według danych meteorologicznych z pobliskiej stacji meteorologicznej przy Instytucie Dendrologii Polskiej Akademii Nauk w Kórniku (52,2447°N, 17,1008°E; odległość 10,5 km od obszaru badawczego), średnia roczna temperatura w latach 2011–2015 (w trakcie prowadzenia badań) wynosiła 9,5°C, a średnioroczne opady wynosiły 528 mm.

Obszar badawczy porastał 135-letni liściasty drzewostan dębowo-grabowy. Wszystkie powierzchnie badawcze były homogeniczne pod względem warunków siedliskowych i struktury lasu. Drzewostan był zdominowany przez dęby szypułkowe (*Quercus robur*), jesiony wyniosłe (*Fraxinus excelsior*) i grab pospolity (*Carpinus betulus*).

Na powierzchniach badawczych występowały zbiorowiska grądu środkowoeuropejskiego *Galio sylvatici-Carpinetum* (R.Tx. 1937) Oberd. 1957, w podzespole *corydalidetosum* Oberd. 1957, z bogatą i dobrze zachowaną warstwą zielną. Wiosną w runie dominował zawilec gajowy (*Anemone nemorosa*), natomiast latem gajowiec żółty (*Galeobdolon luteum*) oraz podagrycznik zwyczajny (*Aegopodium podagraria*). Na badanym obszarze zdiagnozowano gleby murszaste oraz gleby brunatne eutroficzne.

### 3.2. Układ doświadczeń

W celu zweryfikowania hipotez badawczych dotyczących produkcji i dynamiki biomasy roślin runa (hipoteza pierwsza i druga) zbierano materiał roślinny przez trzy lata (2013-2015) na czterech powierzchniach badawczych, stosując metodę żniwną.

W celu zweryfikowania hipotez badawczych dotyczących dynamiki procesu dekompozycji roślin zielnych (hipoteza trzecia, czwarta i piąta) założono trzy eksperymenty dekompozycyjne, wykorzystując w nich metodę woreczków ściółkowych. Do woreczków z moskitiery wykonanej z włókna szklanego o przekroju oczek

1 mm × 1 mm włożono nekromasę różnych gatunków roślin zielnych oraz drzew o znanej suchej masie. W badaniach wykorzystano nekromasę (całe rośliny): *Adoxa moschatellina* L., *Aegopodium podagraria* L., *Alliaria petiolata* (Bieb.) Cav. et Grande, *Anemone nemorosa* L., *Anemone ranunculoides* L., *Asarum europaeum* L., *Convallaria majalis* L., *Corydalis cava* L. (Schweigger et Koerte), *Ficaria verna* Huds., *Galeobdolon luteum* Hudson, *Galium aparine* L., *Impatiens parviflora* DC., *Maianthemum bifolium* L. (F.W. Schmidt), *Mercurialis perennis* L., *Paris quadrifolia* L., *Stachys sylvatica* L. oraz *Urtica dioica* L., a także oddzielnie liście i łodygi *Alliaria petiolata* (Bieb.) Cav. et Grande oraz liście roślin drzewiastych: *Acer pseudoplatanus* L., *Carpinus betulus* L., *Corylus avellana* L., *Fraxinus excelsior* L. i *Quercus robur* L. Obumarłe komponenty wszystkich gatunków roślin zielnych zbierane były w momencie masowego obumierania osobników danego gatunku. Liście drzew i krzewów zbierane były w okresie jesiennym tuż po opadzie w kompleksie leśnym, w którym prowadzone były badania.

W pierwszym doświadczeniu wykorzystano nekromasę (liście + łodygi) czternastu gatunków roślin zielnych, tj. *A. moschatellina* L., *A. podagraria* L., *A. petiolata* (Bieb.) Cav. et Grande, *A. nemorosa* L., *A. ranunculoides* L., *A. europaeum* L., *C. cava* L. (Schweigger et Koerte), *F. verna* Huds., *G. luteum* Hudson, *M. bifolium* L. (F.W. Schmidt), *M. perennis* L., *P. quadrifolia* L., *S. sylvatica* L. oraz *U. dioica* L., a także liście czterech gatunków drzew, tj. *A. pseudoplatanus* L., *C. betulus* L., *F. excelsior* L. i *Q. robur* L. oraz liście jednego gatunku krzewu, tj. *C. avellana* L., którą wyłożono na jednej powierzchni w sześciu blokach badawczych w opisanym powyżej kompleksie leśnym. Doświadczenie to trwało około pół roku w przypadku roślin zielnych (175-182 dni) i około roku (364 dni) dla roślin drzewiastych. Próby zbierano w odstępach tygodniowych (rośliny zielne) lub dwutygodniowych (rośliny drzewiaste).

W drugim doświadczeniu nekromasę (liście + łodygi) trzynastu gatunków roślin zielnych, tj. *A. moschatellina* L., *A. podagraria* L., *A. nemorosa* L., *C. majalis* L., *C. cava* L. (Schweigger et Koerte), *F. verna* Huds., *G. luteum* Hudson, *G. aparine* L., *I. parviflora* DC., *M. bifolium* L. (F.W. Schmidt), *M. perennis* L., *S. sylvatica* L. i *U. dioica* L. oraz liście czterech gatunków roślin drzewiastych, tj. *A. pseudoplatanus* L., *C. betulus* L., *Q.robur* L., *C. avellana* L. wyłożono na czterech powierzchniach w opisanym powyżej kompleksie leśnym. Czas trwania eksperymentu różnił się w zależności od grupy roślin. Utrata masy materiału roślinnego była systematycznie określana w trakcie eksperymentu.

Dla niektórych gatunków stwierdzono, że tempo rozkładu było niższe od założeń, dlatego postanowiono zmienić interwał zbierania próbek i przedłużyć okres zbierania ściółki. Dlatego też czas trwania eksperymentów różnił się w zależności od gatunku, wynosił od 119 dni dla większości gatunków geofitów wiosennych do 851 dni dla drzew i krzewów. Próby zbierano w odstępach tygodniowych (geofity wiosenne), dwutygodniowych (rośliny pełni lata) lub jednomiesięcznych (liście drzew i krzewów).

Trzecie doświadczenie założono na jednej powierzchni w czterech blokach w opisanym powyżej kompleksie leśnym. To doświadczenie dotyczyło tempa rozkładu różnych organów *Alliaria petiolata*, trwało 168 dni w przypadku liści i 532 dni w przypadku łodyg *A. petiolata*. Próby zbierano w odstępach tygodniowych.

### 3.3. Zbiór danych

W celu określenia stanu oraz dynamiki biomasy roślin zielnych, każdorazowo zbieraliśmy nadziemną część roślin z 10 ramek na każdej z 4 powierzchni próbnych (łącznie 40 ramek). Zbieraliśmy całą biomasę nadziemną roślin, przycinając je na poziomie gleby. Jeśli pęd był ukorzeniony wewnątrz ramki, to cała roślina była uwzględniana w próbce, jednak wyłączaliśmy pędy ukorzenione na zewnątrz ramki. Materiał roślinny zbieraliśmy od 12 kwietnia 2013 roku do 30 października 2015 roku. W marcu, kwietniu, maju i czerwcu zbieraliśmy biomasę roślin co 7 dni, podczas gdy w pozostałych miesiącach materiał roślinny był zbierany co 14 dni. Zimą, gdy temperatura była niższa niż 5°C, nie zbieraliśmy biomasy, dlatego w styczniu, lutym i grudniu 2014 roku oraz w lutym 2015 roku zbiory miały miejsce raz w miesiącu. Łącznie zebraliśmy 3360 próbek, podczas 84 zbiorów w terenie. Osobniki każdego gatunku umieszczane były oddzielnie w papierowej kopercie i etykietowane nazwą gatunku, oznaczeniem ramki (nr poletka – nr ramki) i datą zbioru. Rośliny wieloletnie (młode drzewka, rośliny zimozielone) były dzielone na przyrost z bieżącego roku oraz przyrost z poprzednich lat. Próbki były przewożone do laboratorium Zakładu Ekologii Instytutu Dendrologii PAN w Kórniku, suszone w temperaturze 65°C przy wymuszonym obiegu powietrza do ustabilizowanej masy (zazwyczaj przez 3 dni) i ważone z dokładnością do 0,001 g.

Zbioru materiału roślinnego w doświadczeniach dekompozycyjnych dokonywano w odstępach tygodniowych, dwutygodniowych lub miesięcznych (długość interwału regulowano w zależności od tempa rozkładu danego rodzaju materiału, tempo rozkładu

szacowano, dokonując pomiaru ubytków masy na bieżąco). W terenie, w celu uniknięcia strat materiału, każdy woreczek ściółkowy pakowany był do koperty. Następnie przewożono materiał do laboratorium Zakładu Ekologii Instytutu Dendrologii PAN w Kórniku, gdzie woreczki suszono w temperaturze 65°C do stałej masy w suszarce z wymuszonym obiegiem powietrza. Następnie z próbek usunięto wszelki materiał niebędący przedmiotem badań, który znalazł się w woreczkach ściółkowych w czasie ekspozycji w terenie (np. korzenie, mchy, bezkręgowce, piasek, itp.). Każda zaetykietowana próbka została następnie zważona w celu określenia ubytku masy wyjściowej z dokładnością do 0,001 g.

W przypadku drugiego i trzeciego doświadczenia dekompozycyjnego określono ponadto zawartość azotu (N) i węgla (C) w wyjściowym materiale ściółkowym stosowanym w tych badaniach oraz w materiale rozłożonym na poziomie około 80, 60, 40 i 20%. Zawartość C i N oznaczono za pomocą ECS CHNS-O 4010 Elemental Combustion System (Costech Analytical Technologies Inc., USA). Wartości SLA zostały zaczerpnięte z publikacji Paź-Dyderskiej i in. (2020), natomiast innych cech funkcjonalnych roślin z baz danych: LEDA (Kleyer i in. 2008), BiolFlor (Klotz i in. 2002) oraz TRY (Kattge i in. 2011).

### 3.4. Analizy statystyczne

W celu określenia różnic stanów biomasy pomiędzy terminami zbiorów wykonano test Kruskala-Wallisa, a następnie test *posteriori* Tukeya. W celu określenia wpływu terminu zbioru (predyktor) oraz miejsca zbioru (efekt losowy) na stan biomasy warstwy zielnej wykonano liniowy model mieszany.

W celu obliczenia nadziemnej produkcji pierwotnej netto (PPN) zsumowaliśmy maksymalne wartości biomasy dla poszczególnych gatunków występujących podczas sezonu wegetacyjnego, zgodnie ze wzorem: $PPN=\sum_{n=\mathrm{sn}} \mathrm{AB}_{\mathrm{max}}$ ,
gdzie sn to liczba gatunków a $\mathrm{AB}_{\mathrm{max}}$ to najwyższa wartość biomasy indywidualnego gatunku podczas sezonu wegetacyjnego.

W celu charakterystyki procesu dekompozycji w badaniach wykorzystano wzory empiryczne określające tempo dekompozycji (stała *k*; $\mathrm{rok}^{-1}$) oraz czas potrzebny do osiągnięcia połowicznego (*hd*) oraz całkowitego (przyjmowanego w literaturze jako 95% ubytku masy wyjściowej) poziomu rozkładu (*td*) oraz wskaźnik zawartości pierwiastków (*R*).

Stałą *k* określono za pomocą wzorów:

zaproponowanego przez Olsona (1963): $Mt = e^{-kt}$,

gdzie *Mt* jest proporcją masy pozostałej do rozłożenia po czasie *t* ekspozycji w terenie a *k* to stała dekompozycji;

lub Bunnell i in. (1977): $Mt = A*e^{k1t}+(1-A)*e^{k2t}$,

gdzie *Mt* jest proporcją masy pozostałej do rozłożenia po czasie *t* ekspozycji w terenie, *A* jest względnie łatwo rozkładalną frakcją ściółki, *(1-A)* jest trudniej rozkładalną frakcją ściółki, *k1* i *k2* to stałe dekompozycji dla szybko i wolniej rozkładającej się frakcji ściółki.

Na podstawie obliczonej dla każdej ściółki stałej dekompozycji *k*, obliczyliśmy czas połowicznego rozkładu (*hd*):

$hd = ln(0.50)*(-k)^{-1}$

a także czas całkowitego rozkładu (*td*):

$td = ln(1-0.95)*(-k)^{-1}$.

Wskaźnik zawartości pierwiastków (*R*) został obliczony zgodnie z propozycją Wang i in. (2009):

$R\ \% = 100*(MtRt)/(M_0R_0)$,

gdzie $M_0$ (g) to początkowa sucha masa ściółki, *Mt* (g) to sucha masa ściółki pozostała w woreczku po określonym czasie *t*, $R_0$ to koncentracja pierwiastka (mg $g^{-1}$) w masie początkowej ściółki, a *Rt* to koncentracja pierwiastka (mg $g^{-1}$) w masie ściółki pozostałej po czasie *t*.

Istotność różnic w tempie rozkładu poszczególnych typów ściółki określona została przy pomocy jednoczynnikowej analizy wariancji (ANOVA), a następnie testu Tukeya, natomiast wpływ typu ściółki, czasu ekspozycji materiału w terenie, a także interakcji między tymi czynnikami przy pomocy dwuczynnikowej analizy wariancji (ANOVA). Wykonaliśmy również modele liniowe, opisujące tempo dekompozycji jako funkcję grupy funkcjonalnej roślin, czasu ekspozycji materiału w terenie, temperatury i wilgotności.

Proste modele regresyjne zostały użyte do oszacowania zależności tempa dekompozycji liści (wyrażonego stałą *k*) od cech funkcjonalnych roślin.

Analizy statystyczne zostały wykonane w programach: JMP Pro 14.0., JMP Pro 15.0 (SAS Institute Inc. Cary, NC. USA; http://www.sas.com) oraz R (R Core Team 2020).

## 4. Główne wyniki pracy

### 4.1. Udział roślin zielnych w rocznej nadziemnej produkcji netto (PPN)

**Publikacja 1.** *Seasonal dynamics of herbaceous layer biomass and its contribution to annual net primary production in an oak–hornbeam forest.*

W wyniku przeprowadzonych badań wykazano istotne statystycznie różnice w stanach biomasy roślin naczyniowych runa między poszczególnymi terminami zbioru. Najwyższą biomasę obserwowano wiosną (17 kwietnia, 24 kwietnia, 3 maja). Wiosną biomasa wzrastała od minimalnych do maksymalnych wartości w ciągu trzech tygodni. Wyniki wcześniejszych badań sugerowały występowanie dwóch oddzielnych szczytów biomasy w podobnych zbiorowiskach leśnych, za które odpowiadały geofity wiosenne (szczyt wiosenny) oraz gatunki pełni lata (szczyt letni; Jagodziński i in. 2013; Rawlik i Jagodziński 2022). Dynamika stanów biomasy roślin zielnych może być przewidywana na podstawie składu gatunkowego lub składu grup ekologicznych budujących zbiorowisko roślinne oraz ich relacji ilościowych, dlatego analizując kompozycję gatunkową badanych przez nas grądów środkowoeuropejskich podzespołu najbardziej żyznego zakładaliśmy występowanie dwóch szczytów biomasy, jednakże wykres sezonowej zmienności stanów biomasy warstwy zielnej wykazywał jeden szczyt, który pojawiał się wiosną i trwał do wczesnej jesieni. Ten obraz sezonowej dynamiki stanów biomasy był wynikiem szczytów biomasy wiosennych gatunków takich jak *A. nemorosa*, *F. verna* i *C. cava*, a następnie szczytów biomasy grupy roślin, które rozpoczynają wzrost pod koniec wiosny lub na początku lata (pod koniec maja lub pod koniec czerwca), w tym *C. betulus*, *F. excelsior*, *A. moschatellina*, *C. majalis* i *M. bifolium*, które utrzymywały się do późnego lata. W czasie największych stanów biomasy runa dominujący udział w biomasie miało pięć gatunków: *A. nemorosa*, *G. luteum*, *C. betulus*, *F. excelsior* i *M. bifolium*; biomasa innych gatunków nie przekraczała udziału 1,5% w tym okresie.

Jedną z metod oceny udziału warstwy zielnej w rocznej produkcji roślin w lesie jest porównanie jej wartości do wartości opadu organicznego z warstwy drzew. Jednakże badania obejmujące pomiary produkcji warstwy zielnej oraz opadu ściółki na tym samym obszarze są bardzo rzadkie (Landuyt i in. 2019). Wcześniejsze badania wykazały, że wkład warstwy zielnej w PPN w różnych rodzajach lasów zazwyczaj wynosi od 0,5% do 16%, ale może być wyższy (aż do 41% całkowitej rocznej produkcji opadłych liści w lesie) w bardziej otwartych siedliskach leśnych (Gilliam 2007; Muller

2014; Landuyt i in. 2019). Jednakże w lasach liściastych strefy umiarkowanej PPN roślin zielnych jest zazwyczaj mniejszy niż 5% całej PPN (DeAngelis i in. 1981; Welch i in. 2007). PPN warstwy zielnej w czasie niniejszych badań wynosił średnio 85,67 g $m^{-2}$, podczas gdy średnia roczna biomasa opadu z warstwy drzew wynosiła 806,99 g $m^{-2}$. Średni udział warstwy zielnej w rocznej produkcji ściółki wynosił 9,23%, natomiast 13,86% w labilnej frakcji ściółki ulegającej rozkładowi w ciągu pierwszego roku dekompozycji.

### 4.2. Wpływ strategii życiowej na tempo dekompozycji roślin lasu grądowego

**Publikacja 2.** *Short life–fast death: decomposition rates of woody plants leaf- and herb-litter.*

Wyniki przeprowadzonych badań wskazują na istotny statystycznie wpływ gatunku rośliny, czasu ekspozycji oraz interakcji gatunek × czas na rozkład opadłych liści, a także grupy funkcjonalnej, do której należała roślina. Największe różnice w tempie rozkładu między grupami roślin widoczne są na początku procesu dekompozycji. Po około dwóch miesiącach od rozpoczęcia eksperymentu gatunki geofitów wiosennych straciły około 95% biomasy. W tym samym czasie około 69% biomasy roślin zimozielonych, 35% biomasy roślin obumierających w środku lata oraz 30,5% biomasy roślin obumierających jesienią uległo rozkładowi.

Na ogół rozkład opadłych liści gatunków drzewiastych był wyraźnie wolniejszy niż biomasy roślin zielnych. Większość wcześniejszych prac sugeruje, że współczynniki rozkładu ($k$) dla roślin zielnych są wyższe niż jeden, a w niektórych przypadkach znacznie wyższe (Muller 2014), co oznacza, iż rozkład ich biomasy odbywał się znacznie szybciej niż w ciągu jednego roku. Obliczone tempo rozkładu po sześciu miesiącach doświadczenia wynosiło 0,2-0,8 w przypadku liści drzew i 0,2-6,9 w przypadku roślin zielnych. Biomasa liści *F. excelsior* nie rozkładała się istotnie statystycznie wolniej niż liście i pędy niektórych roślin zielnych. Pozostała po około sześciu miesiącach badań masa liści tego gatunku drzewa była bardziej zbliżona do pozostałej po tym samym okresie ekspozycji biomasy *A. petiolata*, *S. sylvatica* i *U. dioica* niż do masy liści innych badanych gatunków drzewiastych. Jest to szczególnie istotne, ponieważ pokazuje, że nekromasa niektórych roślin zielnych nie należy do labilnej frakcji ściółki. Niektóre części tych roślin powinny być sklasyfikowane jako bardziej odporne na rozkład –

wydaje się, iż dotyczy to gatunków o większej alokacji biomasy do łodyg lub o bardziej zlignifikowanych łodygach.

Znaleźliśmy istotne zależności między cechami funkcjonalnymi (specyficzną powierzchnią liści i zawartością suchej masy w liściach) lub chemicznymi (koncentracja azotu w liściach) liści a tempem rozkładu badanych gatunków po sześciu miesiącach eksperymentu. Ponadto, zawartość suchej masy w liściach okazała się najsilniejszym predyktorem tempa rozkładu spośród badanych cech roślin. Proces rozkładu zależał od czasu ekspozycji w terenie, grupy funkcjonalnej roślin oraz średnich dziennych opadów atmosferyczne w trakcie sześciu miesięcy eksperymentu, a także od gatunku. Okazało się, iż wpływ średniej temperatury w trakcie sześciu miesięcy eksperymentu na proces rozkładu nie był istotny statystycznie. W lasach liściastych strefy umiarkowanej dostępność światła jest głównym czynnikiem determinującym strukturę liści, przy czym gatunki geofitów wiosennych charakteryzują się liśćmi bogatymi w składniki odżywcze i wyższym wskaźnikiem specyficznej powierzchni liści w porównaniu do innych grup roślin zielnych lub gatunków drzew, stanowiących późniejsze etapy sukcesji (Rothstein i Zak 2001; Muller 2014; Jagodziński i in. 2016). Wyniki naszych badań potwierdziły, że szybkie tempo rozkładu jest związane z szybkim wzrostem i można je ogólnie przewidzieć na podstawie grupy funkcjonalnej roślin.

### 4.3. Wpływ cech funkcjonalnych na rozkład roślin lasu grądowego

**Publikacja 3.** *The afterlife of herbaceous plant species: A litter decomposition experiment in a temperate oak-hornbeam forest.*

Mimo że pojedynczy model wykładniczy zaproponowany przez Olsona (1963) był powszechnie stosowany w wielu poprzednich badaniach dekompozycji roślin zielnych (Cornwell i Weedon 2014), zalecany jest dwufazowy model wykładniczy zaproponowany przez Bunnella i in. (1977) jako lepiej opisujący rozkład ściółki złożonej z różnych frakcji. Jednakże porównanie tych dwóch modeli na przykładzie roślin zielnych lasu grądowego wskazuje, że dwufazowy model wykładniczy rozkładu tylko nieznacznie lepiej obrazuje proces rozkładu ściółki niż jednofazowy model wykładniczy. Wyraźnie lepsze dopasowanie dwufazowego modelu wykładniczego zaobserwowano tylko w przypadku dwóch gatunków (*G. luteum* i *G. aparine*). Wyniki te wskazują, że proces rozkładu ściółki przebiega równomiernie i nie zaobserwowano wyraźnego

spowolnienia rozkładu w późniejszych stadiach, wynikającego z występowania w większej proporcji trudno rozkładającej się frakcji ściółki.

Według wcześniejszych badań, proces uwalniania różnych pierwiastków chemicznych zależy od pierwiastka, materiału roślinnego, który ulega rozkładowi, a także warunków środowiskowych, w których proces zachodzi (Aponte i in. 2012; Berg i McClaugherty 2014). Ogólnie rzecz biorąc, niektóre zjawiska w dynamice uwalniania poszczególnych pierwiastków chemicznych są podobne w różnych ekosystemach leśnych i rodzajach ściółki, podczas gdy inne są bardzo specyficzne (Aponte i in. 2012). Tempo uwalniania azotu (N) i węgla (C) w całej grupie badanych gatunków było uzależnione od tempa ich rozkładu. Z biomasy geofitów wiosennych pierwiastki uwalniane były najszybciej, znacznie wolniej z biomasy gatunków pełni lata oraz biomasy liści roślin drzewiastych. Zaobserwowaliśmy uwalnianie i immobilizację azotu w początkowej fazie rozkładu biomasy niektórych gatunków (*A. moschatellina*, *G. aparine*, liści i pędów *G. luteum*, *M. bifolium*, *M. perennis*, *Q. robur* oraz *S. sylvatica*). Podobne tendencje zaobserwowano wcześniej (Jacob i in. 2010 lub Kriiska i in. 2021) i zostały one wyjaśnione szybkim wzrostem liczebności mikroorganizmów, który następował po początkowym wymywaniu rozpuszczalnych składników.

Wyniki wcześniejszych badań wskazują, iż funkcjonalne cechy liści, a także jakość ściółki, wyjaśniają dużą część zmienności tempa rozkładu (Cornwell i in. 2008; Weedon i in. 2009; Freschet i in. 2012; Pietsch i in. 2014). Tego typu badania umiejscawiają tempo rozkładu między cechami charakteryzującymi spektrum ekonomiczne roślin (Freschet i in. 2012; Wright i in. 2004), gdzie gatunki o akwizycyjnej strategii ekologicznej, o wysokim SLA i koncentracjach składników odżywczych są powiązane z szybszym tempem rozkładu (Aerts 1997; Freschet i in. 2012; Pietsch i in. 2014), podczas gdy gatunki o konserwatywnej strategii i cechach, takich jak wysokie LDMC i niskie koncentracje składników odżywczych, rozkładają się stosunkowo wolno (Gallardo i Merino 1993; Cortez i in. 2007; Aponte i in. 2012). W przeprowadzonych badaniach uwzględniony został wpływ cech dotyczących rozmiaru (całkowita nadziemna biomasa=TAB, całkowita powierzchnia liści=TLA, biomasa frakcji liści=LMF) na tempo dekompozycji. Jak zakładaliśmy, te cechy miały wpływ na proces rozkładu nekromasy gatunków zielnych. W przypadku badanej grupy roślin leśnych, cechy dotyczące wielkości mają silniejszy wpływ na rozkład niż cechy ekonomiczne (SLA, LDMC, LNC), ponieważ rośliny o małej łącznej biomasie nadziemnej (TAB) i małej

powierzchni liści (TLA) rozkładają się najszybciej. Możemy więc powiedzieć, z pewnym uproszczeniem, że w ramach badanej grupy gatunków duże rośliny o dużej powierzchni liści rozkładają się stosunkowo najwolniej.

### 4.4. Wpływ typu organu roślinnego na tempo dekompozycji oraz uwalniania azotu i węgla u roślin lasu grądowego

**Publikacja 4.** *Differences in C and N release from Alliaria petiolata leaves and stems: consequences for nutrient cycling in forest ecosystems.*

Wyniki wcześniejszych badań nad rozkładem różnych organów roślin nie dały jednoznacznych wyników, ponieważ różniły się dla różnych grup roślin (Bumb i in. 2018; Zuo i in. 2018). Bumb i in. (2018) nie wykazali różnic w tempie rozkładu liści i pędów 16 zielnych gatunków śródziemnomorskich, w badaniach przeprowadzonych na płaskowyżu wapiennym w południowej Francji, co jest sprzeczne z naszymi wynikami. Wyniki naszych badań wskazują, iż biomasa liści *A. petiolata* rozkładała się sześciokrotnie szybciej (czas połowicznego rozkładu 62 dni) niż biomasa łodyg *A. petiolata* (czas połowicznego rozkładu 380 dni). Również tempo uwalniania azotu (N) i węgla (C) było znacznie szybsze w przypadku biomasy liści niż łodyg.

Większość wcześniejszych badań dekompozycji skupiała się na tempie rozkładu liści (Hobbie 2015), pomijając fakt, że duża część materiału organicznego pochodzi z łodyg lub korzeni. Szczególnie w ekosystemach leśnych badania nad rozkładem skupiały się na liściach drzew (Hobbie i in. 2006; Horodecki i Jagodziński 2017, 2019; Horodecki i in. 2019; Urbanowski i in. 2018, 2021a, b). Natomiast wyniki naszych badań podkreślają, iż uwzględnienie tylko rozkładalności liści przy szacowaniu tempa rozkładu całych roślin powoduje poważnie przeszacowanie (4,8-krotnie po pół roku).

## 5. Podsumowanie i wnioski

Wyniki uzyskane w toku realizacji niniejszej pracy doktorskiej uzupełniają wiedzę na temat udziału oraz sezonowego przebiegu produkcji biomasy roślin zielnych w ekosystemach leśnych, a także przebiegu dekompozycji w tej grupie roślin. Dzięki szerokiemu zakresowi analizowanych czynników mogących wpływać na badane procesy, rezultaty przeprowadzonych badań można ekstrapolować na inne układy ekologiczne w lasach liściastych strefy klimatu umiarkowanego. Pozwalają one na lepsze zrozumienie znaczenia roślin zielnych warstwy runa w funkcjonowaniu ekosystemów leśnych.

W wyniku przeprowadzonych badań stwierdzono, że:

- Udział produkcji biomasy warstwy zielnej w rocznej produkcji opadu roślinnego wynosił 9,23% całkowitej ilości opadu roślinnego i 13,86% udziału frakcji łatwo rozkładającej się w trzech badanych sezonach wegetacyjnych; oznacza to, że poprzednie badania nie doszacowywały wkładu warstwy zielnej w roczną produkcję pierwotną netto (PPN) ekosystemów leśnych.
- Sezonowa dynamika biomasy warstwy zielnej wykazała jeden wyraźny szczyt, rozpoczynający się wiosną i trwający do wczesnej jesieni, a nie – jak wskazywały wcześniejsze badania – dwa szczyty.
- Pełny rozkład nekromasy roślin zielnych nie zawsze zachodził w ciągu roku – nie cały opad roślin zielnych należy do labilnej frakcji opadu, jak wskazywały wyniki wcześniejszych badań.
- Tempo rozkładu oraz tempo uwalniania azotu (N) i węgla (C) zależały od grupy funkcjonalnej roślin. Biomasa geofitów wiosennych rozkładała się znacznie szybciej niż biomasa gatunków dominujących w runie lasu grądowego w okresie letnim i jesienią. Tempo rozkładu biomasy niektórych roślin pełni lata było zbliżone do tempa rozkładu biomasy liści drzew.
- W przypadku roślin zielnych warstwy runa leśnego, inaczej niż w przypadku innych grup roślin, cechy dotyczące rozmiaru mają większy wpływ na tempo rozkładu niż cechy ekonomiczne (SLA, LDMC, LNC), ponieważ rośliny o małej całkowitej biomasie nadziemnej i małej łącznej powierzchni liści rozkładają się najszybciej. Wśród cech ekonomicznych najlepszym predyktorem tempa dekompozycji jest zawartość suchej masy w liściach (leaf dry matter content=LDMC).

- Tempo rozkładu nekromasy oraz uwalnianie azotu i węgla z liści *Alliaria petiolata* jest około sześciu razy szybsze niż w przypadku nekromasy łodyg *A. petiolata*. Wyniki naszych badań podkreślają problem braku danych dotyczących tempa rozkładu biomasy organów roślinnych innych niż liście oraz wnioskowania na temat procesu rozkładu całych roślin i wpływu tych roślin na ekosystemy na podstawie badań dotyczących wyłącznie liści.

Wyniki przeprowadzonych badań jednoznacznie wskazują na większe znaczenie warstwy zielnej runa niż dotychczas przypuszczano. Pokazują również, iż wiele funkcjonujących do tej pory ogólnych twierdzeń dotyczących procesów produkcji biomasy oraz dekompozycji roślin tej warstwy było niedopracowanych, opartych na wynikach pojedynczych, wąskich badań. Układ metodyczny opisanych badań pozwolił na dokładniejsze oszacowanie udziału roślin zielnych w produkcji biomasy ekosystemów leśnych oraz szczegółową charakterystykę procesów produkcji i dekompozycji roślin naczyniowych budujących warstwę runa leśnego. Wnioski płynące z zakończonych doświadczeń zachęcają do podjęcia działań ochronnych względem warstwy zielnej lasów, działań naukowych pogłębiających wiedzę na temat jej funkcjonowania, a także działań popularyzatorskich, wskazujących na jej wagę w funkcjonowaniu ekosystemów leśnych. Wyniki niniejszych badań mogą przyczynić się również do dokładniejszego modelowania krążenia węgla i azotu w ekosystemach leśnych.

## 6. Literatura


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**Oświadczenia**

**Oświadczenie kierującego pracą**

Oświadczam, że niniejsza praca została przygotowana pod moim kierunkiem i stwierdzam, że spełnia ona warunki do przedstawienia jej w postępowaniu o nadanie stopnia doktora nauk biologicznych.

Kórnik, 25 sierpnia 2023 r. .....

**Oświadczenie autora pracy**

Świadoma odpowiedzialności prawnej oświadczam, że niniejsza rozprawa doktorska została napisana przeze mnie samodzielnie i nie zawiera treści uzyskanych w sposób niezgodny z obowiązującymi przepisami.

Oświadczam również, że przedstawiona praca nie była wcześniej przedmiotem procedur związanych z uzyskaniem stopnia doktora w innej jednostce.

Oświadczam ponadto, że niniejsza wersja pracy jest identyczna z załączoną wersją elektroniczną.

Kórnik, 25 sierpnia 2023 r. Katarzyna Rawlik

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OŚWIADCZENIE

Oświadczam, że w pracy:

**Rawlik, K.**, Rawlik, M., Jagodziński, A.M. 2023. Seasonal dynamics of herbaceous layer biomass and its contribution to annual net primary production in an oak–hornbeam forest. Forest Ecology and Management 544: 121195. https://doi.org/10.1016/j.foreco.2023.121195

mój wkład polegał na udziale w opracowaniu koncepcji i metodyki badań, przeglądzie literatury związanej z analizowanym zagadnieniem, zbiorze danych w terenie, opracowaniu wyników i ich analizie statystycznej oraz na przygotowaniu manuskryptu pracy; pełniłam również rolę autora korespondencyjnego. **Mój udział procentowy szacuję na 80%.**

**Rawlik, K.**, Nowiński, M., Jagodziński, A.M. 2021. Short life–fast death: decomposition rates of woody plants leaf- and herb-litter. Annals of Forest Science 78: 6. https://doi.org/10.1007/s13595-020-01019-y

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**Rawlik, K.**, Kasprowicz, M., Nowiński, M., Jagodziński, A.M. 2022. The afterlife of herbaceous plant species: A litter decomposition experiment in a temperate oak-hornbeam forest. Forest Ecology and Management 507: 120008. https://doi.org/10.1016/j.foreco.2022.120008

mój wkład polegał na udziale w opracowaniu koncepcji i metodyki badań, przeglądzie literatury związanej z analizowanym zagadnieniem, zbiorze danych w terenie, opracowaniu wyników i ich analizie statystycznej oraz na przygotowaniu manuskryptu pracy; pełniłam również rolę autora korespondencyjnego. **Mój udział procentowy szacuję na 80%.**

**Rawlik, K.**, Jagodziński, A.M. 2022. Differences in C and N release from *Alliaria petiolata* leaves and stems: consequences for nutrient cycling in forest ecosystems. European Journal of Forest Research 141: 769–778. https://doi.org/10.1007/s10342-022-01469-1

mój wkład polegał na udziale w opracowaniu koncepcji i metodyki badań, przeglądzie literatury związanej z analizowanym zagadnieniem, zbiorze danych w terenie, opracowaniu wyników i ich analizie statystycznej oraz na przygotowaniu manuskryptu pracy; pełniłam również rolę autora korespondencyjnego. **Mój udział procentowy szacuję na 90%.**

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OŚWIADCZENIE

Oświadczam, że w pracy:

Rawlik, K., Rawlik, M., **Jagodziński, A.M.** 2023. Seasonal dynamics of herbaceous layer biomass and its contribution to annual net primary production in an oak–hornbeam forest. Forest Ecology and Management 544: 121195. https://doi.org/10.1016/j.foreco.2023.121195

mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań, udziale w interpretacji uzyskanych wyników, udziale w przygotowaniu manuskryptu artykułu i odpowiedzi na recenzje. **Mój udział procentowy szacuję na 10%.**

Rawlik, K., Nowiński, M., **Jagodziński, A.M.** 2021. Short life–fast death: decomposition rates of woody plants leaf- and herb-litter. Annals of Forest Science 78: 6. https://doi.org/10.1007/s13595-020-01019-y

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Rawlik, K., Kasprowicz, M., Nowiński, M., **Jagodziński, A.M.** 2022. The afterlife of herbaceous plant species: A litter decomposition experiment in a temperate oak-hornbeam forest. Forest Ecology and Management 507: 120008. https://doi.org/10.1016/j.foreco.2022.120008

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Rawlik, K., **Jagodziński, A.M.** 2022. Differences in C and N release from *Alliaria petiolata* leaves and stems: consequences for nutrient cycling in forest ecosystems. European Journal of Forest Research 141: 769–778. https://doi.org/10.1007/s10342-022-01469-1

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OŚWIADCZENIE

Oświadczam, że w pracy:

Rawlik, K., **Nowiński, M.**, Jagodziński, A.M. 2021. Short life–fast death: decomposition rates of woody plants leaf- and herb-litter. Annals of Forest Science 78: 6. https://doi.org/10.1007/s13595-020-01019-y

mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań gleboznawczych, wykonaniu analiz gleboznawczych, udziale w interpretacji uzyskanych wyników badań gleboznawczych i udziale w przygotowaniu manuskryptu artykułu. **Mój udział procentowy szacuję na 5%.**

Rawlik, K., Kasprowicz, M., **Nowiński, M.**, Jagodziński, A.M. 2022. The afterlife of herbaceous plant species: A litter decomposition experiment in a temperate oak-hornbeam forest. Forest Ecology and Management 507: 120008. https://doi.org/10.1016/j.foreco.2022.120008

mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań gleboznawczych, wykonaniu analiz gleboznawczych, udziale w interpretacji uzyskanych wyników badań gleboznawczych i udziale w przygotowaniu manuskryptu artykułu. **Mój udział procentowy szacuję na 5%.**

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OŚWIADCZENIE

Oświadczam, że w pracy:

Rawlik, K., **Rawlik, M.**, Jagodziński, A.M. 2023. Seasonal dynamics of herbaceous layer biomass and its contribution to annual net primary production in an oak–hornbeam forest. Forest Ecology and Management 544: 121195. https://doi.org/10.1016/j.foreco.2023.121195

mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań, udziale w analizie danych, interpretacji uzyskanych wyników, udziale w przygotowaniu manuskryptu artykułu i odpowiedzi na recenzje. **Mój udział procentowy szacuję na 10%.**

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Uniwersytet im. Adama Mickiewicza w Poznaniu
Wydział Biologii
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OŚWIADCZENIE

Oświadczam, że w pracy:

Rawlik, K., **Kasprowicz, M.**, Nowiński, M., Jagodziński, A.M. 2022. The afterlife of herbaceous plant species: A litter decomposition experiment in a temperate oak-hornbeam forest. Forest Ecology and Management 507: 120008. https://doi.org/10.1016/j.foreco.2022.120008

mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań fitosocjologicznych, wykonaniu zdjęć fitosocjologicznych, udziale w interpretacji uzyskanych wyników badań fitosocjologicznych i udziale w przygotowaniu manuskryptu artykułu. **Mój udział procentowy szacuję na 5%.**

M. Kasprowicz
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# Seasonal dynamics of herbaceous layer biomass and its contribution to annual net primary production in an oak–hornbeam forest

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ABSTRACT

The role of the herbaceous layer in carbon assimilation and nutrient cycling is still undiscovered and unappreciated. One reason is that simple methods of annual net primary production (ANPP) estimation often underestimate its value, while more accurate methods are too labor-demanding. Moreover, studies on herbaceous layer and litterfall biomass in the same study site are extremely rare and usually conducted during one vegetation season, providing temporally-specific estimates. We hypothesized that (1) the seasonal herb layer biomass dynamics show a two-peak shape and (2) contribution of herbaceous layer biomass production in annual litter production was not more than 5% of tree litterfall. We studied the herb layer and litterfall biomass dynamics in an oak-hornbeam forest in W Poland for three years (January 2013 – October 2015). Samples of the herb layer (ten samples for four sample plots) were collected weekly in March, April and May or every two weeks for the remainder of each year, and litterfall was collected every month. All herb plants were cut at the soil level from circular frames with an area of 0.16 $m^2$. Litterfall was studied with thirty litter traps (height of 15 cm, and catching area of 0.36 $m^2$). We performed Kruskal–Wallis tests with Dunn's post hoc tests to assess differences in variables among all collection times and linear random effects models to assess variance sources. We observed the highest biomass in 2013 on May 3rd (47.05 g $m^{-2}$), and the lowest on October 30th in 2015 (4.69 g $m^{-2}$). The seasonal herb layer biomass dynamic showed a single-peak shape; a very distinct peak occurred in spring and continued in late spring, summer, and early autumn. The spring ephemeral *Anemone nemorosa* had the highest share of herbaceous layer ANPP with 27% and was responsible for the spring biomass peak every season. The mean contribution of the herb layer biomass in annual litterfall was 9.23%. Our results highlight the underestimation of the herb layer role in biomass production in forest ecosystems in previous studies.

## 1. Introduction

Studies on forest ecosystem functioning have paid significantly less attention to understory than to canopy trees, probably because of their small biomass and economic importance (Gilliam 2007; Gilliam 2014; Landuyt et al. 2019; Landuyt et al. 2020b). In particular, studies on overstory aboveground biomass production are considerably more frequent (Tuan et al. 2022; Viet et al. 2022). However, the ecological significance of the herb layer species is well documented. Recent studies highlighted that the herbaceous layer contains 80% of forest plant species biodiversity (Gilliam 2007), including rare species and indicators of site quality (Ellenberg 1988; Dyderski et al. 2017). Additionally, the herb layer competes with woody plant species seedlings and saplings, influencing or even determining overstory composition (Baraloto et al. 2005). The herbaceous layer is also a habitat and source of food for animals (Gill and Beardall 2001; Boch et al. 2013; Smolko et al. 2018). Finally, herbaceous plants can influence soil physicochemical properties (Stefanowicz et al. 2023), as well as the abundance and diversity of arbuscular mycorrhizal fungi and other microorganisms (Zubek et al. 2022).

The accurate estimation of standing biomass is crucial to understanding the seasonality of the herbaceous layer biomass and estimating the annual net primary production (ANPP). Among the various techniques used for biomass estimation, harvesting the aboveground biomass was commonly employed (e.g. Ovington et al. 1963; Zavitkovski 1976; Werger and Van Laar 1985; Rainey et al. 1999). Previous

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studies have emphasized the importance of sample shape and size in obtaining precise results, particularly considering the edge effect and plot heterogeneity (Sala and Austin 2000). Once harvested, biomass should be promptly transported to the laboratory to prevent any losses due to respiration. Subsequently, it is oven-dried and weighed. Depending on the study objectives, the biomass was divided by species (Rainey et al. 1999; Rawlik et al. 2012) or other functional compartments (live plants, dead plants, organs).

Since harvest methods are extensive and labor-intensive, double-sampling techniques have been utilized (Sala and Austin 2000). These methods seek to establish correlations between biomass and less extensive traits. Successful use of cover-biomass correlations has been demonstrated in the case of the herbaceous layer (e.g. Gilliam and Turrill 1993; Gilliam 2006; Gilliam et al. 2016). Accurately estimating herb layer production is challenging due to factors like herbivory, mortality, and seasonally varying biomass losses, which are inherently difficult to measure (Clark et al. 2001). Another methodological challenge is selecting a method that prevents the spatial variability of the understory biomass, which is a natural phenomenon in deciduous forests, from overshadowing its temporal variability. To achieve this, it is necessary to choose the best shape and size of sampling frames, as well as the method of selecting sampling locations. Rectangular frames are considered to best capture the spatial variability of understory plants, as they intersect patches of vegetation with diverse biomass (Bormann 1953). On the other hand, circular frames have the least edge effect (Sala and Austin 2000). The size of the frame is also important and should correspond to the size of vegetation patches in the forest. For each sampling event, the patches to be sampled can be chosen subjectively, aiming to select similar areas in terms of biomass, or randomly. In the case of random selection, due to high variance (spatial heterogeneity), it is important to collect a larger number of samples (Bormann 1953). According to previous studies, the biomass of the herb layer in temperate deciduous forests in Europe ranged between 0 and 500 g $m^{-2}$ (Landuyt et al. 2020a; Rawlik and Jagodziński 2022b). This range is in line with our literature review, expanding the search of cited studies, revealing that herb biomass ranges from 1 g $m^{-2}$ to 536 g $m^{-2}$.

In temperate oak-hornbeam forests, the standing biomass of the herbaceous layer changes with the seasons, which is related to the changes in microclimate and climatic conditions (Czapiewska et al. 2019). Change in microclimatic conditions such as light on the forest floor during the growing season is significant in shaping herb layer vegetation (Axmanová et al. 2012; Czapiewska et al. 2019; Landuyt et al. 2020b). Herbaceous plant species adopt different strategies to thrive in low-light environments, thus, their classification into spring ephemerals, summer-greens, winter-greens, and evergreens (Uemura 1994; Neufeld and Young 2014; Jagodziński et al. 2016). The occurrence of these classes of herbaceous plants across different seasons shows niche separation (i.e. efficient utilization of habitat resources to reduce competition; Díaz and Cabido 2001; Jagodziński et al. 2016). These groups of plants grow and attain their biomass peak at different times, thus previous studies that focused on one peak value of the whole herb layer biomass are insufficient to correctly describe the biomass dynamics (Rawlik and Jagodziński 2022b). Previous research suggested a two-peak pattern in the seasonal dynamics of herbaceous layer biomass. The first peak, driven by the dominance of spring ephemerals, occurs in spring. The second peak, attributed to the prevalence of summer-greens, is expected in late summer or early autumn, consistent with findings in similar plant communities. (e.g. Jagodziński et al. 2013; Czapiewska et al. 2019; Rawlik and Jagodziński 2022b). Moreover, so far there is no information about the full seasonal dynamics of understory biomass (including the winter period) in temperate oak-hornbeam forests. Additionally, some studies described only a summary of the herb layer biomass (not divided into species). Thus, to bridge the knowledge gap, we aimed to describe annual fluctuations of the whole herb layer biomass and individual species.

Net primary production is the difference between gross primary production (total photosynthesis) and total plant respiration in a forest which can be measured as the total new organic matter produced during a chosen time interval (Clark et al. 2001). The most often used method to estimate annual ANPP in forests is to measure the amount of standing biomass produced during the year (Clark et al., 2001). In the case of the herbaceous layer in temperate deciduous forests, the simplest method considers ANPP to be equal to the highest biomass value observed during the year (Rawlik and Jagodziński 2022b). However, this method visibly underestimates ANPP especially in deciduous forest where different groups of herbaceous plants reach biomass peak at different times and die fast just after that time (Rawlik and Jagodziński 2020). For that, Traczyk (1967) proposed a method to assess herb biomass by multiplying the shoot density and shoot biomass measured independently in the field just after each species blossom.

Measurements of whole-forest ANPP are often restricted to summaries of fine litterfall and aboveground biomass increment (Clark et al. 2001). Annual litterfall is usually defined as leaf and other short-lived plant material (e.g. flowers and twigs) production (Clark et al. 2001). The methodology of litterfall biomass assessment is connected with traps which catch litterfall. For proper estimation of litterfall in deciduous forests it is important to collect material continuously throughout the year and litter traps should be emptied even during the period when litterfall is low, to avoid litter loss in the traps (Clark et al. 2001).

Previous research showed that the herb layer contribution to ANPP in different kinds of forests generally ranges between 0.5% and 16%, but can be higher (up to 41% of a forest's annual litterfall) in more open forest stands (Gilliam 2007; Muller 2014; Landuyt et al. 2019). However in temperate deciduous forests it is usually less than 5% (DeAngelis et al 1981; Welch et al. 2007). The majority of forest ecosystem biomass is stored in trunks, branches, and coarse roots, nevertheless, tree leaves contain a significant amount of crucial minerals (N, P, K, Ca, Mg, Fe, etc.) and have a more significant contribution to matter cycling than wood components, as they decompose faster (Rawlik and Jagodziński 2022a; Rawlik et al. 2021; Rawlik et al. 2022; Rawlik et al. 2019). To understand the carbon cycle of forest ecosystems, it is important to know the quantitative relationships between overstory litter and herbaceous layer annual production (Landuyt et al. 2019), especially because both are components of labile fraction of litter. Only a few attempts have been made to study annual herbaceous layer biomass production and litterfall biomass on the same study plot (Gosz et al. 1973; DeAngelis et al. 1981; Welch et al. 2007). Moreover, previous studies were conducted for one season (Gosz et al. 1973; DeAngelis et al. 1981; Welch et al. 2007). Thus, it will be meaningful to further increase the number of attempts to estimate litterfall and herb layer production simultaneously and to improve accuracy in the estimates of forest ecosystem production.

The novelty of this paper is that we assess the full (including winter) seasonal patterns of standing biomass of the herbaceous layer during three vegetation seasons in temperate oak-hornbeam forests. We also present the seasonal dynamics of litterfall from trees and herb layer species. We hypothesized that (1) the seasonal herb layer biomass dynamics show a two-peak shape; with the first occurring in spring and connected with spring dominance of ephemerals in the biomass and the second occurring in late summer or early autumn, connected with the dominance of summer-greens, (2) contribution of herbaceous layer biomass production in annual litter production was not bigger than 5% of tree litterfall, as indicated by previous studies.

## 2. Materials and methods

### 2.1. Study area

The study site was located in the Babki Forest District (W Poland 52.1510° N, 17.0545° E). The study was conducted in an oak-hornbeam forest association (*Galio sylvatici-Carpinetum betuli* (R.Tx. 1937) Oberd. 1957 *corydalidetosum* Oberd. 1957) dominated by 135-year-old oak, hornbeam, and ash trees (Rawlik et al., 2022). The soils of the study site

were Stagnic Gleyic Umbrisols and Brunic Gleyic Umbrisols. The mean annual temperature during 1971– 2010 was 8.8 °C and the annual sum of precipitation was 541 mm (Central Statistical Office 2012). However, during time of fieldwork (2013–2015), the mean annual temperature was higher (9.7 °C) and the annual sum of precipitation was lower (515 mm) based on data from the Kórnik meteorological station (ca. 15 km N of the study site; Rawlik et al. 2022). More details about the study area were described by Rawlik et al. (2022).

### 2.2. Methods

#### 2.2.1. Herb layer biomass collection

Samples were collected from circular frames (0.16 $m^2$) randomly located within four sample plots with an area of 0.25 ha each, located about 50 m apart. We collected 10 frames from 4 sample plots (40 in total) at each collection time in the years 2013, 2014 and 2015. The size of the plots was chosen to allow for easy collection of 10 frames at predetermined harvesting dates over a period of 3 years, each time in a random location. The sample plots were selected to be homogeneous in terms of habitat conditions and forest structure. All sample plots were located in one forest complex, with a similar history of forest management. The understories of all plots were dominated by *Quercus robur*, *Fraxinus excelsior* and *Carpinus betulus*, with basal area of all trees in the overstory ranging from 3.2 to 6.6 $m^2$ $ha^{-1}$. Spatial heterogeneity could not be entirely avoided, even on a local scale, as the herbaceous layer exhibits significant differentiation due to random distribution of light and nutrients, as well as occasional disturbance events. A detailed description of the areas, including the description of stand structure, phytosociological relevés of the plant communities present on the areas, results of soil analyses, and characterization of microclimatic conditions, can be found in our previous publication (Rawlik et al. 2022). These four sample plots serve as technical replications, providing a backup in case any disruption incident occurs on one of the plots. To avoid repetitive sampling of the same (harvested) patches, we marked them with colored sticks. We collected all aboveground biomass as plants were cut at the soil level. We included the whole plant in the sample if a shoot was rooted inside the frame, however we excluded shoots rooted outside the frame. The sampling period was from 12th April 2013 to 30th October 2015. During March, April, May, and June of the sampling year, we collected plant biomass samples every 7 days while in the remaining months, plant materials were collected every 14 days. In winter we sampled once per month when the temperature did not exceed 5 °C (January, February, and December 2014, February 2015). In total, we collected samples in the field 84 times comprising 3360 samples. In the field, each species was collected separately in each frame, placed in a paper bag, and labeled by species, frame, and collection date. Perennial plants (tree saplings, wintergreens) were divided into the current year's increment and the rest of the plant (everything that had grown in previous years). Samples were transported to the laboratory of the Institute of Dendrology PAS in Kórnik, dried at 65 °C with forced air circulation to constant weight (usually 3 days), and weighed with an accuracy of 0.001 g.

#### 2.2.2. Litterfall

Thirty litter traps were installed between sample plots on 6th November 2012 (5 litter traps × 6 blocks). Litter traps were installed between sample plots to avoid any additional negative impact on the herbaceous vegetation associated with the presence of litter traps and monthly collection of material from them. The litter traps were square wooden boxes with permeable synthetic fabric at the bottom and a height of 15 cm, and a catching area of 0.36 $m^2$. The content of litter traps was collected at the beginning of every month, with the exception of months with litterfall close to zero, during the vegetation seasons of 2013, 2014, and 2015. The collection was from 1st December 2012 to 5th December 2015. In total, we collected litterfall samples in the field 27 times: once in 2012, 8 times in 2013, 9 times in 2014, and 9 times in 2015. The litterfall was separated into three components: leaves, woody debris fall (bark, twigs), and other litterfall originating from trees and shrubs, which was unable to classify into the first two categories. After collection samples were transported to the laboratory of the Institute of Dendrology PAS in Kórnik, dried in a dryer with forced air circulation at 65 °C to constant weight (at least 3 days), and then weighed with an accuracy of 0.001 g.

### 2.3. Data analysis

To assess the normality of distributions we performed the Shapiro–Wilk test. Due to the non-normal distribution and heteroscedasticity of herb layer biomass, we used Kruskal–Wallis tests with Dunn's post hoc tests to assess differences in variables among all collection times. To partition variance between temporal-variation and spatial-variation sources we performed a linear random effects model, assuming collection time as a categorical fixed predictor and plot number as a random effect. We decided to assume normal distributions and we did not scale and transform data because the model met the overdispersion test and we obtained easy interpretable data. Scaling, transforming and assuming a gamma or log-normal distribution did not give better results and in the latter case produced significantly overdispersed models. To calculate ANPP we used the method based on the sum of biomass peaks by each species occurring throughout the growing season:

$$\sum_{n=\mathrm{sn}} \mathrm{AB}_{\max}$$

where sn is species number, and $AB_{max}$ is the highest value of standing biomass of an individual herb-layer species during the growing season. For each species recorded in biomass collection frames at a sample plot we used its highest biomass recorded in a certain collection time (for each year separately) and related to the area of 10 frames (even if it only occurred in some of the frames); the obtained values of species biomass per area were summed, although they were recorded in various parts of the year. The calculations of ANPP were made separately for each sample plot. As a result, we obtained values of ANPP for 1–4 plots: in 2013 (four values), 2014 (four values), and 2015 (four values). To estimate ANPP only the current year increments were taken into account. This method was recommended by Rawlik and Jagodziński (2022b) as one of the more precise methods that also does not require the greatest effort.

All analyses were conducted using R software (R Core Team 2020).

## 3. Results

### 3.1. Seasonal changes of herb layer biomass

Our study revealed statistically significant differences among study dates (Fig. 1; Table 1). The highest biomass in 2013 was observed on May 3rd (47.05 g $m^{-2}$), in 2014 on April 17th (34.41 g $m^{-2}$) and in 2015 on April 24th (32.73 g $m^{-2}$) but these values did not differ significantly ($p > 0.05$).

We observed statistically significant differences from the lowest values observed on April 12th 2013 – 8.85 g $m^{-2}$, September 5th in 2014 – 8.35 g $m^{-2,}$ and October 30th in 2015 – 4.69 g $m^{-2}$. The period of the highest biomass states occurred from 26th April to 29th June (2013), from 4th April to 27th June (2014), and from 10th April to 26th June (2015), when biomass amounts generally did not differ significantly. In spring, biomass increased from the minimal to maximal values within three weeks: from April 12th to May 3rd, 2013, from March 28th to April 17th, 2014 and from April 4th to April 24th, 2015 (Fig. 1).

Biomass peaks were dominated by five species: *Anemone nemorosa* – 50.74% (mean share; 42.92% in 2013, 52.24% in 2014 and 57.06% in 2015), *Galeobdolon luteum* – 18.83% (27.09% in 2013, 21.08% in 2014 and 8.31% in 2015), *C. betulus* – 16.32% (11.49% in 2013, 16.17% in 2014 and 21.29% in 2015), *F. excelsior* – 2.63% (3.14% in 2013, 2.89%

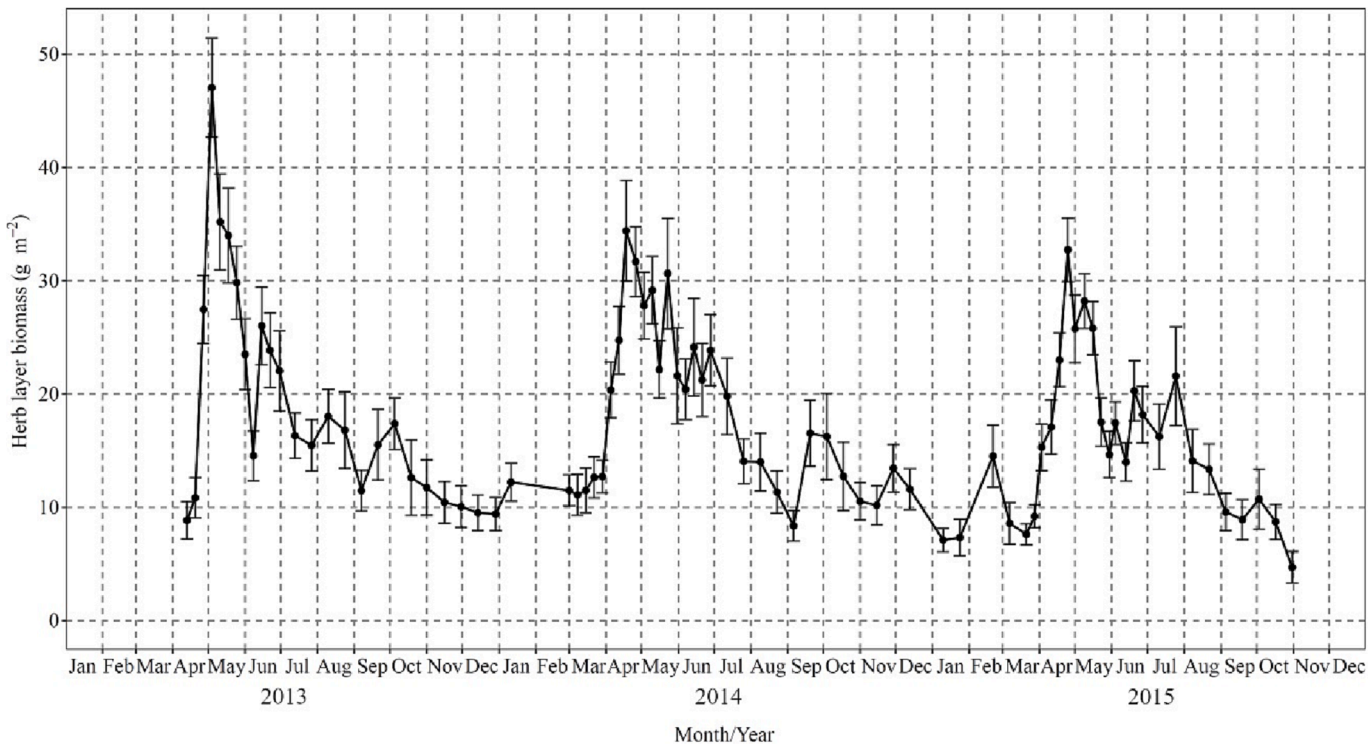


**Fig. 1.** Changes in understory biomass (±SE) during the growing seasons of 2013, 2014, and 2015. The points represent mean values and the vertical lines represent the standard error of the mean.

**Table 1**
Spatial and temporal variation of herb layer biomass showed using linear mixed effects model.

| Herb layer biomass n = 3360 | Random effects | Variance | SD | Mixed model parameters | |
|---|---|---|---|---|---|
| | Plot | 12.42 | 3.524 | $R^2_c$ | 0.2148 |
| | Residuals | 281.15 | 16.768 | $R^2_m$ | 0.1801 |
| | Fixed effects | Estimate | SE | t value | p |
| | (Intercept) | 8.85 | 3.18 | 2.779 | 0.009 |
| | Date of collection | – | – | – | $<10^{-16}$ |

in 2014 and 1.86% in 2015) and *Maianthemum bifolium* – 1.61% (2.39% in 2013, 1.19% in 2014 and 1.25% in 2015); other species did not exceed a 1.5% share in biomass peaks. *A. nemorosa* biomass decreased rapidly just after the biomass peak in the first half of June. From the second half of June and lasting until the end of October, *G. luteum* dominated the biomass with a mean share of 36.67%.

### 3.2. Herb layer biomass production

Herb layer species had different dynamics of biomass increment. As some species accumulate biomass and died within two months (spring ephemerals), others continuously accumulated biomass during the whole growing season. For example, the *A. nemorosa* biomass peak was obtained on May 3rd, 2013, April 17th, 2014, and April 24th, 2015, while *G. luteum* was on June 21st, 2013, June 27th, 2014, and June 19th, 2015. The current year biomass peak of *C. betulus* was on May 10th, 2013, June 13th, 2014 and July 24th, 2015, and that of *F. excelsior* and *M. bifolium* on August 9th, 2013, July 11th, 2014, and July 24th, 2015, and June 14th, 2013, June 6th, 2014 and June 19th, 2015, respectively (Fig. 2). Summing biomass peaks for separate species provided ANPP values closer to reality; for example, we estimated ANPP as 94.03, 86.15, and 76.84 g m$^{-2}$ yr$^{-1}$, in 2013, 2014, 2015 year, respectively, and those values were 1.5 to 2 times higher than biomass peaks in related years.

### 3.3. Biomass of litterfall

In winter and at the beginning of spring (February, March, and April) the litterfall was low (33.20 g m$^{-2}$), but increased slightly during spring and summer (140.14 g m$^{-2}$ from May to September) and the litterfall peak was observed during October and November (545.59 g m$^{-2}$) (Fig. 3). The leaf fall in winter, spring, and summer was 19.63% of annual litterfall, whereas during October and November the majority of leaves fell (80.37% of annual litterfall). Woody debris fall (twigs, bark, etc.) was quite constant throughout the year, with some exceptions in summer and autumn when woody debris fall was high (Fig. 3). Leaves dominated the total bulk of litterfall (mean share: 62.4%), while that of woody debris and other fractions had mean share of 17.1% and 20.4%, respectively. Mean annual litterfall biomass was 806.99 g m$^{-2}$, 762.42 g m$^{-2}$, and 1007.03 g m$^{-2}$ in 2013, 2014, and 2015, respectively (an average of 858.81 g m$^{-2}$).

### 3.4. Share of herbaceous primary production in annual litterfall

ANPP of the herb layer during the study time was 94.03 g m$^{-2}$ in 2013, 86.15 g m$^{-2}$ in 2014, and 76.84 g m$^{-2}$ in 2015 (an average of 85.67 g m$^{-2}$). During all years, annual litterfall exceeded the above-ground herb layer biomass production (Table 2). The mean contribution of the herb layer productivity in annual litter production was 9.23%. The exact relative importance of both studied biomass pools, however, varied depending on the season. The contribution of the understory was the lowest in 2015 (7.09%) and the highest in 2013 (10.44%). The mean contribution of the herb layer biomass in leaves annual litterfall was 13.86%. The contribution of the herb layer biomass in annual leaves litterfall was the lowest in 2015 (11.47%) and the highest in 2013

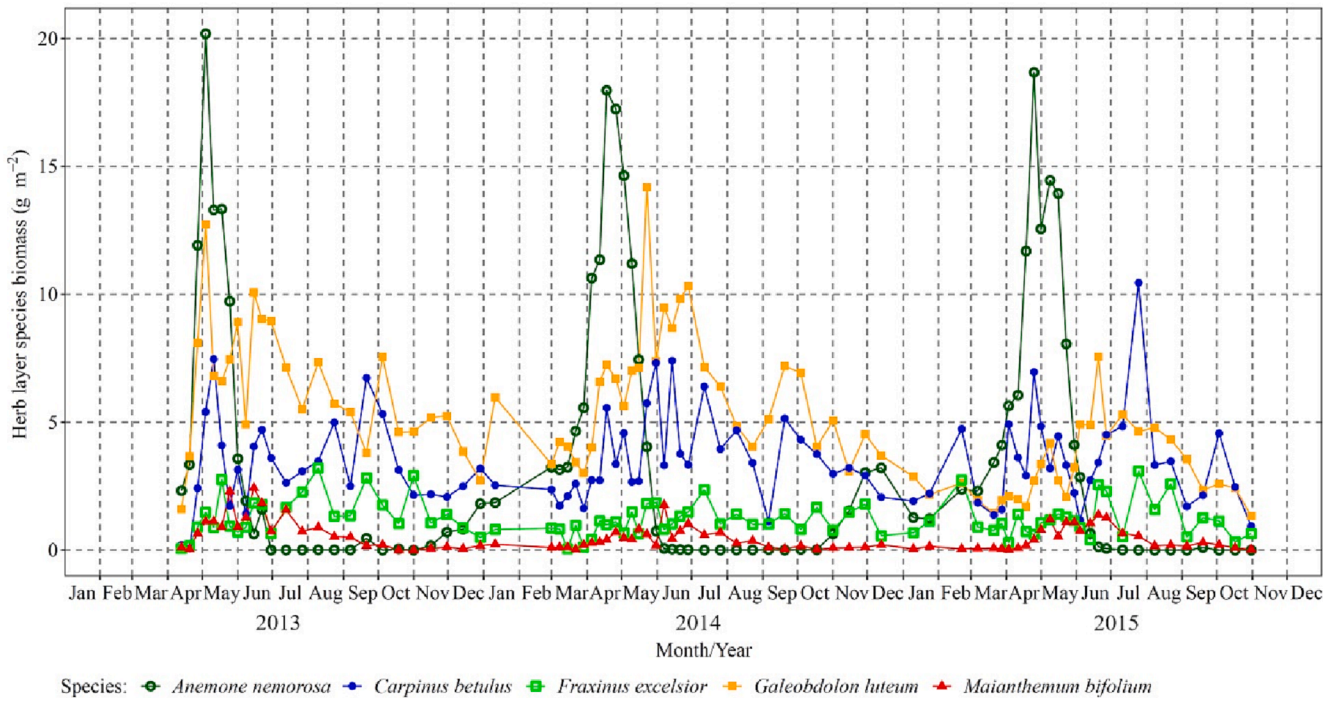


**Fig. 2.** The seasonal dynamics of the biomass for the five dominant ANPP species. The points represent mean values.

(15.69%), while in 2014 it was 14.42%.

## 4. Discussion

Our hypotheses were partially supported by the results of the study. We found statistically significant differences in herb layer biomass and litterfall among study dates. Our study revealed that: (1) the seasonal herb layer biomass dynamics showed a single-peak shape; a very distinct peak occurred in spring and continued in late spring, summer, and late summer to early autumn, and (2) the share of herbaceous layer biomass production in annual litter production was more than 5% of litterfall during the three seasons studied (mean 9.23%).

### *4.1. Seasonal changes of herbaceous biomass*

The highest aboveground herb layer biomass was 45 g m$^{-2}$ which is in line with previous studies from Poland (Table 1 in the Appendix). Landyut et al. (2020b) in their studies conducted in northwestern Europe reported maximal values of the aboveground herb layer to more than 500 g m$^{-2}$ in open forests, where no limitations of light and nitrogen were noticed. Previous studies from our study region reported the lowest aboveground herb layer stand biomass in oak-hornbeam forests in the range from 3.7 g m$^{-2}$ (Jagodziński et al. 2013) and 4.1 g m$^{-2}$ (Rawlik et al. 2012) to 9.6 g m$^{-2}$ (Banasik 1978). The lowest biomass throughout the year was recorded in March, April or November in the previous studies, but in September and December in our studies. As we continued studies in winter, we noticed that biomass production was starting even in winter, when the weather was warm, thus the lowest stand biomass was observed in autumn and winter.

Previous studies showed high variability of herb layer biomass in oak-hornbeam forests in Europe. This is connected with varied species composition, especially different dominance of particular species, distinguishing different forms of oak-hornbeam forests. For example, high values of herb layer biomass in an oak-hornbeam forest were recorded by Werger and Van Laar (1985) in the Netherlands (133.9 g m$^{-2}$), where the dominant herb was *Allium ursinum* that creates dense foliage and taller shoots than *A. nemorosa* that dominates in our plots. The highest values reported by Banasik (1978) from Poland in study areas where *Aegopodium podagraria* dominated biomass production of the herbaceous layer. This can be connected to the fourfold higher individual biomass of *A. podagraria* (0.4254±0.0035 g) than *A. nemorosa* (0.1044±0.0003 g; Paź-Dyderska et al. 2020). Values similar to those obtained in our studies are associated with the dominance of *A. nemorosa* in the herbaceous layer (Rawlik et al. 2012; Jagodziński et al. 2013; Rawlik and Jagodziński 2020; Rawlik and Jagodziński 2022b). Compared to the earlier studies that described the seasonal variation of herbaceous layer biomass production with the dominance of spring ephemerals (Werger and Van Laar 1985; Rawlik et al. 2012; Jagodziński et al. 2013), we observed that the peak time of herbaceous layer biomass occurred two to three weeks earlier in 2014 and 2015, and only 2013 was similar to previous studies. Previous studies have examined the differences in the phenology of flowering onset in spring ephemerals, which have advanced by 5.4 days per decade (Büntgen et al. 2022), and it is projected to increase by approximately one month over a thirty-year period (Puchałka et al. 2022).

Therefore, the observed advance in biomass peak date can be an effect of climate change, however, the limited spatiotemporal scope of our study did not allow for wider conclusions. In our study, the year 2013, characterized by a later occurrence of the biomass peak, exhibited distinct climatic conditions. These included a prolonged duration of snow cover until the first week of April, higher mean temperatures in January, February, and March, significantly higher precipitation in February, lower mean annual temperature (8.8 °C in 2013 compared to 10.2 °C and 10.1 °C in 2014 and 2015, respectively), and higher precipitation (623.2 mm in 2013 compared to 499.6 mm and 423 mm in 2014 and 2015, respectively; Rawlik et al. 2022). For that reason, reaching the biomass peak from winter stagnation relatively fast (three weeks), that we observed in all three years, is an interesting phenomenon, that has not been described so far. Quantifying species-specific biomass accumulation dynamics allows us to determine biomass production with greater precision compared to using a single sampling time.

Only a few studies on herb layer biomass have been conducted over multiple vegetation seasons in temperate deciduous forests (Aulak 1976; Towpasz 1976; Rawlik and Jagodziński 2022b). All of these studies have found differences between seasons, which most of the authors attributed to climatic conditions, especially temperature and precipitation (f.e.

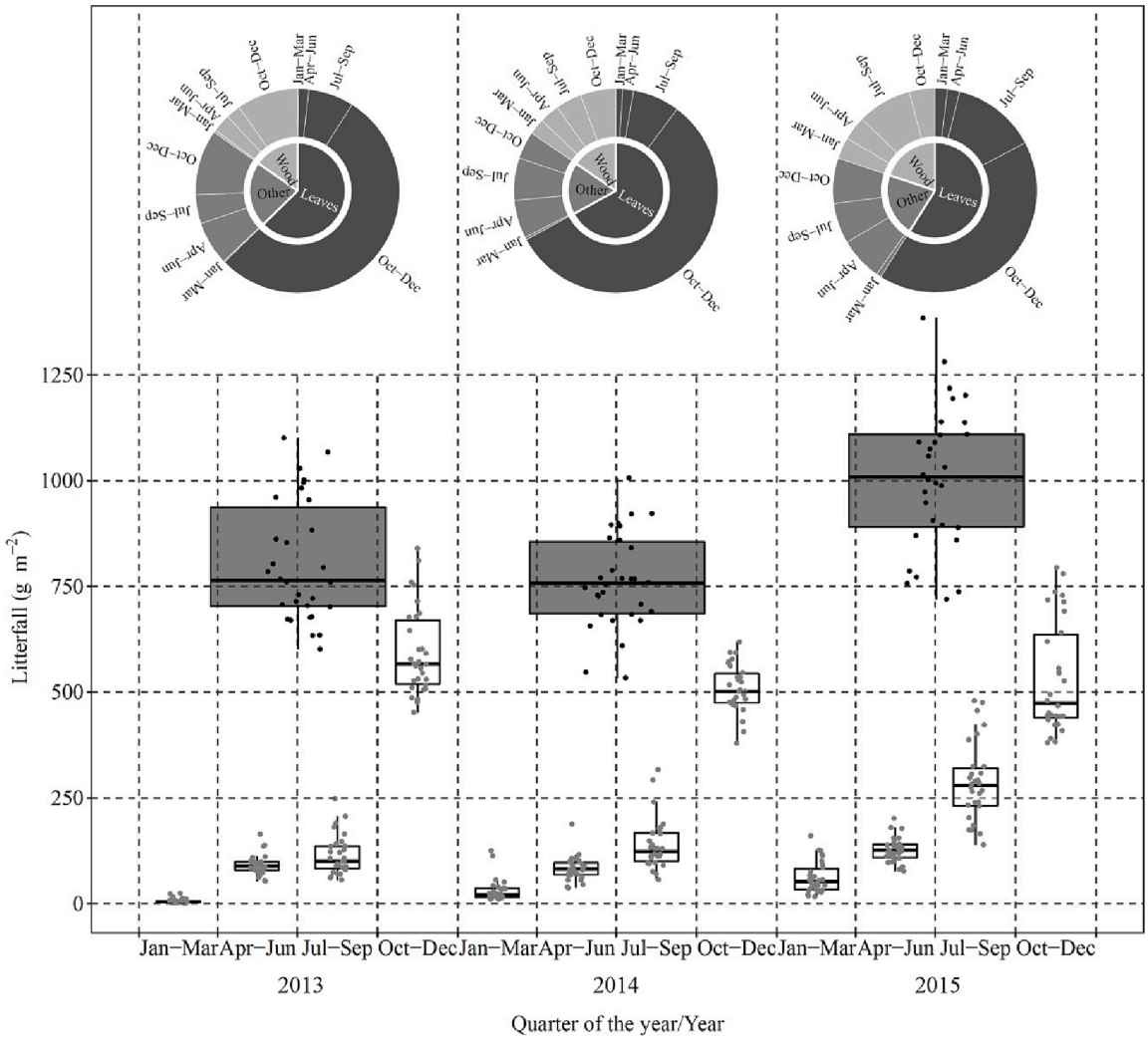


**Fig. 3.** Changes of litterfall from trees and shrubs during seasons 2013, 2014, and 2015.

**Table 2**
Share of herbaceous layer production in annual litter production during seasons 2013, 2014, and 2015 (in g/m$^{-2}$).

| Litterfall | 2013 | | 2014 | | 2015 | |
|---|---|---|---|---|---|---|
| | mean | SE | mean | SE | mean | SE |
| Herbaceous layer | 94.03 | 16.62 | 86.15 | 11.17 | 76.84 | 13.27 |
| Leaves from trees and shrubs | 505.28 | 10.78 | 511.30 | 8.71 | 593.15 | 15.89 |
| Woody debris | 123.56 | 10.98 | 117.79 | 11.79 | 200.40 | 15.19 |
| Others | 178.15 | 15.18 | 133.33 | 8.27 | 213.48 | 11.39 |
| Total litterfall from trees and shrubs | 806.99 | 26.19 | 762.42 | 20.48 | 1007.03 | 30.62 |

Aulak 1976; Towpasz 1976; Rawlik and Jagodziński 2022b). Towpasz (1976) reported that positive temperatures in winter (January, and February) and lower precipitation in March contributed to the limited development of herb layer biomass. This agrees with our results, as we found the highest herb biomass production in the season with the lowest winter temperatures and higher precipitation in March and April (Rawlik and Jagodziński 2022a). A different situation was described by Banasik (1978) from South Poland. In his findings, differences in herb layer production between two consecutive seasons (1967, 1968) were caused by the massive emergence of oak seedlings, which almost completely died in the following year. Therefore, an irregular supply of understory biomass was associated with a mast year and the lack of survival of oak seedlings due to limited light availability.

Previous studies (e.g. Rawlik and Jagodziński 2022b) have reported that the dynamics of the herb layer biomass exhibited a two-peak pattern with the first peak occurring in spring (with the dominance of spring ephemerals) and the second peak occurring in late summer or early autumn (with the dominance of summer-greens). However, in our studies, we observed a distinct single-peak in biomass production that extended from spring to late summer. This pattern was driven by spring biomass peaks of species such as *A. nemorosa*, *Ficaria verna*, and *Corydalis cava* which exhibited slower declines, followed by the biomass peaks of a group of plants that initiate growth in late spring or early summer (late May or late June), including *C. betulus*, *F. excelsior*, *Adoxa moschatellina*, *Convallaria majalis*, and *M. bifolium* that persisted into late summer. Thus, we state that patterns of seasonal variation in the biomass of the herbaceous layer are closely related to quantitative relationships among the ecological groups of plants comprising this forest layer. The seasonal production patterns of herbaceous layer production can be predicted based on the composition of species or functional groups. The literature has highlighted the isolation of the time of spring ephemerals from other herbaceous species, as they form separate communities known as the spring aspect (e.g., Jagodziński et al. 2016; Czapiewska et al. 2019; Rawlik and Jagodziński 2022b). However, our research results indicate the lack of a clear boundary between spring geophytes and summer-flowering plants. Many late-spring plant species complete their life cycles immediately following the dominance of geophytes, resulting in a

seasonal biomass dynamics chart without two distinct peaks.

### 4.2. Biomass of litterfall

Leaves production plays a crucial role in assessing the NPP of forest ecosystems (Petritan et al. 2020) and describing the seasonal litterfall is essential for modelling forest carbon and nutrient cycles (Zhang et al. 2014). Zhang et al. (2014) conducted a comprehensive review of over 400 papers on seasonal litterfall in various forest ecosystems worldwide, and found that the mean annual litterfall varied between 3 and 11 Mg $ha^{-1}$ $y^{-1}$ across different ecosystems. Thus, this is similar to our results, as we obtained values ranging from 7.624 Mg $ha^{-1}$ $y^{-1}$ in 2014 to 10.070 Mg $ha^{-1}$ $y^{-1}$ in 2015. Our results exceed those obtained in northern Poland from oak-hornbeam forest (5.5 to 6.8 Mg $ha^{-1}$; Dziadowiec 2005) and in the western region of Poland from hornbeam-oak-pine (5.8 to 6.6 Mg $ha^{-1}$; Krynytska et al. 2017). The differences in the results could be in the variations in the species composition of the stands, as litterfall production patterns are specific to tree species (Reich et al. 2005; Hobbie et al. 2006). The proportions of leaves, woody debris, and other components in the litterfall biomass were similar to values reported in other studies conducted in similar forest types (Zhang et al. 2014; Krynytska et al. 2017).

We observed relatively high inter-annual variability in litterfall. Among the three seasons studied, the highest litterfall was recorded in 2015, which is somewhat surprising, considering that it was a warm and dry year (Rawlik et al. 2022). Previous studies have indicated a positive correlation between annual litterfall and precipitation, and a negative correlation between annual litterfall and summer temperatures (Novák et al. 2014). In 2015, we observed low temperatures in June and July and high precipitation during those months, which may have influenced leaf production. Additionally, 2015 experienced strong summer winds, which could explain the increased deposition of woody debris, including twigs and branches. Dziadowiec (2005) explained that the components of litterfall most prone to interannual variation are twigs, which can remain dead in tree crowns for an extended period before falling due to strong winds or snow. The next component that shows a different proportion in litterfall between years was fruits (included in "others" component), which are produced abundantly by trees every other year or less frequently (Dziadowiec 2005). In oak-hornbeam forests, this phenomenon is connected with oaks' mast seeding years. During mast years, oak populations produce abundant quantities of seeds that exceed the average amount produced in a non-mast year (Nussbaumer et al. 2016). It is more difficult to explain the higher leaf production despite unfavorable climatic conditions, particularly precipitation. However, in the short period of our study, it was not possible to draw conclusions about the effects of climatic variability on the amount of annual litterfall.

Litterfall seasonal patterns differ within ecosystem types and different tree species (Zhang et al. 2014). Depending on whether these patterns are unimodal, bimodal, or irregular, litter peaks can occur in various months of the year (Zhang et al. 2014). The seasonal patterns of litterfall in temperate forests are typically unimodal, characterized by a prominent peak in autumn (Zhang et al. 2014). This pattern is attributed to the phenomenon of leaf abscission, which primarily occurs during autumn in response to lower temperatures and reduced radiation (Zhang et al. 2014). In our study, we observed that the majority of leaf fall occurred during October and November, which aligns with autumn leaf fall. Consequently, the seasonal patterns of litterfall in our study were unimodal and similar to those reported by Jończak et al. (2016) in a black alder stand in Middle Pomerania. In contrast, Krynytska et al. (2017) described litterfall in the hornbeam-oak-pine forest in Roztoche (W Ukraine) using bimodal models, with the highest litterfall observed in October, and a lower peak in May. The authors suggested that the second peak, which was not observed in our studies, was due to damage to young leaves caused by insects (Krynytska et al. 2017).

### 4.3. Share of herbaceous primary production in annual litterfall

One of the methods for assessing the contribution of herbaceous layer biomass to annual litter production in a forest is by comparing its value to overstory litterfall. However, studies that include both measures on the same site are very rare (Landuyt et al. 2019). Although the contribution of the herb layer in ANPP in temperate deciduous forests is typically less than 5%, nevertheless, some previous studies revealed high variability, indicating that it generally ranges between 0.5% and 16%, and in some cases, it can reach up to 41% (Landuyt et al. 2019). However, the highest values were observed primarily in more open and young stands, where abundant light availability promotes understory development, while foliage production remains relatively low (Landuyt et al. 2019). The results of our study align with the general established by Landuyt et al. (2019), as the average annual litterfall over three years was 9.23% (specifically, 7.09% in 2015, 10.15% in 2014, and 10.44% in 2013).

Previous studies often underestimated herbaceous layer ANPP by using a method based on peak biomass minus minimum biomass. This approach can led to even a 2.5-fold underestimation of ANPP, disregarding temporal biomass variability among species (Rawlik and Jagodziński 2022b). More accurate methods involved tracking biomass dynamics for individual species and determining their specific biomass peaks or biomass and density. Traczyk (1967a) proposed a method that reduced labor intensity by determining shoot biomass and density at the time of peak biomass for each species. Rawlik and Jagodziński (2022b) compared ANPP values based on different methods and recommended the one based on multiplying the shoot biomass and density at the time of the highest values as the most accurate. Double-sampling techniques have been used due to the extensive and labor-intensive nature of harvest methods, establishing correlations between biomass and less extensive traits. Cover-biomass correlations have been successfully utilized for herbaceous layer assessment (e.g., Gilliam and Turrill 1993; Gilliam 2006; Gilliam et al. 2016).The main disadvantage of our study is that we carried out our studies in one forest complex. This may limit the transferability of the results and one should be cautious when inferring results and conclusions for other forests. However, numerous studies based on single sites are providing unique results, which contribute to the further development of large-scale assessments. Such a disadvantage resulting from high labor demand, is usually connected with the collection of data with high temporal (e.g. McMahon and Parker 2015; Czapiewska et al. 2019) or spatial resolution (e.g. Parker et al. 2004; Woziwoda et al. 2019). Despite this disadvantage, assessments of understory biomass production and litterfall with high temporal resolution and conducted over three seasons provide novel data which could be a baseline for further studies.

In addition, understory plants provide food, shelter and habitat, particularly for arthropods (Boch et al. 2013) and large herbivores (e.g. Gill and Beardall 2001; Smolko et al. 2018). Estimating the exact value for biomass lost from the study due to herbivory is challenging, leading to an underestimation of herbaceous layer biomass production. Moreover, the seasonal dynamics of *G. luteum* can indicate herbivore pressure, as in our study, the biomass peak for this species was observed on June 21st, 2013, June 27th, 2014, and June 19th, 2015. These results differ from those reported by Rawlik and Jagodziński (2022b). The above-mentioned authors indicated that the biomass dynamics of *G. luteum* aboveground shoots showed continuous growth during two growing seasons, with the biomass peak value observed during September–November, probably due to lower ungulates pressure, summer-greens can undisturbedly increase their biomass. However, the influence of herbivory on herb layer biomass production is underrepresented in previous studies.

## 5. Conclusions

1. As our studies were conducted for a longer duration and with more frequent measurements compared to previous studies, they provide a more detailed description of herb layer biomass and litterfall biomass dynamics.
2. Previous studies underestimated the contribution of the herbaceous layer to the annual net primary production (ANPP) of forest ecosystems.
3. The seasonal dynamics of the herb layer biomass showed a single-peak shape, with a distinct peak occurring in spring and extending into late spring, summer, and early autumn.
4. The share of herbaceous layer biomass production in annual litter production was 9.23% of total litterfall and 13.86% of the labile fraction during the three growing seasons studied.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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**Appendix Table 1.** Annual net primary production and litterfall of European forests.

| Literature source | Vegetation season | Forest plant community | Study location | Herb layer production (g m$^{-2}$) | Litterfall (g m$^{-2}$) |
|---|---|---|---|---|---|
| **1** | 1963 | Fagetum carpaticum | Ojcowski National Park, Poland | 25.0 | - |
| **1** | 1963 | Pino-Quercetum | Ojcowski National Park, Poland | 80.0 | - |
| **2** | 1964 | Tilio-Carpinetum | Kampinowski National Park, Poland | 16.7 | 373.1 |
| **2** | 1964 | Pino-Quercetum | Kampinowski National Park, Poland | 16.6 | 372.9 |
| **2** | 1964 | Vaccinio myrtilli-Pinetum | Kampinowski National Park, Poland | 13.1 | 324.6 |
| **2** | 1964 | Carici elongatae-Pinetum | Kampinowski National Park, Poland | 55.7 | 409.1 |
| **3** | 1964 | Fagetum carpaticum | Ojcowski National Park, Poland | 46.5 | - |
| **4** | 1967 | Tilio-Carpinetum stachyetosum | Niepołomice Forest, Poland | 55.232 | - |
| **4** | 1967 | Tilio-Carpinetum typicum | Niepołomice Forest, Poland | 32.262 | - |
| **5** | 1968 | Frangulo-Salicetum | Bełdańskie Lake, Poland | 210.4 | 490 |
| **5** | 1968 | Circeo-Alnetum | Bełdańskie Lake, Poland | 225.0 | 364 |
| **5** | 1968 | Tilio-Carpinetum stachyetosum | Bełdańskie Lake, Poland | 72.4 | 714 |
| **5** | 1968 | Tilio-Carpinetum typicum | Bełdańskie Lake, Poland | 575.0 | 640 |
| **6** | 1967 | Vaccinio myrtilli-Pinetum | Piska Forest, Poland | 200.0 | - |
| **6** | 1967 | Vaccinio myrtilli-Pinetum | Piska Forest, Poland | 120.0 | - |
| **6** | 1967 | Vaccinio myrtilli-Pinetum | Piska Forest, Poland | 628.0 | - |
| **7** | 1967 | Cladonio-Pinetum | Kampinowski National Park | 17.6943 | 465.962 |
| **8** | 1967 | Circaeo-Alnetum | Białowieski National Park, Poland | 107.457 | - |
| **9** | 1968 | Vaccinio uliginosi-Pinetum | Kampinowski National Park, Poland | 103.75 | - |
| **10** | 1978 | Stellario-Carpinetum allietosum | Rycholterbos, near Maastricht, Nederlands | 134.0 | - |
| **11** | 2005 | Stellario-Carpinetum | Western Slovakia | 53.6 | - |
| **11** | 2005 | Hacquetio-Carpinetum | Western Slovakia | 102.0 | - |
| **11** | 2005 | Carici pilosae-Carpinetum typicum | Western Slovakia | 43.1 | - |

| | | | | | |
|---|---|---|---|---|---|
| **11** | 2005 | Carici-Carpinetum melicetosum uniflorae | Western Slovakia | 75.0 | - |
| **11** | 2005 | Carici-Carpinetum type with M. perennis | Western Slovakia | 144.7 | - |
| **11** | 2005 | Carici pilosae-Fagetum | Western Slovakia | 61.7 | - |
| **12** | 2006 | Stellario-Alnetum | North Slovakia | 63.7 | - |
| **12** | 2006 | Carici pilosae-Carpinetum | North Slovakia | 56.6 | - |
| **12** | 2006 | Carici pilosae-Fagetum | North Slovakia | 13.4 | - |
| **12** | 2006 | Aceri-Carpinetum | North Slovakia | 24.2 | - |
| **13** | 2010 | Stellario holosteae-Carpinetum betuli | North-West Poland | 35.32 | - |
| **14** | 2010 | Galio sylvatici-Carpinetum betuli | Central Poland | 27.09 | - |
| **15** | 2010-2011 | Stellario holosteae-Carpinetum betuli | North-West Poland | 74.3-94.0 | - |
| **16** | 1973-1974 | Tilio-Carpinetum | South Poland | 122.63-34.13 | - |
| **17** | 1953 | Tilio-Carpinetum | Białowieski National Park, | 20.4 | - |
| **18** | 1967-1968 | Pino-Quercetum | Piski Forest, N-E Poland | 49.61 | 66.375 |
| **19** | 1974-1975 | Vaccinio uliginosi-Pinetum | Roztoczański National Park, Poland | 102.455-165.799 | - |
| **19** | 1974-1975 | Leucobryo-Pinetum moist | Roztoczański National Park, Poland | 93.341-154.377 | - |
| **19** | 1974-1975 | Leucobryo-Pinetum dry | Roztoczański National Park, Poland | 92.194-140.475 | - |
| **20** | 1969-1972 | aspen forest | Northern Wisconsin, USA | 117.5 | - |
| **20** | 1969-1972 | maple-aspen-birch forest | Northern Wisconsin, USA | 63.0 | - |
| **20** | 1969-1972 | birch forest | Northern Wisconsin, USA | 51.0 | - |
| **21** | 1967-1968 | mixed hardwood forest dominated by *Acer saccharum* | Brownfield woods, Illinois, USA | 68.0-175.0 | - |

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RESEARCH PAPER

# Short life–fast death: decomposition rates of woody plants leaf- and herb-litter

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## Abstract

• ***Key message*** **Decomposition of forest herb species litter was not always completed in less than a year and was not always faster than decomposition of tree leaf litter in an oak-hornbeam forest in Western Poland. Litter decomposition of herbaceous plants is connected with their life strategy and functional traits of their leaves.**

• ***Context*** Forest understories are frequently ignored in ecological research on decomposition, although they play an important role in biomass and nutrient cycling in forest ecosystems.

• ***Aims*** We hypothesized that the decomposition process of herbaceous species was completed in less than a year, as opposed to tree leaf litter. The second aim of our study was to determine if life strategy affects the rate of litter decomposition.

• ***Methods*** We performed the decomposition experiment in the oak-hornbeam forest in Czmoń (Western Poland) using the litter bag method to determine decay constants ($k$) for all species studied. The influence of species identity, functional group, and functional traits of leaves and other effects on the decomposition process was assessed.

• ***Results*** The decomposition process was significantly dependent on the functional group of plants, time of exposure in the field, species identity, and precipitation. We found a significant correlation between leaf traits and decay rates of the species studied.

• ***Conclusion*** Litter decomposition of herbaceous plants is connected with their life strategy and functional traits of their leaves in an oak-hornbeam forests.

**Keywords** Ecosystem processes · Decomposition · Functional groups · Leaf litter · Life strategy · Understory vegetation

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**Contribution of the co-authors** Katarzyna Rawlik: designed the research, formulated research problem and developed the methodology; collected the data; analyzed the data and wrote the first draft of the manuscript; contributed critically to the drafts and gave final approval for publication.
Mirosław Nowiński: collected the data; analyzed the data; contributed critically to the drafts and gave final approval for publication.
Andrzej M. Jagodziński: designed the research, formulated a research problem and developed the methodology; analyzed the data and wrote the first draft of the manuscript; contributed critically to the drafts and gave final approval for publication

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## 1 Introduction

Forest understories are frequently ignored in ecological research on productivity, probably due to their relatively small (ca. 1–2%) contribution to total plant biomass of ecosystems. However, herbaceous species have great importance for forest nutrient retention (Bormann et al. 1968; Muller and Bormann 1976; Muller 2014). The herb layer can provide up to 16% of annual litter fall in forests (Gilliam 2007; Muller 2014). Moreover, in temperate deciduous forests herbaceous species supply litter to the litter horizon continuously during the growing season, thus not only in an autumnal pulse like tree leaf litter (Wise and Shaefer 1994). Additionally, foliar concentrations of some nutrients (N, P, K, Mg) are higher in herbaceous than in tree species (Gilliam 2007). It is particularly important that, on average, the herbaceous layer contains 80% of forest plant species biodiversity and rare herb species can be useful as indicators of biodiversity or site quality (Gilliam 2007;

Spyreas and Matthews 2006). Moreover, by competition with natural woody plant species regeneration, the herb layer influences or even determines overstory composition (Baraloto et al. 2005). The biomass of herb species is also an important source of food for animals (Dzięciołowski 1970).

The decomposition of organic matter is a crucial process in ecosystem functioning because it is responsible for replenishing the pool of soil nutrients available to plants, returning huge amounts of carbon dioxide to the atmosphere, and creating long-term storage of carbon as soil organic matter (Berg and McClaugherty 2014). In recent decades, the number of studies describing organic matter decomposition has increased rapidly. An important subset of those studies has been experiments comparing decomposition rates of litter from different species in common garden conditions (e.g., Hobbie 1996; Hobbie et al. 2006). These kinds of studies are keys for estimating species effects on litter decomposition and to create ecosystem models that help to illuminate their inner organization (Hobbie et al. 2006). Moreover, they are crucial for understanding the consequences of changes in plant biodiversity for ecosystem functioning (Chapin 2003; Handa et al. 2014; Liang et al. 2016). The majority of decomposition experiments in forest ecosystems have focused on woody species foliage (e.g., Dziadowiec 1987, 1990; Hobbie et al. 2006; Horodecki and Jagodziński 2017, 2019; Horodecki et al. 2019; Jackson et al. 2013; Jurkšienė et al. 2017) and wood (e.g., Bantle et al. 2014; Harmon et al. 2000). The limited studies available on decomposition in deciduous forests have focused on herb species decomposition rates (Halabuk and Gerhátová 2011; Mayer 2008; Rodgers et al. 2008; Wise and Shaefer 1994) and interactions with soil organisms (Wise and Shaefer 1994). Most of those studies noted that herb species litter in temperate deciduous forests was fully decomposed within 6 months after senescence (Halabuk and Gerhátová 2011; Mayer 2008; Muller 2014; Rodgers et al. 2008). Only herb species biomass dominated by sedges, shrubs, and mosses (Hobbie 1996) or ferns and shrubs (MacLean and Wein 1978) required more than 1 year to decompose completely.

Decomposition rates depend on climate, litter quality, and communities of soil organisms (Berg and McClaugherty 2014; Cornwell et al. 2008; Kamczyc et al. 2019; Urbanowski et al. 2018). Microclimates in temperate deciduous forest understories vary during the growing season, due to changing solar zenith angle and canopy phenology (Noda et al. 2015). Seasonal changes in the availability of light in the understory of deciduous forests are strictly connected with changes in other microclimatic conditions, like temperature and moisture (Graves 1990). This seasonality results in the occurrence of different phenological strategies among herb species in deciduous forests, including spring ephemeral, summer-green, winter-green, and evergreen species (Neufeld and Young 2014; Uemura 1994). These strategies represent a kind of niche separation, which allows the species to utilize habitat resources efficiently and avoid competition (Díaz and Cabido 2001; Jagodziński et al. 2016; Scherer-Lorenzen 2008).

Plant adaptations to variation in the physical environment is reflected in plant biological traits and connected with their different functions within an ecosystem. They determine the potential of a given species to establish or persist under any given set of environmental conditions (Díaz and Cabido 2001). The connection between plant adaptation strategies and decomposability is crucial for understanding vegetation–soil feedbacks. There is a general concept that functional traits of leaves (Leaf Economic Spectrum; Wright et al. 2005) influence leaf litter decomposition and nutrient release (Cornelissen and Thompson 1997; Zukswert and Prescott 2017). According to this concept species of plants with conservative resource strategies (high leaf dry matter contents (LDMC)), low nutrient concentrations, and low specific leaf area (SLA), decompose slower than fast-growing, acquisitive species (Díaz et al. 2016; Freschett et al. 2010, 2012; Wright et al. 2005). Studies that conceptualize decomposition within the tradeoff between defense and photosynthetic production have been frequently conducted for leaves of trees (Makkonen et al. 2012; Melilo et al. 1982; Zukswert and Prescott 2017) or herbaceous species of grasslands (Cornelissen and Thompson 1997; Cornwell et al. 2008). Previous research indicated that spring ephemerals have typical short-lived, sun-type leaves. They have the greatest metabolic activity, the highest rates of photosynthesis, and leaf N contents among all phenological groups of herbs (Muller 2014; Rothstein and Zak 2001). Generally, foliar nutrient concentrations of herbs are higher than overstory species (Muller 2014). In many previous studies, it was found that decomposition rate was strongly positively correlated with leaf N concentration and negatively with leaf life span (Bakker et al. 2011; Cornwell et al. 2008; Wright et al. 2005). To our knowledge, there is no information about differences in decomposition rates among species representing different life strategies of forest understory plant species in a temperate deciduous forest. Although functional traits of plants are nowadays widely accepted as potentially powerful indicators of the ecology of species, only a few forest understory species have been included in studies (Ma et al. 2010; Poorter and De Jong 1999; Rawlik and Jagodziński 2020; Rawlik et al. 2018; Rothstein and Zak 2001; Wang et al. 2010), and most frequently these species were pooled with other herbaceous plants. Many studies have demonstrated that plant traits have afterlife effects via their impacts on decomposition rates, however, it is still not clear whether patterns found on a global scale are reproducible at local scales, in specific growth forms (Kleyer et al. 2018), or different organs (Hobbie 2015).

Many studies researching correlations among plant traits or their correlations with decomposition included only one organ (e.g., stems or leaves), avoiding a whole-plant perspective (Kleyer and Minden 2015). These studies concerned homogeneous components of plants, usually focused on leaves (Hobbie 1992), even though a large part of herbaceous litter comes from stems or roots. Differences in structural and physiological traits between organs, connected with their different biological functions, might cause differential decomposability (Freschet et al. 2012). In this study, we wanted to know the true biological rate of biomass decomposition of the species included; therefore, we used mixed aboveground biomass (including leaves and shoots). Moreover, we decided to compare decomposition rates of leaves and blooming shoots (material dominated by shoots) of one herb species (*Aegopodium podagraria*) to assess differences in decomposition rates of different organs.

Our primary objective was to compare decomposition rates of oak-hornbeam forest herb species with different ecological requirements, phenology, and life-history traits. The second aim of our study was to compare the decomposition rates of these plants with leaf litter of tree species occurring in the overstory. We hypothesized that (1) biomass of herbaceous plants in a temperate deciduous forest decomposes completely in less than a year (decomposition constants $k > 1$) (Muller 2014 and literature cited therein). We also hypothesized that (2) spring ephemerals decompose faster than summer and autumn species (Jagodziński et al. 2016; Neufeld and Young 2014), and (3) herb species biomass decomposes faster than that of tree leaves (Mayer 2008; Muller 2014).

## 2 Materials and methods

### 2.1 Study area

This study was conducted in the Czmoń Forest (Babki Forest District, W Poland; 52° 09′ 05.76″ N, 17° 03′ 00.68″ E; 76 m a.s.l.), in the temperate climatic zone. Mean annual temperature in this area was 8.7 °C, and mean annual precipitation was 514 mm in 1971–2010, and 9.2 °C and 535 mm in 2001–2010 (Central Statistical Office 2020). According to meteorological data from a nearby meteorological station (Institute of Dendrology, Polish Academy of Sciences, Kórnik; 52° 14′ 41″ N, 17° 06′ 03″ E; 10.5 km from the study area) the mean annual temperature in 2011–2013 was 9.1 °C (Fig. 6a in the Appendix) and mean annual precipitation was 573 mm (Fig. 7 in the Appendix). In the year preceding the experiment (2011), the mean annual temperature was 9.5 °C, which was higher than during a typical year in the study area. More specifically, during the 12 months preceding the experiment (June 2011–May 2012), the average monthly temperature was as follows: 19.0 °C in June, 18.2 °C in July, 19.7 °C in August, 14.7 °C in September, 9.1 °C in October, 3.2 °C in November, 3.3 °C in December, 0.4 °C in January, − 4.6 °C in February, 5.8 °C in March, 9.0 °C in April, 15.2 °C in May. In the year preceding the experiment (2011), the annual precipitation was 431 mm, which was less than during a typical year in the study area. In the 12 months preceding the experiment (June 2011–May 2012), the monthly sum of precipitation was as follows: 59.3 mm in June, 108.1 mm in July, 78.8 mm in August, 24.7 in September, 26.8 mm in October, 0.7 mm in November, 48.0 mm in December, 74.5 mm in January, 44.2 mm in February, 10.3 mm in March, 30.5 mm in April, 40.8 mm in May. Air temperature at the meteorological station was measured at the level of 2 m. During the experiment (28 May 2012–26 October 2013), we also measured temperatures at the ground level every hour using four data loggers evenly distributed within the stand (HOBO U23-001 Pro v2 Temperature/Relative Humidity, Onset Computer Corporation, Bourne, Massachusetts, USA) (Fig. 6b in the Appendix). Since we compared the decomposition rates of the species studied after ca. 6 months from the beginning of the experiment, we show detailed temperature and precipitation conditions for this period (Table 4 in the Appendix). There were differences in average air temperatures, ground temperatures, and total precipitation among the five dates of the field experiment.

The study area was located in a deciduous forest complex, covered by a 97-year-old oak-hornbeam stand (Table 5 in the Appendix). Detailed descriptions of the study area were given by Horodecki et al. (2014), Rawlik et al. (2015), and Wiczyńska et al. (2013).

We determined soil particle-size distribution, soil pH in $H_2O$ and in 1 M KCl, physicochemical soil characteristic (Table 6 in the Appendix). These properties were measured in two soil samples collected in October 2013.

The number of sample plots and growing seasons included in the study was limited by the high labor demand for sampling senescent herbaceous plants and preparing the litter bag experiment. We are aware that chances to generalize results from our study are limited by the low replicability (one sample plot and one growing season). However, despite the lack of replications, our assessments of the effects of life-history traits on biomass decomposition, inclusion of stem and leaf biomass to estimate ecologically relevant decomposition of aboveground herbaceous biomass, and comparisons of herbaceous biomass with tree leaf litter decomposition, gives unique insight into the complexity of decomposition at this site. In addition, our study provides novel data that could be used in designing further studies.

## 2.2 Species studied

We chose 14 vascular plant species, which are the most abundant in the understories of fertile deciduous forests in Central Europe and present within the research site (Ellenberg 1988), i.e., *Adoxa moschatellina* L., *Aegopodium podagraria* L., *Alliaria petiolata* (Bieb.) Cav. et Grande, *Anemone nemorosa* L., *Anemone ranunculoides* L., *Asarum europaeum* L., *Corydalis cava* L. (Schweigger et Koerte), *Ficaria verna* Huds., *Galeobdolon luteum* Hudson, *Maianthemum bifolium* L. (F.W. Schmidt), *Mercurialis perennis* L., *Paris quadrifolia* L., *Stachys sylvatica* L., and *Urtica dioica* L. Additionally, we studied the five most abundant tree and shrub species in the overstory and undergrowth of the forest stand, i.e., *Acer pseudoplatanus* L., *Carpinus betulus* L., *Corylus avellana* L., *Fraxinus excelsior* L., and *Quercus robur* L. We chose these herb and woody plant species because they have a strong influence on ecosystem functioning, due to the fact that abundance of species is correlated with their importance to ecosystem function (Grime 2001), and because these species differ in their ecological requirements, phenology, and life-history traits (Table 1).

## 2.3 Methods

We harvested herbaceous plants during one growing season (2012) at the time when most of the plants within each population began senescing. In most cases, we collected senescent aboveground biomass (mixed leaves and stems). In the case of *A. podagraria*, we collected leaves and blooming shoots separately. During autumn 2012, we collected freshly fallen leaves of the mentioned tree species from stands in the vicinity of the sample plot. After collection material was dried in the laboratory at 65 °C to a constant weight in a dryer with forced air circulation (UFE 600, Memmert GmbH+Co.KG, Germany). Dried litter was weighed using BP 210 S (http://www.sartorius.dataweigh.com) and Mettler Toledo PG 1003-S (http://www.mt.com) scales with an accuracy of 0.001 g and placed into "litter bags" made of fiberglass netting (15 cm × 15 cm) with a mesh size of 1 mm.

Those bags were filled with 3.9–4.2 g (*U. dioica*), 1.9–3.2 (the remaining herb species), or 8.0–8.3 g (tree leaves) of litter and labeled. In total, 2658 litter bags were placed in the forest at five dates, according to the time of senescence of most plants of the particular taxon (Table 1). The decision on mesh size for our experiment took into account that it can modify activities of mesofauna and macrofauna, microclimatic conditions, and material leaching out of litter bags. Results of choosing different mesh sizes were shown by many previous methodological studies (Bradford et al. 2002; Harmon et al. 1999; Slade and Riutta 2012; Wise and Shaefer 1994). Thus, our choice was a compromise. The masses put in litter bags differed for particular species to avoid excessive compaction of the material. Moreover, the amount of material was adjusted to each material type, to standardize litter densities and textures inside the bags. For all herbaceous species, we placed a mix of leaves and shoots in litter bags, in proportions similar to what occurs in specimens in the field.

For *A. europaeum*, we decided to start the experiment according to the time of senescence of most of last-year's leaves. For *G. luteum*, we decided to start the experiment according to the time of senescence of most of the current year's leaves. Our main criterion (time of senescence of most plants of the particular taxon) was used to separate spring ephemerals and summer-green plants. Summer-green plants were further separated into two groups, mid-summer, and autumn-senescing plants. We decided to use different starting times of the experiment for particular groups of plants because the aim of our studies was to find real, biological rates of decomposition of the species studied. We established one research plot (ca. 0.25 ha in total). Litter bags were randomly placed on this research plot in six sets of samples. Distance between every set of samples was ca. 10 m. On the research plot we established samples of all species harvested in each term of collection (six samples per collection term).

Six randomly selected litter bags of each species were collected every week for herb species or every 2 weeks for tree species (Rawlik et al. 2020). The time of exposition in the field was generally about one half year (175 or 182 days) for herb species and 364 days for leaves of trees. After drying at 65 °C to a constant weight in a dryer with forced air circulation (UFE 600, Memmert GmbH+Co.KG, Germany), litter was removed from bags, and cleaned to remove sand, fungi and roots, and then weighed. The mass loss of the plant material was determined systematically during the experiment. For some species, we noticed that the decomposition rate was lower than previously assumed, and thus, we decided to extend the period of litter collection (see Table 7 in the Appendix). Thus, we decided to continue the experiment for longer durations for blooming shoots of *A. podagraria* (406 days) and *M. bifolium* (238 days), and leaves of *A. podagraria* (203 days), *M. perennis* (203 days), *S. sylvatica* (203 days), and *U. dioica* (203 days).

We are aware of the limitations of the litter bag method, due to artifacts the method has compared to real biological decomposition rates. Mainly, drying plant material can slow the decomposition rate because the chemical composition of samples may be changed, making dried material less attractive for consumers. Secondly, putting material into litter bags influences decomposition. In this context chosen mesh size is important. Mesh size is important because of the exclusion of macrofauna and different impacts of

microclimate, and thus biological activity and control on handling effects and increased exposure to abiotic factors (Bradford et al. 2002). The litter bag mesh size chosen for our experiment was a compromise between the smallest mesh, which inhibits meso- and macrofauna from entering litter bags, and the largest mesh, which leads to material leaching out of the bags. Moreover, in our studies, it was important to treat all samples in the same way, to enable making comparisons among them.

### 2.4 Data analysis

For each litter bag, we determined the proportion of initial litter mass remaining. We analyzed decay constants ($k$) by fitting the data for each species (the proportion of initial mass remaining was calculated by dividing the mass at each harvest date by the initial mass) with a negative exponential decay model. We used linear regressions of log-transformed proportions of initial mass remaining against time (Berg and McClaugherty 2014; Hobbie 1996; Olson 1963) using the following formula:

$$X = e^{-kt},$$

where $X$ is the proportion of remaining biomass at time $t$ and $k$ is the decay rate.

Differences in the rates of decomposition among the species studied were assessed using a one-way analysis of variance (ANOVA), followed by Tukey's test. After that, we used Bonferroni correction, meaning that we tested hypotheses at $\alpha = 0.000877$. We used the Bonferroni correction to control the family-wise error rate (FWER). The FWER is the probability of rejecting at least one true $H_i$, that means making at least one type I error. The Bonferroni correction rejects the null hypothesis for each $p_i = \alpha/m$, thereby controlling the FWER at $\leq \alpha$. The influence of the studied factors (species, time of exposure in the field, their interaction) on litter decomposition rates was assessed using two-way ANOVA. We checked the normality and homogeneity of the distribution of variables in each group compared by ANOVA. The assumptions of normality and homogeneity were not always valid; however, we decided to assume a normal distribution of data, as due to high sample size we may assume that with increasing sample size distribution of a variable in the whole population tends to a normal distribution, according to the central limit theorem.

Functional trait data were obtained from BiolFlor (Klotz et al. 2002), the LEDA trait database (Kleyer et al. 2008), and the TRY database (Kattge et al. 2011). We focused on morphological and chemical traits of living leaves known to affect components of the carbon and/or nitrogen cycles at the leaf, whole-plant, and ecosystem levels (Cornelissen et al. 1999; Reich et al. 1999): specific leaf area (SLA), leaf nitrogen (N) content per leaf dry mass (LNC), and leaf dry matter content (LDMC). The traits involved in this study were chosen to represent the trade-off between fast acquisition and conservation of resources. Moreover, these traits are correlated with leaf litter traits, traits of other organs, as well as with decomposition rates of leaves and decomposition rates of other organs (Freschet et al. 2012). Four species (*A. moschatellina*, *A. ranunculoides*, *C. cava*, *P. quadrifolia*) were excluded from the analysis of LNC impact on the decay process because of a lack of data. We evaluated simple linear regression models of species-specific $k$ and the above-mentioned plant traits as independent variables. Moreover, we used principal components analysis (PCA) to assess the correlations between plant traits and decomposition rates. We performed an analysis of variance of a mixed-effects linear model, describing differences in mass loss as a function of functional group, exposition time, temperature, and precipitation. To account for species-dependence of samples representing particular species we treated species as random factors with random slopes (we expected different trajectories of decomposition rates for each species).

All analyses were conducted in JMP Pro 14.0 (SAS Institute Inc. Cary, NC. USA; http://www.sas.com).

## 3 Results

### 3.1 Litter decomposition of understory herb species

We found statistically significant effects of herb species ($p < 0.0001$, $df = 14$, $F = 350.6065$), time ($p < 0.0001$, $df = 1$, $F = 1707.408$) and interaction of species × time ($p < 0.0001$, $df = 14$, $F = 36.503$) on litter decomposition. After ca. 2 months of incubation, spring ephemeral species (*A. moschatellina* and *C. cava*) reached 95% biomass losses. After the same time of decomposition in the forest, losses of biomass were the highest for the second group of spring ephemerals, i.e. *A. moschatellina*, *P. quadrifolia*; on average 95 % of litter decayed. At the same time, ca. 92 % of the first group of spring ephemerals (*C. cava*, *A. ranunculoides*, *F. verna*, and *A.nemorosa*), 69% of winter-green plants (*A. europaeum* and *G. luteum*), 35% of mid-summer senescing plants (*M. bifolium*, *A. podagraria* (blooming shoots), *A. petiolata*) and 30.5% of autumn-senescing plants (*A. podagraria* (leaves), *M. perennis*, *U. dioica*, and *S. sylvatica*) decomposed. Later, after ca. 6 months of incubation, rates of decomposition of litter for most of the herb species were considerably slower than at the start of the process. Six-month decay constants of spring ephemerals decreased, with the lowest value for *A. moschatellina* ($k = 4.7$) and the highest for *A. ranunculoides* ($k = 6.9$).

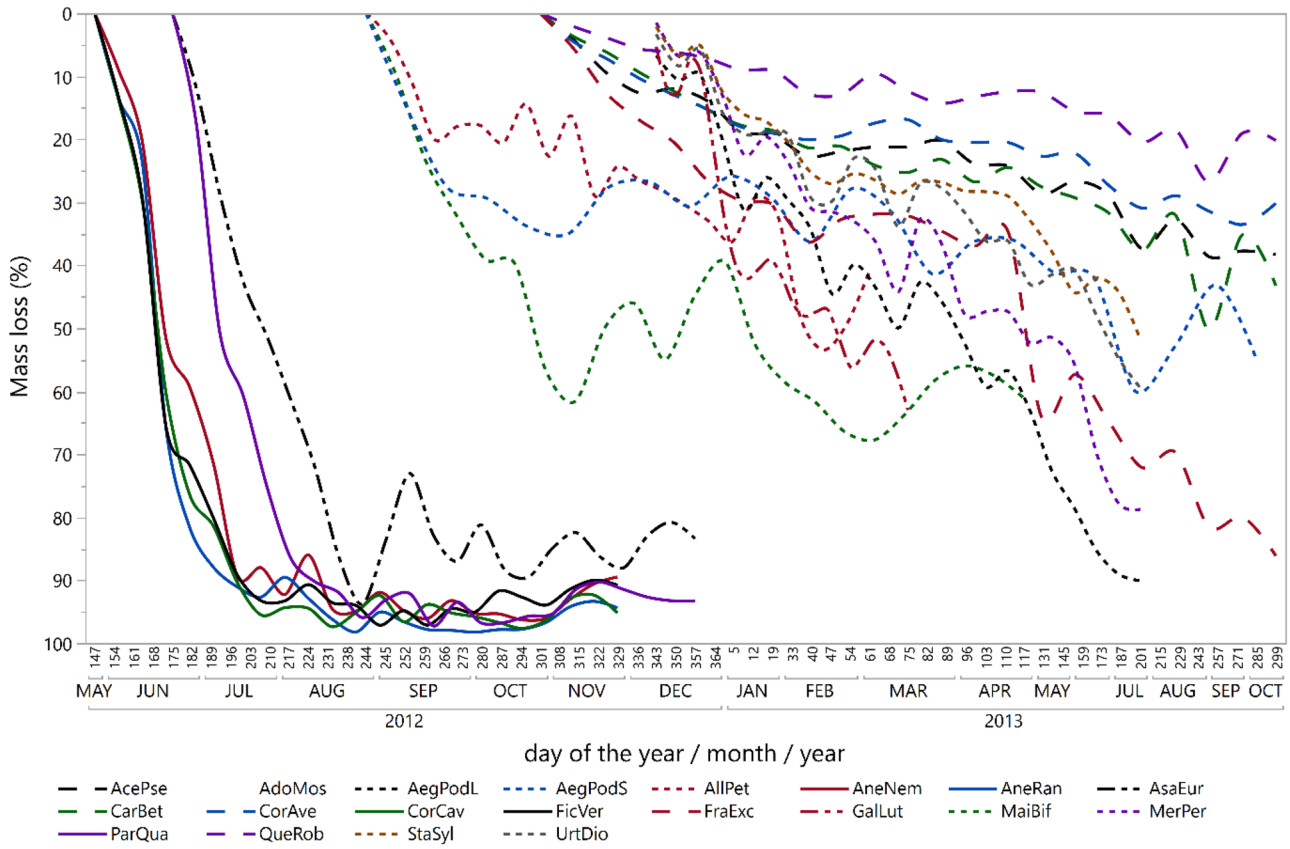


**Fig. 1** Decomposition (percentage of mass loss) for all plant species studied during the experiment by date during the years 2012 and 2013. Explanations of abbreviations: AcePse - *Acer pseudoplatanus*; AdoMos - *Adoxa moschatellina*; AegPodL - *Aegopodium podagraria* leaves; AegPodS - *Aegopodium podagraria* shoots; AllPet - *Alliaria petiolata*; AneNem - *Anemone nemorosa*; AneRan - *Anemone ranunculoides*; AsaEur - *Asarum europaeum*; CarBet - *Carpinus betulus*; CorAve - *Corylus avellana*; CorCav - *Corydalis cava*; FicVer - *Ficaria verna*; FraExc - *Fraxinus excelsior*; GalLut - *Galeobdolon luteum*; MaiBif - *Maianthemum bifolium*; MerPer - *Mercurialis perennis*; ParQua - *Paris quadrifolia*; QueRob - *Quercus robur*; StaSyl - *Stachys sylvatica*; UrtDio - *Urtica dioica*

Mid-summer senescing plants decomposed the slowest ($k$ range 0.2–3.2). During 182 days (ca. 6 months) of the experiment 95% of the biomass of all spring ephemeral species decomposed (Table 2). Plants that senesced during the mid-summer (*M. bifolium*, *A. petiolata*, *A. podagraria* (blooming shoots)) decomposed the slowest (Figs. 1 and 2). Biomass losses of *A. moschatellina* and *C. cava* were the most rapid—96% and 95% of the initial litter mass decayed during 63 days, respectively. After the same time of decomposition, 94% of *P. quadrifolia* and *F. verna*, 91% of *A. ranunculoides*, 90% of *A. europaeum*, 88% of *A. nemorosa*, 54% of *M. bifolium*, 48% of *G. luteum*, 34% of *A. podagraria* (leaves), 33% of *A. podagraria* (blooming shoots), 33% of *M. perennis*, 30% of *U. dioica*, 25% of *S. sylvatica*, and 18% of *A. petiolata* litter decomposed (Fig. 1). During ca. 6 months of the experiment, 95% of the biomass of *C. cava*, 94% of *A. ranunculoides*, 93% of *P. quadrifolia*, 91% of *F. verna*, and *A. moschatellina* decomposed (Table 2). After the same time of decomposition, 89% of the biomass of *A. nemorosa*, 87% of leaves of *A. podagraria*, 81% of *A. europaeum*, and 73% of *M. perennis* decomposed. Biomass of *M. bifolium*, *U. dioica*, *S. sylvatica*, and *A. petiolata* were 68, 50, 42, and 41% decomposed, respectively, whereas 28% of blooming shoots of *A. podagraria* decomposed.

### 3.2 Litter decomposition of the overstory species

We found statistically significant influence of woody plant species ($p < 0.0001$, $df = 4$, $F = 616.6597$), time ($p < 0.0001$, $df = 1$, $F = 916.3222$), and interaction of species × time ($p < 0.0001$, $df = 4$, $F = 70.108$) on litter decomposition. After ca. 6 months in the field decay rates of decomposition of tree foliage litter ranged from 0.2 to 0.8. *Q. robur* litter had the lowest decomposition rate (12%). At the same time, 21% of *C. avellana* leaf biomass, 24% of *C. betulus*, 25% of *A. pseudoplatanus*, and 43% of *F. excelsior*

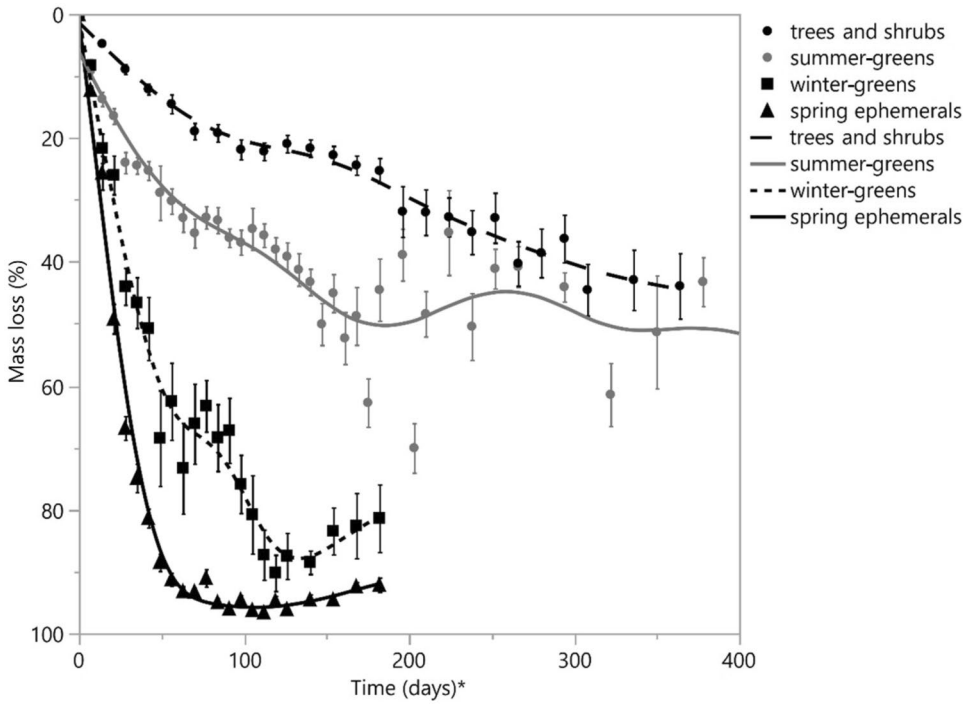


**Fig. 2** Decomposition (mean percentage of initial mass loss) of all functional groups of plants studied during the experiment. *Time of the exposition in the field = time from the start of the experiment, which varied in time of the year for different functional groups as shown in Fig. 1

decomposed (Fig. 1). After 1 year of exposure in the field, 20% of *Q. robur*, 30% of *C. avellana*, 38% of *A. pseudoplatanus*, 43% of *C. betulus*, and 86% of *F. excelsior* decomposed. The foliage of trees had decay rates ranging from 0.2 to 1.9 during the first year of decomposition. *F. excelsior* leaf biomass decomposed significantly faster than leaves of other tree species (Table 7 in the Appendix).

### 3.3 Herbs vs. deciduous tree species litter decomposition

In general, litter decomposition for woody plant species was distinctly lower than for herbaceous species. The decay rates calculated for 6 months ranged from 0.2 to 0.8 and 0.2 to 6.9, respectively. *F. excelsior* leaf biomass did not decompose significantly slower than *A. podagraria* (both leaves and blooming shoots), *A. petiolata*, *M. perennis*, *U. dioica*, or *S. sylvatica* litter during ca. 2 months and *A. petiolata*, *A. podagraria* (blooming shoots), *U. dioica*, or *S. sylvatica* litter during 6 months of exposure in the field (Figs. 1 and 2; Table 7 in the Appendix). The value of mass remaining after ca. 6 months of the study reached by this tree species foliage was more similar to values reached by *A. petiolata*, *S. sylvatica*, and *U. dioica* than to the other woody species studied.

The species studied may be arranged from the fastest to slowest decomposition rate determined after ca. 6 months of the study: *A. ranunculoides*, *C. cava*, *A. nemorosa*, *F. verna*, *P. quadrifolia*, *A. moschatellina*, *A. europaeum*, *A. podagraria* leaves, *M. perennis*, *M. bifolium*, *U. dioica*, *S. sylvatica*, *A. petiolata*, *F. excelsior*, *C. betulus*, *A. pseudoplatanus*, *C. avellana*, *Q. robur*, and *A. podagraria* blooming shoots (Table 2).

### 3.4 Predictors of decay

We found significant regressions between morphological (SLA and LDMC) or chemical (LNC) leaf traits and decay rates of the species studied after six months of the experiment (Fig. 3, Table 3). Moreover, LDMC was a stronger predictor of decay rates than SLA and LNC. The regressions between *k*-values and traits are visualized in Fig. 3. Variation among traits studied was effectively captured by PCA. The principal ordination axis (PC1) accounted for 65.2% of the total trait variation, and together with the first two principal axes, accounted for 85.8% (Fig. 4). *K* decay and SLA contributed to the first axis, as well as LDMC, but in opposite directions, whereas LNC was correlated with the second axis. The decomposition process depended on fixed effects (time of exposition in the field, the functional group of plants, and mean total daily precipitation during 6 months of the experiment), as well as on species identity (random intercept) (Table 3). Impact of the other fixed effect (mean temperature during 6 months of the experiment) on the decay process was not statistically significant (Table 3). We found statistically significant differences in the rate of litter decomposition among all functional groups studied (Fig. 5).

**Table 1** Description and life history traits of the species included in the study

| Species | Life form[1] | Life span | Functional group[2] | Strategy[3] | Leaf persistence[4] | LDMC (mg $g^{-1}$) | SLA ($cm^2$ $g^{-1}$) | LNC (mg $g^{-1}$) | Date of the start of the experiment | Number of litter bags |
|---|---|---|---|---|---|---|---|---|---|---|
| *Anemone nemorosa* | G | Perennial | se | CSR | V | 205.0 | 277.1 | 26.77 | 26.05.2012 | 132 |
| *Anemone ranunculoides* | G | Perennial | se | CSR | V | 184.1 | 365.3 | - | 26.05.2012 | 132 |
| *Corydalis cava* | G | Perennial | se | CSR | V | 139.9 | 510.0 | - | 26.05.2012 | 132 |
| *Ficaria verna* | G/H | Perennial | se | CSR | V | 117.5 | 317.9 | 33.00 | 26.05.2012 | 132 |
| *Asarum europaeum* | H | Perennial | wg | CS | I | 145.8 | 275.2 | 31.80 | 23.06.2012 | 132 |
| *Adoxa moschatellina* | G | Perennial | se | CSR | V | 136.7 | 384.5 | - | 23.06.2012 | 132 |
| *Paris quadrifolia* | G | Perennial | se | CSR | S | 176.0 | 350.0 | - | 23.06.2012 | 132 |
| *Alliaria petiolata* | C/H | Annual/perennial | ms | CR | I | 161.3 | 404.4 | 37.22 | 01.09.2012 | 126 |
| *Maianthemum bifolium* | G | Perennial | ms | S | S | 238.6 | 331.4 | 24.90 | 01.09.2012 | 144 |
| *Aegopodium podagraria*S | H | Perennial | ms | C | S | 230.0 | 297.7 | 21.49 | 01.09.2012 | 198 |
| *Aegopodium podagraria*L | H | Perennial | as | C | S | 230.0 | 297.7 | 21.49 | 08.12.2012 | 132 |
| *Galeobdolon luteum* | C | Perennial | as | CS | I | 270.0 | 253.5 | 18.19 | 08.12.2012 | 78 |
| *Mercurialis perennis* | G | Perennial | as | CS | S | 224.5 | 256.8 | 24.74 | 08.12.2012 | 132 |
| *Stachys sylvatica* | H | Perennial | as | CS | S | 207.0 | 421.2 | 22.89 | 08.12.2012 | 132 |
| *Urtica dioica* | C | Perennial | as | C | S | 212.5 | 261.6 | 40.53 | 08.12.2012 | 132 |
| *Corylus avellana* | N | Perennial | ts | C | S | 283.8 | 205.4 | 24.20 | 27.10.2012 | 132 |
| *Acer pseudoplatanus* | M | Perennial | ts | C | S | 262.5 | 167.6 | 23.80 | 27.10.2012 | 132 |
| *Carpinus betulus* | M | Perennial | ts | C | S | 254.4 | 236.7 | 20.85 | 27.10.2012 | 132 |
| *Fraxinus excelsior* | M | Perennial | ts | C | S | 256.5 | 135.6 | 22.61 | 27.10.2012 | 132 |
| *Quercus robur* | M | Perennial | ts | C | S | 280.0 | 153.4 | 21.99 | 27.10.2012 | 132 |
| Source[5]: | 1 | 1 | | 1 | 1 | 2 | 2 | 3 | | |

*Aegopodium podagraria*S - *Aegopodium podagraria* blooming shoots; *Aegopodium podagraria*L - *Aegopodium podagraria* leaves

[1]Life forms: H - hemicryptophytes; C - chamaephytes; G - geophytes; T - therophytes

[2]Functional group: se - spring ephemerals; wg - winter-green plants; ms - mid-summer senescing plants; as - autumn-senescing plants; ts - trees and shrubs

[3]Life strategies: C - competitive; CR - competitive/ruderal; CSR - competitive/stress-tolerant/ruderal; CS - competitive/stress-tolerant; S - stress-tolerant

[4]Leaf persistence: S - summer green; I - persistent green; V - spring green

[5]Source of data: 1 - BiolFlor (Klotz et al. 2002); 2 - LEDA trait database (Kleyer et al. 2008), 3 - TRY database (Kattge et al. 2011)

**Table 2** Results of the exponential decay model during 6 months of decomposition in the field. $k_6$ is the decay rate assessed after 6 months of the experiment in the field and $r_6$ is Pearson's correlation coefficient—values marked with the same letter do not differ significantly at $p < 0.0001$, based on one-way ANOVA and Tukey's a posteriori test. The last three columns show a decay time for 50%, 90%, and 95% litter mass loss

| Species | Parameter | | | | | |
|---|---|---|---|---|---|---|
| | $k_6$ (years$^{-1}$) | $r_6$ | | Decay time (days) | | |
| | | | | 50% | 90% | 95% |
| *Corydalis cava* | 6.4 | − 0.68 | a | 28 | 56 | 63 |
| *Anemone ranunculoides* | 6.9 | − 0.74 | a | 28 | 56 | 84 |
| *Anemone nemorosa* | 6.2 | − 0.75 | ab | 28 | 70 | 91 |
| *Adoxa moschatellina* | 4.7 | − 0.54 | cd | 14 | 63 | 63 |
| *Ficaria verna* | 5.4 | − 0.63 | bc | 28 | 56 | 98 |
| *Paris quadrifolia* | 5.0 | − 0.60 | cd | 21 | 49 | 84 |
| *Maianthemum bifolium* | 1.4 | − 0.57 | fg | 56 | - | - |
| *Aegopodium podagraria*L | 3.2 | − 0.87 | e | 98 | 203 | - |
| *Mercurialis perennis* | 2.1 | − 0.87 | f | 140 | - | - |
| *Aegopodium podagraria*S | 0.2 | − 0.18 | h | 322 | - | - |
| *Stachys sylvatica* | 0.9 | − 0.84 | gh | 203 | - | - |
| *Asarum europaeum* | 4.1 | − 0.58 | de | 35 | 63 | - |
| *Urtica dioica* | 1.1 | − 0.82 | fgh | 203 | - | - |
| *Galeodbolon luteum* | - | - | - | 77 | - | - |
| *Alliaria petiolata* | 0.9 | − 0.78 | gh | - | - | - |
| *Fraxinus excelsior* | 0.8 | − 0.80 | gh | 196 | - | - |
| *Carpinus betulus* | 0.5 | − 0.86 | gh | - | - | - |
| *Corylus avellana* | 0.3 | − 0.76 | gh | - | - | - |
| *Acer pseudoplatanus* | 0.4 | − 0.82 | gh | - | - | - |
| *Quercus robur* | 0.2 | − 0.79 | h | - | - | - |

*Aegopodium podagraria*S - *Aegopodium podagraria* shoots; *Aegopodium podagraria*L - *Aegopodium podagraria* leaves

## 4 Discussion

Our hypotheses were only partially supported by the results of the experiment. We found statistically significant differences in litter decomposition among the plant species studied. Our study revealed that: (1) decomposition of herbaceous plants (including stems) was not always completed in less than a year, (2) spring ephemerals had higher decomposition rates than species which dominate the understory during summer and autumn, and (3) decomposition rates of herb species biomass were not always higher than that of tree leaves.

Few published papers on biomass and nutrient cycling of forests have addressed the dynamics of herbaceous material decomposition. Most of them suggest that decay rates ($k$) for herbaceous plants are higher than one, being in some cases considerably higher (Muller 2014). Exceptions are tundra vegetation dominated by mosses, sedges, or woody understory species (Hobbie 1996), and bulked herbaceous litter, dominated by ferns and woody understory species in a mixed hardwood stand in Canada (MacLean and Wein 1978). This is not in accordance with our study. In most cases, decomposition of herb litter biomass was completed much faster than within 1 year. During our experiment (ca. 6 months) decomposition

**Table 3** Linear mixed model analysis of plant functional group effects on decomposition. Time of exposure in the field (duration of the experiment), mean temperature during 6 months of the experiment, and mean total daily precipitation during 6 months of the experiment were fixed effects and plant species were random effects (random intercepts and slopes among species) on the decay process

| Variable | Sum of squares | Mean square | NumDF | DenDF | $F$ | Pr(> $F$) |
|---|---|---|---|---|---|---|
| Functional group of plants | *1017* | *338.93* | *3* | *10.6* | *7.3* | *0.006* |
| Time of exposure in the field | *92,448* | *2254.82* | *41* | *594.9* | *48.3* | *< 0.0001* |
| Mean temperature | 1 | 0.68 | 1 | 10.5 | 0.01 | 0.91 |
| Mean total daily precipitation | *259* | *259.28* | *1* | *10.5* | *5.5* | 0.04 |
| Random effect–intercept | SD = 3.75 | Random effect–slope | SD = 0.07 | | | |

Parameters in italics are statistically significant

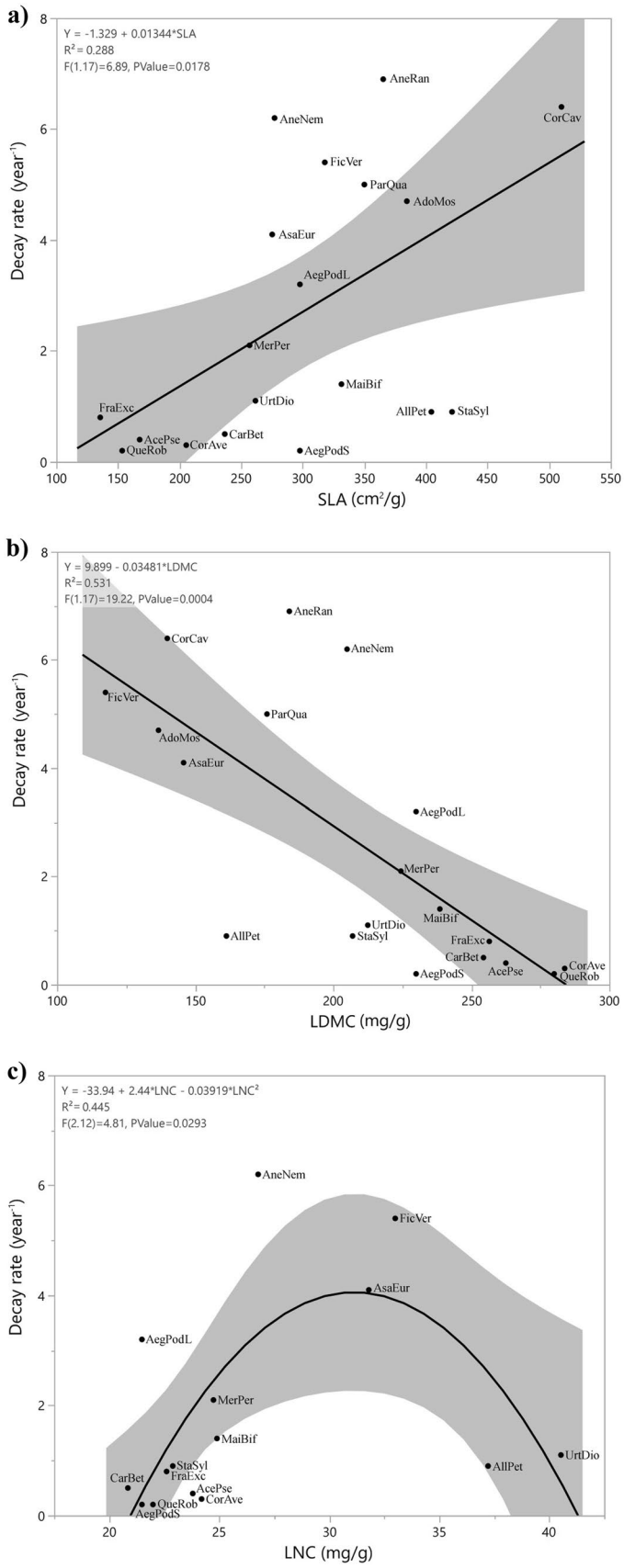


**Fig. 3** Results of regressions of the decay rate (decay constant after 6 months of decay) of each litter species with functional traits: **a** SLA vs. decay rates; **b** LDMC vs. decay rates; **c** LNC vs. decay rates. The gray area shows 95% confidence intervals for the predicted values. Explanations of abbreviations: AcePse - *Acer pseudoplatanus;* AdoMos - *Adoxa moschatellina*; AegPodL - *Aegopodium podagraria* leaves; AegPodS - *Aegopodium podagraria* shoots; AllPet - *Alliaria petiolata*; AneNem - *Anemone nemorosa*; AneRan - *Anemone ranunculoides*; AsaEur - *Asarum europaeum*; CarBet - *Carpinus betulus*; CorAve - *Corylus avellana*; CorCav - *Corydalis cava*; FicVer - *Ficaria verna*; FraExc - *Fraxinus excelsior*; GalLut - *Galeobdolon luteum*; MaiBif - *Maianthemum bifolium*; MerPer - *Mercurialis perennis*; ParQua - *Paris quadrifolia*; QueRob - *Quercus robur*; StaSyl - *Stachys sylvatica*; UrtDio - *Urtica dioica*

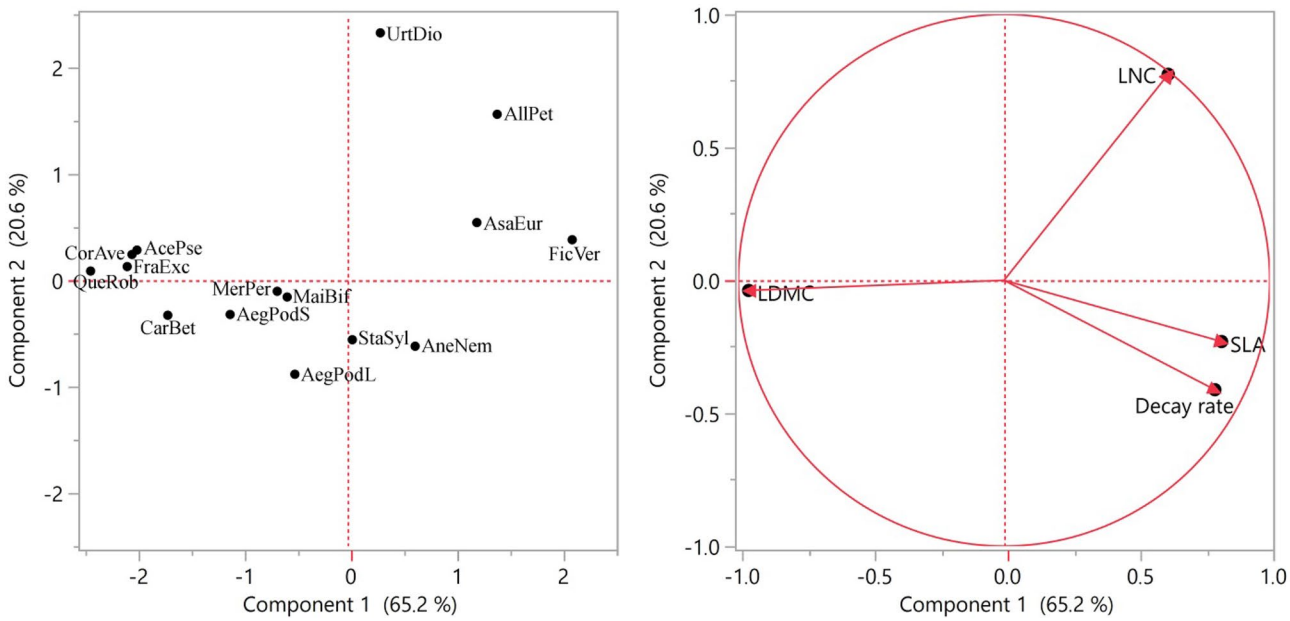


**Fig. 4** Results of principal components analysis. Explanations of abbreviations: AcePse - *Acer pseudoplatanus*; AdoMos - *Adoxa moschatellina*; AegPodL - *Aegopodium podagraria* leaves; AegPodS - *Aegopodium podagraria* shoots; AllPet - *Alliaria petiolata*; AneNem - *Anemone nemorosa*; AneRan - *Anemone ranunculoides*; AsaEur - *Asarum europaeum*; CarBet - *Carpinus betulus*; CorAve - *Corylus avellana*; CorCav - *Corydalis cava*; FicVer - *Ficaria verna*; FraExc - *Fraxinus excelsior*; GalLut - *Galeobdolon luteum*; MaiBif - *Maianthemum bifolium*; MerPer - *Mercurialis perennis*; ParQua - *Paris quadrifolia*; QueRob - *Quercus robur*; StaSyl - *Stachys sylvatica*; UrtDio - *Urtica dioica*

rates of six species included in the spring ephemeral group reached $k$ values in the range of 4.7–6.9, while mid-summer senescing summer-green plants (three species) ranged from 0.2–1.4, autumn-senescing summer-green plants (four species) ranged from 0.9 to 3.2, and winter-green *A. europaeum* reached 4.1. According to Muller (2014), the decomposition

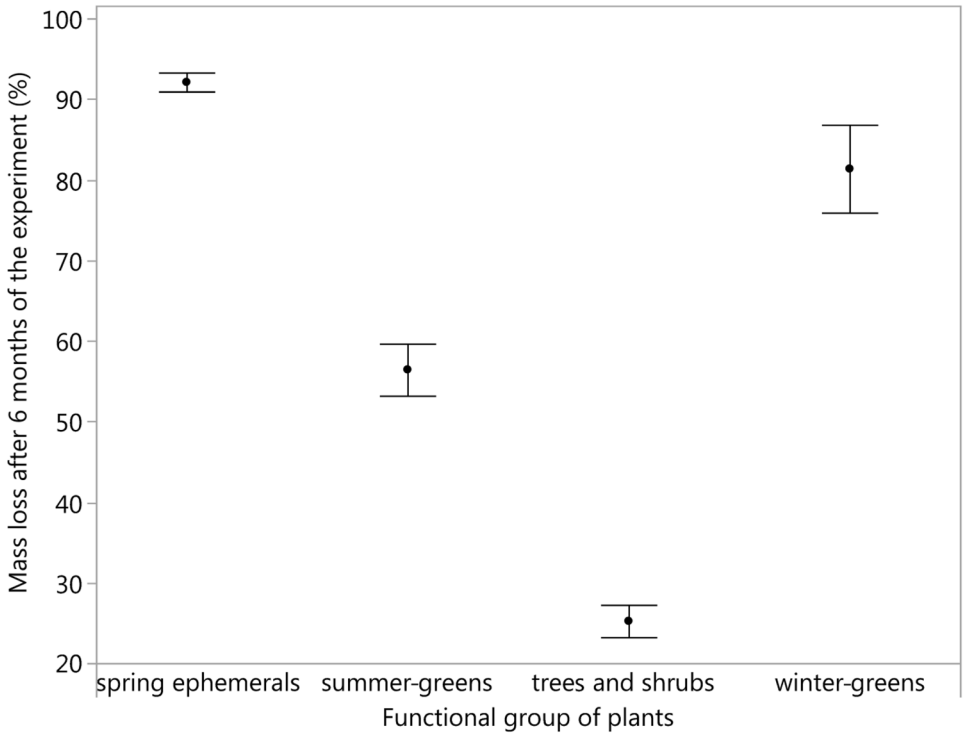


**Fig. 5** Differences among functional groups of plants based on the Tukey HSD test ($p < 0.0001$)

rates of herbaceous species during 12 months of field exposure reached values in the range of 0.61–3.31. This was likely related to the species taken into account in Muller's (2014) review, as only two species are in common between that study and our study, namely, *A. nemorosa* and *M. perennis*. Data about these species were obtained from Wise and Shaefer (1994), who found statistically significant differences between decomposition rates of these species connected with three litter bag mesh sizes used in their experiment. In the treatment similar to ours (1 mm mesh size), they found 12-month decomposition constants $k$ of 13.99 and 10.58 for *A. nemorosa* and *M. perennis*, respectively. Our study had 6-month decomposition constants of 6.2 and 2.1 for *A. nemorosa* and *M. perennis*, respectively. However, the results cited were obtained in beech forests on mull soils, where mean annual temperatures during the period of the study, were 6, 6.7, and 6 °C, and mean annual precipitation was 706, 726, and 717 mm. We conducted our studies in drier and warmer conditions, which may have significantly influenced $k$ constants since mean temperature and precipitation are key factors determining decomposition rate (Aerts 1997; Hobbie 1996; Trofymow et al. 2002). In contrast, Halabuk and Gerhátová (2011) in SW Slovakia found results similar to our study, in similar environmental and climatic conditions (an ecotone of the hornbeam-oak forest situated in a region with a mean annual temperature of 9.3 °C and total annual precipitation of 580 mm). They found decomposition rates of $k = 2.41$ for *M. perennis* and $k = 2.44$ for *A. petiolata* during a 324-day experiment. In an experiment conducted in North America by Rodgers et al. (2008), green rosettes of *A. petiolata* decomposed in about 6 months, and senesced litter of *A. petiolata* decomposed in about one year. These results are very close to our 0.9 decomposition rate for *A. petiolata*, although those studies were conducted at five different sites including deciduous, coniferous, and mixed forests. In our study, decomposition constants of *A. petiolata* and blooming shoots of *A. podagraria* were lower than one. These species (especially *A. podagraria* blooming shoots) decomposed as slowly as tree leaves during our experiment. These two plant species had the highest contributions of stems to aboveground biomass among the species studied (Paź-Dyderska et al. 2020). For these two species, the decomposition rate visibly decreased during decomposition. In our opinion, this is connected with the differences in organ-specific decomposition rate $k$. Every sample is a mix of leaves and shoots in proportions similar to what occurs in specimens in the field. After the first stage of decomposition, when leaves have decomposed, the process slows down, and rates of mass losses between dates of sample collection are stable or even decreasing. Biomass allocation to organs that differ in the way that they decompose (e.g., stems and leaves) affects decomposition itself (Hobbie 1996). However, this has not been confirmed by studies of Bumb et al. (2018), which showed the same leaf and shoot decomposability of sixteen Mediterranean species. More in-depth studies are needed to understand how the decomposability of different plant organs is correlated and if these processes are controlled by the same functional traits (Freschet et al. 2012; Hobbie 2015). The duration of our experiment was only half of a year for most of the species. In the case of spring ephemerals, this was enough time to complete decomposition, but in other cases, we considered only part of the process that included decay of the labile part of the plant material.

Cornwell et al. (2008) found that decomposition and nutrient cycling processes across biomes were affected by the functional group of plant species. This has been described for a wide range of temperate plant species (Cornelissen and Thompson 1997), in Alaskan tundra (Hobbie 1996), lowland tropical forest (Santiago 2010), Mediterranean forests (De la Riva et al. 2019), rainforests (Jackson et al. 2013), experimental grasslands (Scherer-Lorenzen 2008), old-fields (Kazakou et al. 2006), alpine meadow (Jiang et al. 2013), alpine snow beds (Carbognani et al. 2014), and post-mining sites (Rawlik et al. 2019). There is little information available about tradeoffs between plant traits (Kleyer et al. 2018), and between plant functional traits and decomposition, in forest herb species. Plant functional groups were also connected with similar SLA, LDMC, and LNC (Cornwell et al. 2008). It was previously reported that these traits have an "after-life effect" on decomposition (Freschet et al. 2010, 2012; Jackrel and Wootton 2015; Santiago 2010). Freschet et al. (2012) reported that structural (lignin, DMC) and chemical (N) traits together were better predictors for decomposition rates of several high-turnover organs (leaves, fine stems, and reproductive parts) than structural traits alone, whereas leaf nitrogen content influenced leaf decomposition, but this relationship was not apparent in any other organs. Results of our studies focused on the decomposition of aboveground biomass of herbaceous plants, confirmed patterns reported by Freschet (2012). The best predictor for decomposition rates in our studies was LDMC. The results obtained were similar to those reported in previous studies, although we decided to use values obtained from global databases of functional traits. This method has limitations, as it is known that measurements of traits and decay rates on the same species, conducted at different sites, can potentially add noise to the analyses (Zanne et al. 2015).

In temperate deciduous forests, light availability is a major factor that determines leaf structure, with spring ephemeral species exhibiting nutrient-rich leaves with higher SLA relative to other herb species groups or late-successional canopy tree species (Jagodziński et al. 2016; Muller 2014; Rothstein and Zak 2001). Therefore, leaf traits associated with canopy openness determine litter decomposition rates. This is in accordance with our results showing decreasing decay rates in this order: spring ephemerals (high N concentration, high SLA), mid-summer, and autumn-senescing summer-green

herbaceous species. Our study further confirmed that fast decomposition rates were related to fast growth and can be generally predicted from functional plant group. Higher decomposition rates for spring ephemerals are supposedly connected with their traits as well as with ecological function in forest ecosystems. Results of previously published papers suggest that the spring ephemeral group of plants act as a "vernal dam" for nutrients. According to this theory spring ephemerals, by nutrient uptake and storage before canopy leaf-out, prevent nutrient losses by spring flow of soil water (Muller and Bormann 1976; Muller 2014; Rothstein and Zak 2001). Fast decomposition of the litter of this phenological group of herbaceous species may be the main part of their function in nutrient cycling, because it allows a huge pool of nutrients to be returned to the soil, making them available for trees at the time of their most intensive physiological activity. The remaining herb species with lower decomposition rates can be very important for nutrient storage in plant biomass. However, a broader study is needed to understand the function of herbaceous species in nutrient cycling in deciduous forest systems.

Most recent research results suggest that decomposition of tree leaf litter requires longer than one year for completion. Moreover, for leaves of woody species, decomposition rates have most often been reported in the range from 0.3 to 0.8 (see Muller 2014 and literature cited therein). This is generally in accordance with our studies showing that ca. 6-month decomposition rates of four oak-hornbeam tree species were in the range cited above (*F. excelsior* $k = 0.8$, *C. betulus* $k = 0.5$, *A. pseudoplatanus* $k = 0.4$, *C. avellana* $k = 0.3$, and *Q. robur* $k = 0.2$).

Our results are similar to previous estimates of tree foliage decomposition in areas of similar climatic and environmental conditions, although the variability of values is high because decay processes are sensitive to even small microclimatic and climatic fluctuations. In the experiment provided by Dziadowiec (1987) in an oak-linden-hornbeam forest in the Białowieża Forest, 65% of the initial biomass of *A. pseudoplatanus* and 36.5% of *Q. robur* leaves decomposed after 1 year in the field. This author also reported similar results from an oak-hornbeam forest near Toruń in Poland (Dziadowiec 1990). After 1 year of the experiment, 46% of the initial biomass of *C. betulus* leaf litter and 36% of *Q. robur* leaves decomposed. For those species, we found 43.3% and 20.2% of biomass decomposed, respectively, at the same time. Faster decomposition in Białowieża can be connected with bigger litter bag mesh size (2 mm) and more humid climatic conditions (Dziadowiec 1987). Hobbie et al. (2006) reported decomposition results for *Q. robur* leaves in central Poland similar to our results ($k$ range after 1 year of exposure in the field of 0.21–0.24 vs. 0.23). However, in the case of the experiment cited above, decomposition constants were lower than in our experiment for *A. pseudoplatanus* (0.29 vs. 0.47) and *C. betulus* (0.30 vs. 0.54). Although several studies described tree leaf litter decomposition rates much higher than for herbaceous litter, research focused on oak-hornbeam forest tree species from other parts of those species geographical distributions are still limited (Jacob et al. 2009; Slade and Riutta 2012).

One of the key certainties in decomposition in forest ecosystems is the faster decomposition of herb litter than tree leaf biomass (Halabuk and Gerhátová 2011; Mayer 2008; Muller 2014), as most reported tree foliage has decomposition rates of $k < 1$ and most herbaceous litter of $k > 1$. We did not find significant differences between the decomposition of tree leaves and summer-green herb species after six months of the study. This is particularly important because it shows that not all herb species litter is part of the labile litter fraction. Some parts of those plant materials should be categorized as more resistant to decomposition—this seems to be a fact for species with a higher allocation of biomass to stems or with more lignified stems. In contrast, our study indicated that *F. excelsior* leaf litter can be included in the labile pool of litter which decomposes and returns nutrients to available nutrient pools quickly. Unfortunately, our studies focused on the first stages of the decomposition process, and differences between decomposition of herb and tree species foliage may be more visible in the later stages of decomposition.

Previous studies recognized that climatic factors such as mean annual temperature, mean annual precipitation and annual actual evapotranspiration regulate litter decomposition rate (Berg and McClaugherty 2014; Zhang et al. 2008). Generally, higher temperatures and precipitation stimulate mass loss during decomposition (Hobbie 1996; Mueller et al. 2016; Trofymow et al. 2002). In this context, reported differences in decomposition rates of the species we studied can be partly explained by changes in microclimatic conditions, and by their life history traits. At the same time, climate conditions have impacts on both litter quality (Coûteaux et al. 1995) and plant traits. Moreover, it is difficult to separate the influence of climate from the influence of litter quality on decomposition processes (Berg and McClaugherty 2014). As summarized by Aerts (1997), climate, litter chemistry, and litter decomposition are connected by a triangular relationship. As we mentioned above (introduction), we found differences between average air temperatures, ground temperatures, and total precipitation during the field incubation of litter for different groups of plants, e.g., during the 6-month experiment for the 1st group of plants mean ground temperature was more than 10 °C higher than during the 6-month experiment

for tree leaves. Total precipitation also differed for the periods of field experiments for different groups of plants. Our results indicated that microclimatic conditions stimulated decomposition when spring ephemeral litter decays in forest ecosystems and precipitation had a statistically significant impact on the decay process. Our study seemed to suffer because different times of incubation, which made it impossible to disentangle the influences of different climatic conditions and litter quality on the decomposition process. However, our studies aimed to find real, biological rates of decomposition of the species studied. Generally, we conducted our study with weather conditions similar to average conditions of the last decade (mean annual temperature: 9.1 °C in 2011–2013 vs. 9.2 in 2001–2010 and mean annual precipitation: 573 mm vs. 535 in the same periods of time, respectively). Moreover, we included microclimatic conditions as fixed effects into linear mixed models, to assess the impact of technical limitations of our studies on the results obtained.

In our studies, we make an effort to find real biological rates of decomposition of the species studied. However, we are aware of the limitations of research methods used in decomposition research. Kurz-Besson et al. (2005) compared the results of litter bag and direct observation methods and found higher mass losses measured by litter bags than by direct observation. These results were in agreement with previous results (De Santo et al. 1993) and were probably connected with a higher and more stable moisture content of litter in litter bags than in surrounding litter. In light of these findings, our results could overestimate decomposition rates; however, the studies mentioned took place with different material (Scots pine needles) and habitat. On the other hand, taking into account the results obtained by Bradford et al. (2002), our results could underestimate decomposition rates. According to these results, using litter bags of 1 mm mesh size decreased decomposition by 20% at 35 days because of macrofauna exclusion. Despite these limitations, the litter bag method is highly repeatable, relatively inexpensive, and widely used in decomposition studies (Harmon et al. 1999).

## 5 Conclusions

1. The decomposition process was dependent on the functional group of plants, time of exposure in the field, species identity, and precipitation.
2. Spring ephemerals had higher decomposition rates than species that dominate the understory of oak-hornbeam forest during summer and autumn.
3. The decomposition of herbaceous plants was not always completed in less than a year—not all litter of herbaceous species is part of the labile litter fraction.
4. Functional traits of leaves of herbaceous plants were correlated with their decomposition. The best predictor for decomposition rates in our studies was leaf dry matter content (LDMC).

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**Data availability** The datasets generated and analyzed during the current study are available in the FigShare repository, https://doi.org/10.6084/m9.figshare.12987410.v3.

## Appendix

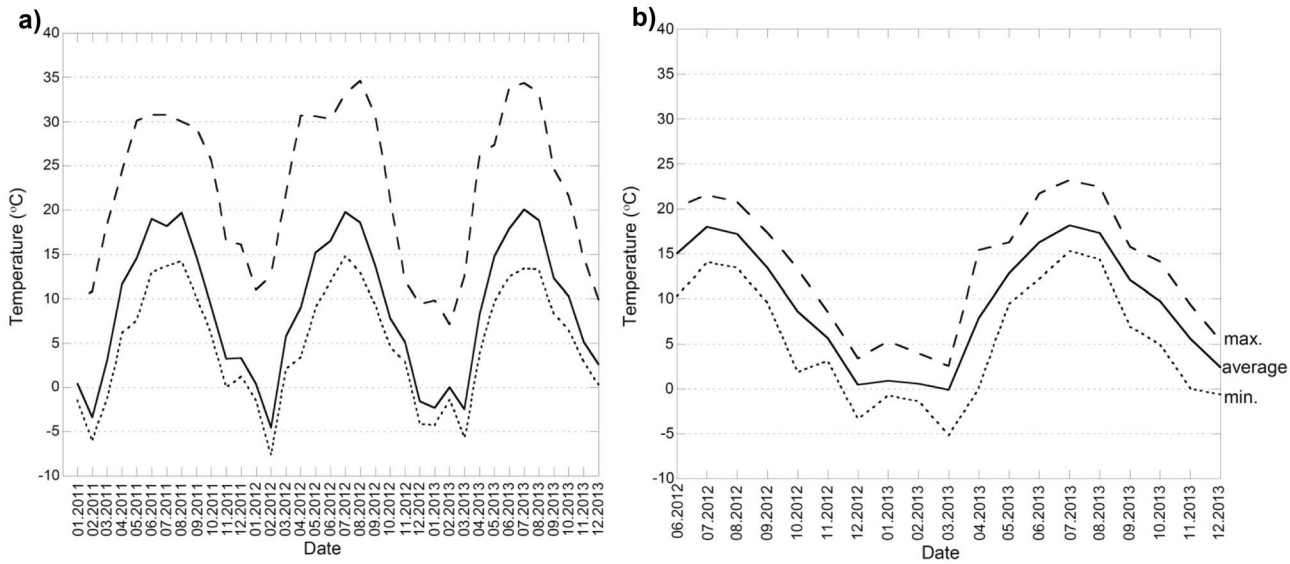


**Fig. 6** Temperatures during the course of the research. **a** Air temperature data from the meteorological station in Kórnik including the year prior to start of the research and the 2 years during the research project. **b** Temperature of the ground surface on sample plots measured by HOBO data-loggers

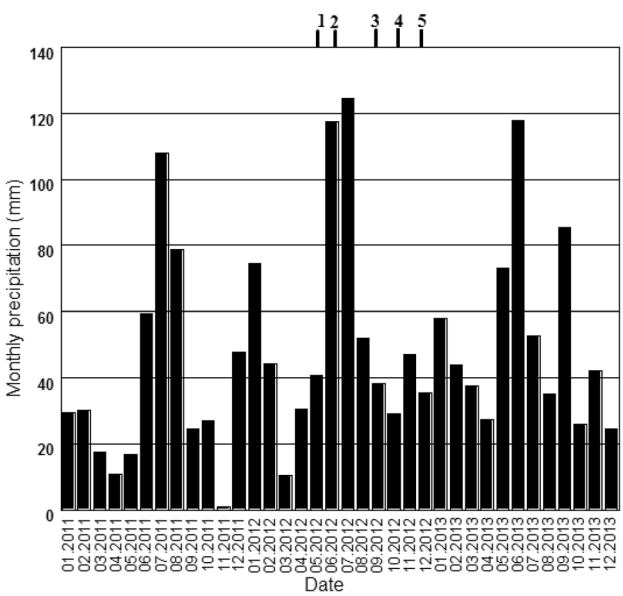


**Fig. 7** Monthly precipitation during the course of the research. Data was from the meteorological station in Kórnik including the year prior to start of the research and the 2 years during the research project: 1- beginning of the experiment for the first group of plants; 2- beginning of the experiment for the second group of plants; 3- beginning of the experiment for the third group of plants; 4- beginning of the experiment for the fourth group of plants; 5- beginning of the experiment for the fifth group of plants

**Table 4** Meteorological characteristics during the experiment. Ranges and mean values were given for 2- and 6-month periods from the beginning of the experiments, where leaf litter in litterbags was placed in the forest (5 terms)

| Date | Air temperature (°C) at the meteorological station | | | | | | | | Ground temperature (°C) in the forest | | | | | | | | Total daily precipitation (mm) at the meteorological station | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | During 2 months | | | | During 6 months | | | | During 2 months | | | | During 6 months | | | | During 2 months | | | | During 6 months | | | |
| | Range | Mean | SD | SE | Range | Mean | SD | SE | Range | Mean | SD | SE | Range | Mean | SD | SE | Range | Mean | SD | SE | Range | Mean | SD | SE |
| 26.05.2012 | 10.0–24.4 | 17.5 | 3.5 | 0.5 | − 1.8–24.7 | 13.9 | 6.0 | 0.4 | 10.3–21.1 | 16.0 | 2.8 | 0.4 | 1.9–21.6 | 13.3 | 4.8 | 0.4 | 0–40.5 | 4.0 | 7.6 | 1.0 | 0–40.5 | 2.2 | 5.0 | 0.4 |
| 23.06.2012 | 14.4–24.7 | 19.1 | 3.1 | 0.4 | − 9.9–24.7 | 11.3 | 8.1 | 0.6 | 13.8–21.6 | 17.4 | 2.4 | 0.3 | − 3.3–21.6 | 11.3 | 6.3 | 0.5 | 0–22.2 | 3.0 | 5.4 | 0.7 | 0–22.2 | 1.8 | 3.6 | 0.3 |
| 01.09.2012 | 1.4–19.1 | 11.3 | 3.5 | 0.5 | − 9.9–19.1 | 3.8 | 6.8 | 0.5 | 3.6–17.3 | 11.5 | 2.8 | 0.4 | − 3.3–17.3 | 4.9 | 5.2 | 0.4 | 0–10.7 | 1.2 | 2.4 | 0.3 | 0–13.4 | 1.5 | 2.3 | 0.2 |
| 27.10.2012 | -9.9–8.7 | 1.6 | 4.8 | 0.6 | − 10.8–16.8 | 1.0 | 5.6 | 0.4 | − 3.3–8.5 | 3.4 | 2.9 | 0.4 | − 5.2–15.4 | 2.5 | 3.8 | 0.3 | 0–13.4 | 1.2 | 2.2 | 0.3 | 0–13.4 | 1.7 | 2.4 | 0.2 |
| 08.12.2012 | -9.9–6.5 | -1.6 | 5.2 | 0.7 | − 10.8–25.7 | 4.8 | 8.1 | 0.6 | − 3.3–5.3 | 0.8 | 1.7 | 0.2 | − 5.2–21.7 | 5.4 | 5.9 | 0.4 | 0–8.6 | 1.9 | 2.2 | 0.3 | 0–24.7 | 2.3 | 3.3 | 0.3 |

**Table 5** Description of study site

| Main plant communities | *Galio sylvatici-Carpinetum typicum*, *Galio sylvatici-Carpinetum corydaletosum* |
|---|---|
| Most common herb species | *Adoxa moschatellina*, *Anemone nemorosa*, *A. ranunculoides*, *Aegopodium podagraria*, *Asarum europaeum*, *Corydalis cava*, *Ficaria verna*, *Galeobdolon luteum*, *Milium effusum* |
| Most common tree species | *Fraxinus excelsior*, *Quercus robur*, *Carpinus betulus* |
| Most common shrub species | *Corylus avellana* |
| Mean height of trees | 20.2 m (the highest trees reach 31.8 m) |
| Density of trees | 230 specimens per hectare |
| Soil type | Gleyic Umbrisol (Arenic), Epidistric Gleyic Cambisol (Humic, Arenic) |

**Table 6** Physicochemical properties of the soil on the sample plot

| Profile no. | Soil horizon | Depth (cm) | Percentage content of fractions with particle diameter (mm) | | | Granulometric group | $C_{org}$ | $N_{tot}$ | C/N | Humus content | pH reaction | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Sand (0.05–2 mm) | Silt (0.002–0.05 mm) | Clay (< 0.002 mm) | | % | | | % | In $H_2O$ | In KCl |
| 1 | Ol | 3–1(0) | - | - | - | - | 43.191 | 1.686 | 25.6 | 74.46 | 5.45 | 5.02 |
| | Ofh | 1–0 | - | - | - | - | 42.285 | 1.675 | 25.2 | 72.90 | 5.98 | 5.51 |
| | Au | 0–30 | 77 | 18 | 5 | LoSa | 2.558 | 0.248 | 10.3 | 4.41 | 4.31 | 3.47 |
| | AC | 30–48 | 83 | 14 | 3 | LoSa | 0.598 | 0.057 | 10.5 | 1.03 | 4.95 | 3.93 |
| | C1g | 48–61 | 89 | 6 | 5 | Sa | 0.116 | 0.008 | 14.5 | 0.20 | 5.79 | 4.26 |
| | C2g | 61–150 | 92 | 7 | 1 | Sa | 0.065 | 0.006 | 10.8 | 0.11 | 6.90 | 5.18 |
| 2 | Ol | 3–1(0) | - | - | - | - | 45.920 | 1.444 | 31.8 | 79.17 | 4.90 | 4.47 |
| | Ofh | 1–0 | - | - | - | - | 34.422 | 1.400 | 24.6 | 59.34 | 5.65 | 5.12 |
| | A | 0–26 | 77 | 19 | 4 | LoSa | 1.353 | 0.092 | 14.7 | 2.33 | 4.33 | 3.46 |
| | Bw | 26–60 | 81 | 12 | 7 | LoSa | 0.463 | 0.044 | 10.5 | 0.80 | 5.01 | 3.95 |
| | BC | 60–80 | 89 | 7 | 4 | Sa | 0.145 | 0.013 | 11.2 | 0.25 | 6.02 | 4.32 |
| | Cg | 80–150 | 96 | 3 | 1 | Sa | 0.116 | 0.011 | 10.5 | 0.20 | 6.83 | 5.27 |

LoSa - loamy sand; Sa - sand; $C_{org}$ (%) - organic carbon content determined using the Tiurin method (in accordance with the PN-ISO 14235:2003 standard); $N_{tot}$ (%) - total nitrogen content determined using the modified Kjeldahl method (in accordance with the PN:ISO 11261:2002 standard); C:N - $C_{org}$ to $N_{tot}$ ratio; pH $H_2O$, measured in 1:5 soil suspension in $H_2O$ obtained by the potentiometric method in distilled water (in accordance with the ISO 10390:2005 standard)

**Table 7** Decomposition (percentage of initial mass remaining) during the time of the experiment

| Interval (days) | Species | Mean rest of litter (%) | SE (%) | Results of ANOVA |
|---|---|---|---|---|
| 7 | CorCav | 13.82 | 1.44 | a |
| | AneNem | 9.19 | 1.07 | abcd |
| | AneRan | 12.88 | 2.29 | ab |
| | FicVer | 12.08 | 1.35 | ab |
| | AsaEur | 6.7 | 1.07 | bcd |
| | ParQua | 11.59 | 1.26 | abc |
| | AdoMos | 13.7 | 2.57 | ab |
| | MaiBif | 13.76 | 0.88 | a |
| | AegPodS | 13.77 | 1.36 | a |
| | AllPet | 8.16 | 0.83 | abcd |
| | MerPer | 4.68 | 0.66 | d |
| | UrtDio | 6.91 | 0.96 | abcd |
| | AegPodL | 11.33 | 1.83 | abc |
| | StaSyl | 5.29 | 1.03 | cd |
| | GalLut | 9.76 | 1.49 | abcd |
| 14 | CorCav | 16.53 | 2.87 | def |
| | AneNem | 10.68 | 2.33 | efg |
| | AneRan | 15.89 | 0.96 | def |
| | FicVer | 19.35 | 3.92 | cde |
| | AsaEur | 27.73 | 1.92 | bc |
| | ParQua | 39.63 | 4.04 | ab |
| | AdoMos | 51.36 | 2.68 | a |
| | MaiBif | 23.27 | 1.2 | cd |
| | AegPodS. | 23.26 | 2.21 | cd |
| | AllPet | 16.09 | 1.61 | cdef |
| | MerPer | 7.97 | 1.07 | fgh |
| | UrtDio | 9.38 | 1.33 | fg |
| | AegPodL | 9.9 | 0.91 | efg |
| | StaSyl | 7.73 | 0.98 | fgh |
| | GalLut | 15.49 | 2.49 | def |
| | CorAve | 5.1 | 0.63 | gh |
| | FraExc | 6.66 | 1.09 | gh |
| | CarBet | 4.2 | 0.36 | gh |
| | AcePse | 5.03 | 1.46 | gh |
| | QueRob | 2.44 | 0.18 | h |
| 21 | CorCav | 48.5 | 6.35 | abc |
| | AneNem | 36.1 | 3.43 | cdef |
| | AneRan | 39.79 | 4.53 | cde |
| | FicVer | 45.61 | 5.33 | bcd |
| | AsaEur | 29.34 | 5.91 | def |
| | ParQua | 58.7 | 1.74 | ab |
| | AdoMos | 66.21 | 2.00 | a |
| | MaiBif | 25.21 | 1.67 | efg |
| | AegPodS | 26.44 | 2.92 | efg |
| | AllPet | 21.28 | 1.71 | fgh |
| | MerPer | 8.00 | 1.51 | i |
| | UrtDio | 10.85 | 1.22 | hi |
| | AegPodL | 12.7 | 0.87 | ghi |
| | StaSyl | 10.26 | 1.13 | hi |
| | GalLut | 22.54 | 1.85 | efgh |
| 28 | CorCav | 63.94 | 3.15 | abc |
| | AneNem | 56.04 | 5.61 | bcd |
| | AneRan | 75.29 | 2.25 | a |

**Table 7** (continued)

| Interval (days) | Species | Mean rest of litter (%) | SE (%) | Results of ANOVA |
|---|---|---|---|---|
| | FicVer | 71.49 | 4.65 | ab |
| | AsaEur | 48.82 | 4.88 | cde |
| | ParQua | 62.16 | 5.34 | abc |
| | AdoMos | 71.63 | 2.86 | ab |
| | MaiBif | 35.56 | 6.6 | efg |
| | AegPodS | 31.13 | 2.92 | efgh |
| | AllPet | 16.63 | 2.81 | hijk |
| | MerPer | 18.76 | 1.75 | ghijk |
| | UrtDio | 20.67 | 2.23 | ghij |
| | AegPodL | 30.24 | 3.56 | fghi |
| | StaSyl | 14.47 | 1.25 | ijkl |
| | GalLut | 39.05 | 2.45 | def |
| | CorAve | 8.09 | 0.7 | jkl |
| | FraExc | 14.69 | 2.24 | hijkl |
| | CarBet | 7.08 | 0.51 | kl |
| | AcePse | 10.97 | 1.12 | jkl |
| | QueRob | 4.49 | 0.74 | l |
| 35 | CorCav | 77.45 | 4.55 | ab |
| | AneNem | 59.57 | 5.85 | bcd |
| | AneRan | 81.65 | 3.66 | a |
| | FicVer | 71.47 | 5.00 | abc |
| | AsaEur | 51.4 | 7.66 | cde |
| | ParQua | 76.75 | 2.72 | ab |
| | AdoMos | 82.39 | 6.93 | a |
| | MaiBif | 38.07 | 2.37 | defg |
| | AegPodS | 29.63 | 3.94 | efgh |
| | AllPet | 18.26 | 0.56 | gh |
| | MerPer | 21.76 | 1.52 | fgh |
| | UrtDio | 17.21 | 1.75 | h |
| | AegPodL | 28.74 | 1.28 | fgh |
| | StaSyl | 16.93 | 0.6 | h |
| | GalLut | 41.68 | 2.49 | def |
| 42 | CorCav | 80.76 | 2.28 | ab |
| | AneNem | 69.04 | 3.91 | bc |
| | AneRan | 87.62 | 1.00 | a |
| | FicVer | 78.80 | 1.71 | ab |
| | AsaEur | 60.31 | 6.83 | c |
| | ParQua | 85.56 | 2.68 | a |
| | AdoMos | 86.12 | 4.3 | a |
| | MaiBif | 42.52 | 2.84 | d |
| | AegPodS | 29.85 | 2.73 | def |
| | AllPet | 21.48 | 1.78 | fg |
| | MerPer | 18.67 | 0.86 | fg |
| | UrtDio | 20.00 | 2.26 | fg |
| | AegPodL | 26.08 | 1.57 | ef |

**Table 7** (continued)

| Interval (days) | Species | Mean rest of litter (%) | SE (%) | Results of ANOVA |
|---|---|---|---|---|
| | StaSyl | 17.55 | 1.12 | fg |
| | GalLut | 39.19 | 3.7 | de |
| | CorAve | 11.94 | 1.46 | gh |
| | FraExc | 18.38 | 1.4 | fg |
| | CarBet | 11.11 | 1.01 | gh |
| | AcePse | 12.77 | 1.12 | gh |
| | QueRob | 6.2 | 0.37 | h |
| 49 | CorCav | 87.55 | 3.2 | a |
| | AneNem | 86.8 | 3.06 | a |
| | AneRan | 89.25 | 2.31 | a |
| | FicVer | 87.52 | 2.55 | a |
| | AsaEur | 68.41 | 7.72 | a |
| | ParQua | 90.63 | 2.75 | a |
| | AdoMos | 88.91 | 6.48 | a |
| | MaiBif | 40.56 | 10.03 | b |
| | AegPodS | 33.71 | 1.66 | bc |
| | AllPet | 12.09 | 2.14 | c |
| 56 | CorCav | 94.19 | 1.99 | a |
| | AneNem | 89.33 | 1.77 | ab |
| | AneRan | 93.83 | 0.60 | a |
| | FicVer | 91.12 | 1.55 | ab |
| | AsaEur | 79.18 | 7.19 | b |
| | ParQua | 89.31 | 4.23 | ab |
| | AdoMos | 89.44 | 3.67 | ab |
| | MaiBif | 56.56 | 3.45 | c |
| | AegPodS | 33.47 | 1.23 | de |
| | AllPet | 23.77 | 2.03 | efg |
| | MerPer | 25.37 | 3.06 | efg |
| | UrtDio | 19.82 | 2.62 | efgh |
| | AegPodL | 30.56 | 1.34 | def |
| | StaSyl | 21.32 | 1.57 | efg |
| | GalLut | 45.75 | 2.69 | cd |
| | CorAve | 14.17 | 0.90 | fgh |
| | FraExc | 24.05 | 4.22 | efg |
| | CarBet | 13.99 | 1.11 | fgh |
| | AcePse | 12.17 | 1.15 | gh |
| | QueRob | 6.4 | 0.54 | h |
| 63 | CorCav | 95.46 | 0.91 | a |
| | AneNem | 88.22 | 1.97 | a |
| | AneRan | 90.95 | 2.99 | a |
| | FicVer | 94.23 | 1.10 | a |
| | AsaEur | 90.13 | 2.52 | a |
| | ParQua | 94.27 | 1.50 | a |
| | AdoMos | 95.87 | 1.58 | a |
| | MaiBif | 53.80 | 3.28 | b |
| | AegPodS | 33.50 | 5.48 | cde |

**Table 7** (continued)

| Interval (days) | Species | Mean rest of litter (%) | SE (%) | Results of ANOVA |
|---|---|---|---|---|
| | AllPet | 17.81 | 2.13 | e |
| | MerPer | 32.96 | 3.23 | cde |
| | UrtDio | 29.64 | 5.90 | cde |
| | AegPodL | 34.40 | 2.91 | cd |
| | StaSyl | 25.34 | 2.69 | de |
| | GalLut | 47.98 | 5.62 | bc |
| 70 | CorCav | 94.11 | 0.85 | ab |
| | AneNem | 92.45 | 1.36 | ab |
| | AneRan | 89.66 | 1.57 | ab |
| | FicVer | 92.73 | 1.17 | ab |
| | AsaEur | 84.53 | 4.92 | b |
| | ParQua | 93.27 | 1.55 | ab |
| | AdoMos | 96.96 | 0.55 | a |
| | MaiBif | 62.38 | 5.70 | c |
| | AegPodS | 35.41 | 3.55 | def |
| | AllPet | 18.67 | 1.97 | ghi |
| | MerPer | 32.36 | 3.36 | defg |
| | UrtDio | 30.26 | 1.92 | efgh |
| | AegPodL | 44.64 | 3.30 | de |
| | StaSyl | 27.08 | 2.93 | fgh |
| | GalLut | 47.63 | 4.71 | cd |
| | CorAve | 17.64 | 1.26 | hi |
| | FraExc | 29.95 | 1.68 | efgh |
| | CarBet | 17.66 | 1.43 | hi |
| | AcePse | 18.30 | 0.91 | ghi |
| | QueRob | 8.92 | 0.52 | i |
| 77 | CorCav | 94.34 | 1.53 | a |
| | AneNem | 85.76 | 4.96 | ab |
| | AneRan | 92.81 | 1.39 | a |
| | FicVer | 90.56 | 5.46 | a |
| | AsaEur | 70.32 | 6.88 | bc |
| | ParQua | 91.15 | 2.96 | a |
| | AdoMos | 91.23 | 2.45 | a |
| | MaiBif | 48.92 | 5.38 | cde |
| | AegPodS | 26.32 | 4.15 | ef |
| | AllPet | 30.20 | 3.95 | ef |
| | MerPer | 32.77 | 4.07 | ef |
| | UrtDio | 24.07 | 2.47 | f |
| | AegPodL | 40.06 | 1.22 | def |
| | StaSyl | 26.03 | 2.41 | f |
| | GalLut | 56.11 | 3.05 | cd |
| 84 | CorCav | 97.09 | 0.77 | a |
| | AneNem | 92.99 | 0.97 | ab |
| | AneRan | 95.17 | 1.06 | ab |
| | FicVer | 93.50 | 2.36 | ab |
| | AsaEur | 84.13 | 3.40 | b |

**Table 7** (continued)

| Interval (days) | Species | Mean rest of litter (%) | SE (%) | Results of ANOVA |
|---|---|---|---|---|
| | ParQua | 95.94 | 1.25 | a |
| | AdoMos | 94.79 | 2.07 | ab |
| | MaiBif | 53.52 | 2.54 | c |
| | AegPodS | 30.28 | 3.14 | de |
| | AllPet | 24.19 | 2.01 | de |
| | MerPer | 34.78 | 3.71 | cde |
| | UrtDio | 22.62 | 4.44 | ef |
| | AegPodL | 42.33 | 6.18 | cd |
| | StaSyl | 24.91 | 3.50 | de |
| | GalLut | 52.56 | 4.09 | c |
| | CorAve | 19.02 | 1.74 | ef |
| | FraExc | 29.87 | 2.44 | de |
| | CarBet | 18.43 | 1.30 | ef |
| | AcePse | 19.25 | 1.13 | ef |
| | QueRob | 9.05 | 0.91 | f |
| 91 | CorCav | 96.65 | 1.10 | a |
| | AneNem | 95.81 | 0.47 | a |
| | AneRan | 98.46 | 0.21 | a |
| | FicVer | 93.08 | 3.47 | a |
| | AsaEur | 80.49 | 6.87 | b |
| | ParQua | 96.72 | 0.90 | a |
| | AdoMos | 95.00 | 2.02 | a |
| | MaiBif | 45.43 | 3.10 | cd |
| | AegPodS | 33.10 | 1.88 | de |
| | AllPet | 26.48 | 2.68 | e |
| | MerPer | 40.68 | 2.63 | cde |
| | UrtDio | 30.59 | 3.30 | de |
| | AegPodL | 46.68 | 2.92 | cd |
| | StaSyl | 29.48 | 2.57 | de |
| | GalLut | 53.86 | 1.88 | c |
| 98 | CorCav | 92.85 | 2.32 | ab |
| | AneNem | 91.90 | 2.54 | ab |
| | AneRan | 94.78 | 0.75 | ab |
| | FicVer | 97.08 | 0.46 | a |
| | AsaEur | 88.67 | 2.56 | b |
| | ParQua | 92.88 | 1.88 | ab |
| | AdoMos | 97.18 | 0.79 | a |
| | MaiBif | 53.27 | 3.10 | cd |
| | AegPodS | 23.32 | 3.53 | gh |
| | AllPet | 26.79 | 3.37 | gh |
| | MerPer | 43.43 | 2.65 | def |
| | UrtDio | 33.60 | 1.72 | fgh |
| | AegPodL | 50.24 | 3.48 | cde |
| | StaSyl | 27.03 | 1.47 | gh |
| | GalLut | 62.99 | 4.95 | c |

**Table 7** (continued)

| Interval (days) | Species | Mean rest of litter (%) | SE (%) | Results of ANOVA |
|---|---|---|---|---|
| | CorAve | 19.74 | 1.30 | hi |
| | FraExc | 35.56 | 1.88 | efg |
| | CarBet | 21.00 | 1.29 | ghi |
| | AcePse | 21.81 | 1.01 | ghi |
| | QueRob | 10.87 | 0.67 | i |
| 105 | CorCav | 96.74 | 0.44 | a |
| | AneNem | 94.98 | 0.60 | a |
| | AneRan | 96.70 | 0.56 | a |
| | FicVer | 94.72 | 1.42 | a |
| | AsaEur | 80.76 | 6.32 | b |
| | ParQua | 97.01 | 0.59 | a |
| | AdoMos | 96.92 | 0.15 | a |
| | MaiBif | 52.63 | 4.34 | c |
| | AegPodS | 26.27 | 2.86 | d |
| | AllPet | 27.96 | 2.42 | d |
| 112 | CorCav | 93.96 | 1.54 | ab |
| | AneNem | 96.62 | 0.49 | ab |
| | AneRan | 97.79 | 0.65 | a |
| | FicVer | 97.48 | 0.25 | a |
| | AsaEur | 87.26 | 4.07 | b |
| | ParQua | 97.06 | 0.61 | ab |
| | AdoMos | 96.43 | 1.40 | ab |
| | MaiBif | 46.81 | 2.51 | c |
| | AegPodS | 30.88 | 9.31 | cde |
| | AllPet | 30.95 | 2.04 | cde |
| | MerPer | 38.62 | 4.13 | cd |
| | UrtDio | 28.61 | 1.46 | de |
| | AegPodL | 47.00 | 3.44 | c |
| | StaSyl | 26.96 | 1.35 | def |
| | CorAve | 19.90 | 0.51 | ef |
| | FraExc | 33.64 | 2.38 | cde |
| | CarBet | 20.77 | 2.86 | ef |
| | AcePse | 22.33 | 1.31 | ef |
| | QueRob | 13.90 | 1.43 | f |
| 119 | CorCav | 94.78 | 2.64 | a |
| | AneNem | 93.66 | 1.98 | a |
| | AneRan | 97.77 | 0.33 | a |
| | FicVer | 94.21 | 1.74 | a |
| | AsaEur | 90.17 | 2.92 | a |
| | ParQua | 95.33 | 0.89 | a |
| | AdoMos | 92.76 | 1.98 | a |
| | MaiBif | 37.46 | 9.17 | bc |
| | AegPodS | 33.06 | 2.88 | bc |
| | AllPet | 34.45 | 2.42 | bc |
| | MerPer | 47.90 | 2.81 | bc |
| | UrtDio | 31.74 | 1.33 | c |
| | AegPodL | 52.61 | 2.46 | b |

**Table 7** (continued)

| Interval (days) | Species | Mean rest of litter (%) | SE (%) | Results of ANOVA |
|---|---|---|---|---|
| | StaSyl | 28.33 | 2.65 | c |
| 126 | CorCav | 95.45 | 0.86 | ab |
| | AneNem | 94.52 | 0.76 | ab |
| | AneRan | 98.23 | 0.26 | a |
| | FicVer | 95.69 | 0.44 | ab |
| | AsaEur | 87.44 | 3.70 | b |
| | ParQua | 96.29 | 0.50 | ab |
| | AdoMos | 96.07 | 0.95 | ab |
| | MaiBif | 43.18 | 8.15 | de |
| | AegPodS | 24.16 | 3.23 | fg |
| | AllPet | 36.12 | 1.78 | def |
| | MerPer | 47.47 | 3.24 | cd |
| | UrtDio | 36.25 | 4.54 | def |
| | AegPodL | 59.38 | 1.77 | c |
| | StaSyl | 28.42 | 1.95 | efg |
| | CorAve | 17.93 | 0.86 | gh |
| | FraExc | 31.97 | 1.46 | defg |
| | CarBet | 23.63 | 0.78 | fg |
| | AcePse | 21.22 | 0.38 | fgh |
| | QueRob | 9.65 | 0.81 | h |
| 133 | MerPer | 46.80 | 2.07 | ab |
| | UrtDio | 35.42 | 2.95 | bc |
| | AegPodL | 56.85 | 2.78 | a |
| | StaSyl | 28.39 | 3.38 | c |
| 140 | CorCav | 96.82 | 0.39 | ab |
| | AneNem | 95.36 | 0.77 | abc |
| | AneRan | 97.79 | 0.22 | a |
| | FicVer | 91.50 | 4.13 | abc |
| | AsaEur | 88.44 | 1.90 | c |
| | ParQua | 91.07 | 1.92 | bc |
| | AdoMos | 94.43 | 1.44 | abc |
| | MaiBif | 57.58 | 3.30 | d |
| | AegPodS | 29.74 | 1.55 | fg |
| | AllPet | 29.11 | 2.35 | fg |
| | MerPer | 51.31 | 2.77 | de |
| | UrtDio | 41.74 | 2.58 | ef |
| | AegPodL | 60.18 | 3.10 | d |
| | StaSyl | 32.65 | 2.21 | fg |
| | CorAve | 16.89 | 0.40 | hi |
| | FraExc | 32.15 | 1.49 | fg |
| | CarBet | 25.31 | 1.21 | gh |
| | AcePse | 21.23 | 1.96 | ghi |
| | QueRob | 12.42 | 0.99 | i |
| 147 | MerPer | 52.61 | 3.91 | b |
| | UrtDio | 43.21 | 2.52 | bc |
| | AegPodL | 69.98 | 3.51 | a |
| | StaSyl | 34.23 | 3.00 | c |
| 154 | CorCav | 97.04 | 1.24 | a |

**Table 7** (continued)

| Interval (days) | Species | Mean rest of litter (%) | SE (%) | Results of ANOVA |
|---|---|---|---|---|
| | AneNem | 96.414 | 0.574 | a |
| | AneRan | 97.18 | 0.77 | a |
| | FicVer | 94.08 | 1.85 | a |
| | AsaEur | 83.40 | 3.76 | b |
| | ParQua | 91.10 | 1.81 | ab |
| | AdoMos | 92.52 | 2.36 | ab |
| | MaiBif | 58.82 | 3.20 | c |
| | AegPodS | 33.08 | 2.99 | def |
| | AllPet | 43.11 | 2.75 | d |
| | CorAve | 20.44 | 1.11 | fg |
| | FraExc | 35.08 | 1.92 | de |
| | CarBet | 23.30 | 1.80 | efg |
| | AcePse | 20.42 | 2.30 | fg |
| | QueRob | 14.32 | 1.63 | g |
| 161 | MerPer | 51.38 | 9.75 | ab |
| | UrtDio | 39.71 | 7.45 | b |
| | AegPodL | 75.24 | 2.80 | a |
| | StaSyl | 42.76 | 3.35 | b |
| 168 | CorCav | 92.09 | 2.20 | ab |
| | AneNem | 91.91 | 0.95 | ab |
| | AneRan | 93.55 | 1.96 | a |
| | FicVer | 90.51 | 2.24 | ab |
| | AsaEur | 82.55 | 5.26 | b |
| | ParQua | 92.97 | 1.78 | a |
| | AdoMos | 93.10 | 1.65 | a |
| | MaiBif | 64.33 | 2.32 | c |
| | AegPodS | 35.66 | 1.16 | d |
| | CorAve | 20.31 | 1.43 | ef |
| | FraExc | 36.44 | 1.50 | d |
| | CarBet | 27.31 | 1.72 | de |
| | AcePse | 24.88 | 0.58 | de |
| | QueRob | 12.84 | 1.20 | f |
| 175 | MerPer | 72.65 | 1.87 | b |
| | UrtDio | 49.83 | 1.92 | c |
| | AegPodL | 86.53 | 2.78 | a |
| | StaSyl | 41.76 | 3.90 | c |
| 182 | CorCav | 95.19 | 0.35 | ab |
| | AneNem | 89.47 | 4.77 | ab |
| | AneRan | 94.38 | 0.92 | a |
| | FicVer | 90.76 | 2.38 | ab |
| | AsaEur | 81.35 | 5.45 | bc |
| | ParQua | 93.26 | 1.79 | ab |
| | AdoMos | 90.62 | 3.84 | ab |
| | MaiBif | 67.94 | 2.85 | c |
| | AegPodS | 27.90 | 2.95 | def |
| | AllPet | 41.00 | 2.42 | de |

**Table 7** (continued)

| Interval (days) | Species | Mean rest of litter (%) | SE (%) | Results of ANOVA |
|---|---|---|---|---|
| | CorAve | 21.32 | 0.74 | fg |
| | FraExc | 42.88 | 2.81 | d |
| | CarBet | 23.89 | 1.09 | efg |
| | AcePse | 25.10 | 1.27 | efg |
| | QueRob | 12.36 | 0.84 | g |
| 196 | AegPodS | 38.81 | 4.17 | b |
| | CorAve | 22.77 | 0.62 | bc |
| | FraExc | 66.20 | 10.77 | a |
| | CarBet | 28.05 | 1.34 | bc |
| | AcePse | 29.05 | 1.21 | bc |
| | QueRob | 12.62 | 1.59 | c |
| 203 | MerPer | 78.72 | 7.71 | ab |
| | UrtDio | 59.45 | 4.15 | bc |
| | AegPodL | 90.05 | 3.37 | a |
| | StaSyl | 51.78 | 4.74 | c |
| 210 | MaiBif | 56.79 | 2.94 | a |
| | AegPodS | 39.93 | 4.03 | b |
| | CorAve | 23.38 | 0.48 | cd |
| | FraExc | 64.03 | 4.15 | a |
| | CarBet | 28.57 | 2.27 | bc |
| | AcePse | 26.54 | 1.24 | c |
| | QueRob | 15.50 | 0.73 | d |
| 224 | AegPodS | 41.73 | 4.17 | b |
| | CorAve | 22.57 | 0.61 | cd |
| | FraExc | 55.47 | 2.49 | a |
| | CarBet | 29.89 | 2.28 | c |
| | AcePse | 27.43 | 1.38 | c |
| | QueRob | 15.78 | 2.84 | d |
| 238 | MaiBif | 61.13 | 2.6 | a |
| | AegPodS | 44.41 | 6.57 | ab |
| | CorAve | 29.60 | 2.33 | bc |
| | FraExc | 65.49 | 8.60 | a |
| | CarBet | 31.33 | 1.25 | bc |
| | AcePse | 30.13 | 1.55 | bc |
| | QueRob | 18.32 | 2.54 | d |
| 252 | AegPodS | 41.05 | 3.18 | b |
| | CorAve | 23.12 | 1.84 | cd |
| | FraExc | 63.07 | 6.41 | a |
| | CarBet | 32.73 | 2.03 | bc |
| | AcePse | 27.94 | 3.89 | bcd |
| | QueRob | 13.22 | 1.23 | d |
| 266 | AegPodS | 40.74 | 3.31 | b |
| | CorAve | 30.88 | 3.73 | bc |
| | FraExc | 72.40 | 5.25 | a |
| | CarBet | 36.79 | 1.49 | b |
| | AcePse | 37.31 | 2.88 | b |
| | QueRob | 20.39 | 2.94 | c |
| 280 | CorAve | 30.69 | 2.73 | bc |
| | FraExc | 69.41 | 5.63 | a |
| | CarBet | 40.99 | 2.87 | b |

**Table 7** (continued)

| Interval (days) | Species | Mean rest of litter (%) | SE (%) | Results of ANOVA |
|---|---|---|---|---|
| | AcePse | 36.25 | 5.54 | bc |
| | QueRob | 20.31 | 3.03 | c |
| 294 | AegPodS | 44.01 | 2.37 | b |
| | CorAve | 28.77 | 2.60 | cd |
| | FraExc | 70.48 | 3.74 | a |
| | CarBet | 30.77 | 1.91 | bcd |
| | AcePse | 32.33 | 4.22 | bc |
| | QueRob | 18.63 | 2.28 | d |
| 308 | CorAve | 30.16 | 3.73 | b |
| | FraExc | 79.76 | 4.69 | a |
| | CarBet | 48.78 | 5.98 | b |
| | AcePse | 37.27 | 7.34 | b |
| | QueRob | 26.41 | 3.60 | b |
| 322 | AegPodS | 61.38 | 5.10 | |
| 336 | CorAve | 33.64 | 1.73 | b |
| | FraExc | 79.79 | 3.57 | a |
| | CarBet | 36.33 | 5.50 | b |
| | AcePse | 37.88 | 11.14 | b |
| | QueRob | 19.82 | 4.39 | b |
| 350 | AegPodS | 51.29 | 9.11 | |
| 364 | CorAve | 30.16 | 3.13 | bc |
| | FraExc | 86.13 | 3.09 | a |
| | CarBet | 43.32 | 7.15 | b |
| | AcePse | 38.32 | 7.02 | bc |
| | QueRob | 20.23 | 5.47 | c |
| 378 | AegPodS | 43.18 | 3.94 | |
| 406 | AegPodS | 55.01 | 4.94 | |

AcePse - *Acer pseudoplatanus*; AdoMos - *Adoxa moschatellina*; AegPodL - *Aegopodium podagraria* leaves; AegPodS - *Aegopodium podagraria* shoots; AllPet - *Alliaria petiolata*; AneNem - *Anemone nemorosa*; AneRan - *Anemone ranunculoides*; AsaEur - *Asarum europaeum*; CarBet - *Carpinus betulus*; CorAve - *Corylus avellana*; CorCav - *Corydalis cava*; FicVer - *Ficaria verna*; FraExc - *Fraxinus excelsior*; GalLut - *Galeobdolon luteum*; MaiBif - *Maianthemum bifolium*; MerPer - *Mercurialis perennis*; ParQua - *Paris quadrifolia*; QueRob - *Quercus robur*; StaSyl - *Stachys sylvatica*; UrtDio - *Urtica dioica*

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# The afterlife of herbaceous plant species: A litter decomposition experiment in a temperate oak-hornbeam forest

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ABSTRACT

Understanding the mechanisms of singular species and their traits impacts on ecosystem functions, is crucial in the era of unprecedented anthropogenic changes of the environment, e.g. to predict changes in carbon and nutrient cycling connected with species shifts. It may allow us to take protective measurements and mitigate the negative effects of global changes. Litter decomposition is a crucial process shaping nutrient cycling in ecosystems. Studies on decomposition in forest ecosystems are mainly limited to foliar litter. In contrast to woody plant species, our knowledge of decomposition of herbaceous plants is scarce. Thus, unanswered questions remain about the model that best describes the decomposition process of herbaceous plants. The relationship of decomposition rate to functional traits is unknown for this species pool. We used the litter bag method to determine the decomposition rate of 13 herbaceous plant species and four overstory tree species growing in a temperate oak-hornbeam forest. We showed that the litter decomposition rate and C and N release were higher in spring ephemerals than summer green herbaceous species, as the plants with small total individual aboveground biomass (TAB) and small total leaf area (TLA) decomposed the fastest. Our results demonstrate that in this generally acquisitive group of plants, size traits have a stronger impact on decomposition than economic traits. For almost all species, the two-phase exponential decay model explains the course of herbaceous species litter decomposition only slightly better than the single exponential model.

## 1. Introduction

The herbaceous species layer is considered an important reservoir of forest biodiversity and rare species (Gilliam 2007). Moreover, it is a source of habitat and food for invertebrates and herbivores (Boch et al. 2013; Gill and Beardall 2001; Smolko et al. 2018). The understory layer impacts overstory composition by competition with tree species regeneration (Baraloto et al. 2005). The limited available studies are related to the importance of the herb layer in ecosystem function in temperate forests (Gilliam 2007, 2014; Landuyt et al. 2019). In the past, the small contribution of the herbaceous layer to standing forest biomass was highlighted (Gilliam 2007). Nevertheless, herbaceous species have great importance for forest functioning, by influencing water cycling (Thrippleton et al. 2016) and nutrient cycling (e.g. Elliott et al. 2014; Muller 2014).

The latest scientific reports indicate that the biomass of the understory, generally ranging between 0 and 500 g/m$^2$ (Landuyt et al. 2020; Rawlik and Jagodziński 2021) can reach values comparable to the biomass of leaves produced in the overstory (generally ranging between 100 and 900 g/m$^2$ (Sayer 2006), which highlights the large contribution of the herbaceous layer to the labile part of the litter. More than 90% of N and P required for plant growth is released in the decomposition process (Chapin 2003; Qu et al. 2020). In this context, herbaceous species should be very important, as their nutrient concentrations were on average between 1.5 and 5 times higher than those found in overstory leaves, depending on the nutrient considered (Landuyt et al. 2019). Moreover, the importance of spring ephemerals in nutrient circulation is particularly high, as early in the spring, when trees are still dormant, they capture a significant amount of nutrients from the soil, preventing their leakage (Mabry et al. 2008). Patterns of decomposition and nutrient release in herbaceous species have not been studied so far. Moreover, herbaceous litter is generally considered as more decomposable than tree leaf litter (Muller 2014), and the herb layer inputs litter continuously, during the whole year, as opposed to the leaf litter of

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trees (Muller 2014). Additionally, Wang et al. (2021) showed that herbaceous species litter significantly influences decomposition of tree species litter, although the direct of changes strongly depends on herb species identity. Nitrogen rich tissues of spring ephemerals do not accelerate decomposition rate because N is not a limiting resource in temperate deciduous forests, while phosphorous rich tissues of summer greens can enhance decomposition. However, our previous study (Rawlik et al. 2021) showed that herbaceous litter decomposition was not always completed in less than a year and was not always faster than the decomposition of tree leaf litter in an oak-hornbeam forest in Western Poland. The novelty of this paper is that for the first time we assess the influence of functional group of herbaceous plants on patterns of the latest stages of the decomposition process, for the most abundant oak-hornbeam herb species, as we prolonged the experiment duration, in comparison with preliminary studies (Rawlik et al. 2021). Spring ephemerals develop aboveground organs and assimilate carbon in early spring before full canopy closure, thereby avoiding shading by the tree canopy (Rawlik and Jagodziński 2020; Uemura 1994). Globally, all plant species producing short-lived leaves with high photosynthetic rates and low structural costs, decompose faster than plants producing leaves with the opposite traits (Reich et al. 1997; Wright et al. 2004), thus we hypothesize that spring ephemerals decompose faster than summer-greens. Summer-greens develop aboveground organs more slowly, during the whole growing season (Rawlik and Jagodziński 2020; Uemura 1994). Moreover, we studied patterns of nutrient release of the species studied. Finally, for the first time, we assessed size traits, nitrogen and carbon concentration influences on decomposition and nutrient release rates, taking into account a wider pool (in comparison with preliminary studies; Rawlik et al. 2021) of oak-hornbeam herbaceous species.

Decomposition of plant litter is a large component of the flux of carbon from biosphere to atmosphere (Schimel 1995). The rate of decomposition influences important ecosystem processes such as net ecosystem exchange, carbon storage and nutrient cycling, thus models developed in simple empirical works are directly used in global models of the carbon cycle (Brovkin et al. 2012). Although large numbers of different models of decomposition processes exist, the most often used is the single exponential model, proposed by Olson (1963; Berg and McClaugherty 2014). This model is relatively simple and good for the early stage of decay, as it assumes that the decomposition rate is constant and that all material is decomposed (Gholz et al. 2000). This model has been criticized many times, as adequate only for homogenous material composed of molecules with equal decomposability (Wider and Lang 1982; Cheshire et al. 1988; Prescott 2005; Adair et al. 2008). A second model, developed and based on the assumption that the litter substrate is mixed material composed of fractions with different decomposition rates, is a two-phase double exponential model (Berg and McClaugherty 2014). Herbaceous litter is a mixed material, made of easily decomposable leaves and more difficult to decompose stems, thus a two-phase double exponential model should better describe the process of its decomposition (Berg and McClaugherty 2014). Moreover, a single exponential model fits early stages of decomposition, when about 20% of initial mass is remaining, whereas a two-phase double exponential model better describes the whole decomposition process (Berg and McClaugherty 2014). Decomposition dynamics are the most well described for needle and leaf litter of trees (Berg and McClaugherty 2014) and it is important to check if herbaceous species litter reflects general patterns linked to ecological strategies of plants, and thus functional traits.

Understanding the importance of abiotic and biotic factors which control decomposition is another important theme in ecosystem research (Cornwell and Weedon 2014). There is a general concept that structural and chemical leaf traits (Leaf Economic Spectrum = LES) as well as whole plant traits (Plant Economic Spectrum = PES) have afterlife effects on litter decomposability (Cornelissen et al. 2004), as interspecific variation in fresh leaves and litter traits are strongly correlated and reflect litter attractiveness for decomposers (e.g. Freschet et al. 2012). Especially leaf persistence (LP) (Cornelissen and Thompson 1997), lignin content (Meentemeyer 1978), physical toughness (Pérez-Harguindeguy et al. 2000), polyphenol content (Coq et al. 2010), specific leaf area (SLA), and leaf dry matter content (LDMC) (Kazakou et al. 2006; Horodecki et al. 2019) were reported as traits affecting decomposition rates (Table 1). Also, chemical traits of leaves, such as nitrogen (N), phosphorus (P), and calcium (Ca) contents (Aerts 1997), pH (Cornelissen et al. 2006) and the ratios of nutrient concentrations (e.g, C:N, N:P) were used as significant predictors of leaf litter decomposition rates (Freschet et al. 2012; Patoine et al. 2020) (Table 1). Afterlife effects of functional traits on decomposition are well documented for leaf litter in most cases (Cornwell et al. 2008, Fujii et al. 2018, Guo et al. 2019), while for other organs such clear patterns have not yet been found (Tuo et al. 2021), although some studies on other organs (root, stem, bark, wood) were conducted (Silver and Miya, 2001; Van Geffen et al., 2010; Vivanco and Austin, 2006). Few studies have explored the effects of size traits (traits connected with biomass allocation) on decomposition. Van Geffen et al., 2010 described positive effects of small stem size (diameter) on wood decomposition for 15 Bolivian tree species. Pietsch et al. (2014) described a negative correlation between maximal height and wood decomposition rate. Our previous research indicated that life strategy affects early-stage decomposition rates in herbaceous species (Rawlik et al. 2019; Rawlik et al. 2021) and it is connected with resource-economic traits, mainly SLA, LDMC, and leaf nitrogen concentration (LNC; Rawlik et al. 2021). LDMC was a stronger predictor of decay rates than SLA and LNC. Thus, spring ephemerals, with the highest SLA, LNC, and the lowest LDMC among all phenological groups of oak-hornbeam herbaceous species, decomposed the fastest (Rawlik et al. 2021). However, some part of the variation in decomposition rate was not explained by the impact of economic traits. Some species with high SLA and LDMC but with low leaf mass fraction (LMF) decomposed more slowly. Results of studies of decomposability of different plant organs showed that biomass allocation, especially the relative proportion of leaf versus non-leaf organs, is a central aspect of whole-plant effects on labile soil organic matter dynamics (Freschet et al. 2013). Considering that fine stem and fine root litters of species decompose roughly twice slower than their leaf litter (Freschet et al. 2013), decomposition of whole herbaceous plant litter (mixed leaves and

**Table 1**
Explanation of abbreviations and relationships of studied functional traits to decomposition according to the literature.

| Functional trait | Abbreviation | Relation to decomposition rate | Literature source |
|---|---|---|---|
| Leaf persistance | LP | Negative | Cornelissen and Thompson (1997) |
| Leaf dry matter content (mg/g) | LDMC | Negative | Garnier et al. 2004, Bumb et al. (2018) |
| Proportion of carbon content to nitrogen content | C/N ratio | Negative | Cornwell et al. (2008), Van Geffen et al., 2010 |
| Initial litter nitrogen concentration per mass (%) | N content | Positive | Pietsch et al. (2014), Zuo et al. (2018) |
| Initial litter carbon concentration per mass (%) | C content | Negative | Cornwell et al. (2008), Freschet et al. (2012) |
| Leaf mass fraction (proportion) | LMF | – | – |
| Total leaf area ($cm^2$) | TLA | – | – |
| Total individual aboveground biomass (g) | TB | – | – |
| Specific leaf area ($cm^2/g$) | SLA | Positive | Cornwell et al. (2008), Pietsch et al. (2014) |

stems) should be much slower than predicted from leaf economic functional traits only. In our study we explored the decomposition process of whole plants (litter included senescent leaves as well as stems), thus we suppose that size traits could be more important in explanation of decomposition rate variation than leaf traits, as tall plants invest more in structural or defense related compounds (e.g. microtubules, phloem proteins), connected with support and transport functions (Freschet et al. 2010; Bumb et al. 2018).

We hypothesized that: (H1) decomposition and nutrient release rates of spring ephemerals are much higher than for summer-greens and leaves of woody species, (H2) the two-phase exponential decay model better explains the litter decomposition of herbaceous plant species than the one-phase exponential model, due to the fact that herb litter is a mixed material with leaves and shoots, and (H3) traits related to plant size (TAB, TLA) affect decomposition in the studied species, more than "economic traits" (SLA, LNC, LDMC, LMF).

## 2. Materials and methods

We used data from an original experiment (2011–2015) combined with data from functional trait databases to test relationships between leaf and whole-plant economic traits and litter decay rates.

### 2.1. Experimental site

The research area was established in Central Wielkopolska within a large compact oak-hornbeam forest complex, near Czmoń (52.1510°N, 17.0545°E; Table 1 in the Appendix). The mean annual temperature in this area was 8.7 °C, and mean annual precipitation was 514 mm in 1971–2010, and 9.2 °C, and 535 mm in 2001–2010, respectively (Central Statistical Office, 2020). According to meteorological data from a nearby meteorological station (Institute of Dendrology, Polish Academy of Sciences, Kórnik; 52.2447°N, 17.1008°E; 10.5 km from the study area), the mean annual temperature in 2011–2015 (during the experiment) was 9.5 °C and mean annual precipitation was 528 mm (Table 2, 3 in the Appendix). The study area was located in a deciduous 135-year-old oak-hornbeam stand (Table 1, 4 in the Appendix), comprising the plant association of *Galio sylvatici-Carpinetum* (R.Tx. 1937) Oberd. 1957, subassociation *corydalidetosum* Oberd. 1957, with a rich, well-developed herbaceous layer (Table 5 in the Appendix). The soils were described as Stagnic Gleyic Gleysols (Arenic, Humic) (Table 6 in the Appendix).

During the experiment we also measured temperatures at every sample plot, at the ground level every hour using data loggers evenly distributed within the stand (HOBO U23-001 Pro v2 Temperature, Onset Computer Corporation, Bourne, Massachusetts, USA) (Table 3 in the Appendix).

We established four study plots (from 400 $m^2$ to 2500 $m^2$) with homogenous vegetation layers (herbs, shrubs and trees), in terms of cover and species composition. Within these stands we measured all diameters at breast height (i.e., 1.3 m, henceforth DBH) and height (H) for at least 50% of overstory trees (Table 4 in the Appendix).

Moreover, on every sample plot phytosociological relevés were taken on two dates, in accordance with the phenological optimum of the studied community, according to the method of Braun-Blanquet (1964), with 7 classes of cover-abundance (5 = cover > 75%; 4 = 50–75%; 3 = 25–50%; 2 = 5–25%; 1 = numerous or scattered, but cover < 5%; + = few, with small cover; and r = rare, solitary, with small cover). The taxonomic nomenclature followed is that of Mirek et al. (2002) for vascular plants, and Ochyra et al. (2003) for mosses (Table 5 in the Appendix).

Soil properties were measured based on soil pit excavation (1.5 m deep) in the center of each study site, collected in October 2013. We determined soil particle-size distribution, soil pH in $H_2O$ and in 1 M KCl, physicochemical soil characteristic (Table 6 in the Appendix).

To characterize light availability on the forest floor, on June 2015 we measured canopy light absorption (characterized by diffuse non-interceptance—DIFN) using an LAI-2200 plant canopy analyzer (Li-Cor Inc., Lincoln, NE, USA) (Table 1 in the Appendix).

### 2.2. Species studied

To assess the influence of functional traits on decomposition processes in forest herb species we chose 13 vascular plant species that dominated in our sample of plot cover (see Table 2 in Appendix): *Adoxa moschatellina*, *Aegopodium podagraria*, *Anemone nemorosa*, *Convallaria majalis*, *Corydalis cava*, *Ficaria verna*, *Galeobdolon luteum*, *Galium aparine*, *Impatiens parviflora*, *Maianthemum bifolium*, *Mercurialis perennis*, *Stachys sylvatica* and *Urtica dioica* (Table 2).

To determine which herbaceous species were merged in terms of similarity of the functional traits studied and the rate of decomposition we used Ward hierarchical method (Ward and Hook 1963). Based on the dendrogram developed with above mentioned method, we showed that the analyzed species, in terms of all the examined functional traits, differentiated themselves into three distinct groups. The first group (spring ephemerals) includes four species: *A. moschatellina*, *F. verna*, *A. nemorosa*, *C. cava*, the second group (summer-greens I) includes five species: *A. podagraria*, *C. majalis*, *S. sylvatica*, *U. dioica* and *I. parviflora,* while the third group (summer-greens II) includes: *G. aparine*, *M. perennis*, *M. bifolium* and *G. luteum* (Fig. 1). Moreover, we also studied the decomposition rates of three tree (*Acer pseudoplatanus*, *Carpinus betulus*, *Quercus robur*) and one shrub species (*Corylus avellana*) to compare them directly to the decomposition process of herbaceous litter.

### 2.3. Litterbag experiment

We harvested plants from October 2012 to November 2013. We collected material from each species at the time when most of the plants within each population began senescing. We used material collected from the close vicinity of all our sample plots. We transported the collected biomass to the laboratory and dried it to a constant mass in a dryer with forced air circulation at 65 °C. After that, we installed known masses of plants inside the litter bags. The masses varied from 1.8 to 3.2 g for herbaceous species, and from 8.0 to 8.4 g for woody species. These masses were different for different species to avoid excessive compaction of material in litter bags. For all species, we placed whole specimens (mix of leaves and shoots). 'Litter bags' were made of fiberglass netting (15 × 15 cm) with a mesh size of 1 mm. The bags were permanently closed and labeled. In total we set up 3900 litter bags.

To answer our scientific questions we established two experiments. Firstly, we established four sample plots to assess the decomposition rates of different functional groups of herbaceous species (the 1st experiment; see Table 3). We placed three litter bags on every sample plot for every species for every harvest time (12 replications per collection period). We established this experiment at different dates, according to the time of senescence of most plants of the particular taxa, to assess true biological decomposition rates, in conditions as similar to natural as possible. Litter bags were randomly placed inside research plots, on the soil surface, lightly covered by surrounding litter. The second experiment (the 2nd experiment; Table 3) was established on the 8th of December 2012 to compare decomposition rates of litter originated from woody plants with summer green herbaceous species, as we had similar results for decomposition rates of these two groups in previous studies (Rawlik et al. 2021). We placed one litter bag in the case of trees and shrubs and two litter bags in the case of herbaceous species on each of six sample plots for every harvest time (6 replications in the case of trees and shrubs per harvest time; 12 replications in the case of herbaceous species per harvest time).

In both experiments we collected litter bags every week for spring ephemerals, two weeks for summer greens, or one month for trees and shrubs. Therefore, number of samples collected differed, from 11 for the most decomposable spring ephemeral to 39 for one of the summer

**Table 2**
Functional traits of the herbaceous species included in the study.

| Species | SLA[1] | TLA[2] | TB[3] | LMF[4] | LDMC[5] | LP[6] | LCC[7] | LNC[8] | C/N [9] | Functional group[10] |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Adoxa moschatellina*** | 276.50 | 36.72 | 0.26 | 0.71 | 136.67 | 1 | 40.70 | 1.53 | 31.25 | 1 |
| ***Aegopodium podagraria*** | 271.67 | 74.19 | 0.42 | 0.96 | 230.00 | 2 | 40.70 | 2.93 | 15.68 | 2 |
| ***Anemone nemorosa*** | 276.97 | 21.11 | 0.10 | 0.76 | 205.00 | 1 | 36.98 | 2.54 | 16.98 | 1 |
| ***Convallaria majalis*** | 253.42 | 89.04 | 0.43 | 0.92 | 221.50 | 2 | 40.64 | 2.19 | 21.65 | 2 |
| ***Corydalis cava*** | 396.27 | 35.51 | 0.13 | 0.68 | 139.91 | 1 | 37.75 | 2.82 | 15.62 | 1 |
| ***Ficaria verna*** | 269.70 | 16.76 | 0.12 | 0.68 | – | 1 | 40.37 | 2.39 | 19.69 | 1 |
| ***Galeobdolon luteum*** | 299.32 | 33.09 | 0.22 | 0.55 | – | 4 | 47.08 | 1.34 | 42.98 | 3 |
| ***Galium aparine*** | 449.18 | 17.99 | 0.09 | 0.49 | 140.00 | 3 | 45.02 | 1.34 | 39.13 | 3 |
| ***Impatiens parviflora*** | 863.27 | 115.9 | 0.34 | 0.52 | 76.47 | 2 | 40.75 | 2.74 | 17.36 | 2 |
| ***Maianthemum bifolium*** | 309.10 | 16.10 | 0.07 | 0.86 | 238.58 | 2 | 43.53 | 1.31 | 38.78 | 3 |
| ***Mercurialis perennis*** | 460.07 | 72.74 | 0.33 | 0.41 | 224.50 | 2 | 43.12 | 1.68 | 29.92 | 3 |
| ***Stachys sylvatica*** | 412.28 | 162.95 | 0.88 | 0.57 | 207.00 | 2 | 41.02 | 1.57 | 30.59 | 2 |
| ***Urtica dioica*** | 394.15 | 161.07 | 0.62 | 0.64 | 212.50 | 2 | 41.01 | 3.24 | 14.77 | 2 |
| Source[11]: | 1 | 1 | 1 | 1 | 2 | 3 | 4 | 4 | 4 | 4 |

[1] SLA – specific leaf area ($cm^2/g$).
[2] TLA – total leaf area ($cm^2$).
[3] TB – total individual aboveground biomass (g).
[4] LMF – leaf mass fraction (proportion).
[5] LDMC – leaf dry matter content (mg/g).
[6] LP – leaf persistence: 1 – spring green, 2 – summer green, 3 – overwintering green, 4 – persistent green.
[7] C content – initial litter carbon concentration per mass (%).
[8] N content – initial litter nitrogen concentration per mass (%).
[9] C/N ratio – proportion of carbon content to nitrogen content.
[10] Functional group: 1 – spring ephemerals, 2 – summer-greens I, 3 – summer-greens II.
[11] Source of data: 1 – Paź-Dyderska et al. 2020, 2 – LEDA trait database (Kleyer et al. 2008), 3 – BiolFlor (Klotz et al. 2002), 4 – original data;

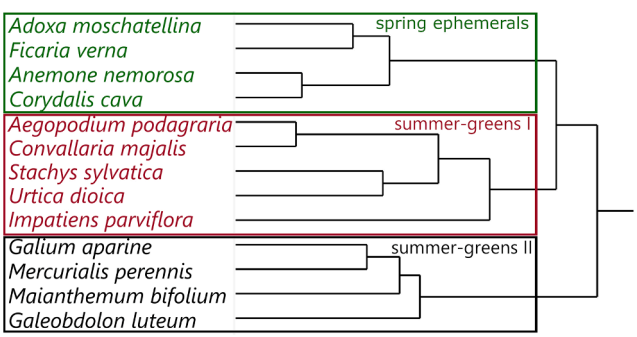


**Fig. 1.** Dendrogram plotted based on the tested functional traits.

greens (Table 3). The duration of the experiment also differed among the functional groups. The mass loss of the plant material was determined systematically during the experiment, for some species we noticed that the decomposition ratio was lower than previously assumed, and thus we decided to change the interval of sample collection and extend the period of litter collection. Thus, the duration of experiments was different for different species, at least 119 days for most decomposable spring ephemeral species to 851 days for trees and shrubs (Table 3). After drying, we removed litter from bags, and we cleaned it to remove sand, fungus, and roots, and then we weighed it to determine the percent of initial litter mass remaining. This is an experiment with repeated measures (at least 11 times per species), therefore we had enough measures to model decomposition curves for each of the species studied.

### 2.4. Functional traits

We obtained functional traits data from Paź-Dyderska et al. (2020), who provided measurements of the species studied from Poland, in an area of climatic conditions similar to our study area. Only values of LDMC were obtained from LEDA databases (Kleyer et al. 2008), and LP from BiolFlor databases (Klotz et al. 2002), as these values were not available from the mentioned paper. Global trait databases, in the cases of the species studied, most often include only measurements of a few individuals collected in Western Europe, mismatching local climate conditions. Therefore, we believe that our study will result in data with smaller potential noise coming from the variability of traits among different habitat and climatic conditions (Zanne et al. 2015). We determined nutrient contents in the initial litter material and four times (when around 80, 60, 40, and 20% of each species material was decomposed) during the experimental period. Contents of C and N were determined with an ECS CHNS–O 4010 Elemental Combustion System (Costech Instruments, Italy/USA). In these studies, we decided to check how economic traits (LP, SLA, LDMC, LMF), size traits (TLA, TAB), and chemical traits (LCC, LNC, C/N) of litter affect decomposition rate.

### 2.5. Statistical analyses

We assumed that the decomposition process over time will be described by two models:

a single exponential model proposed by Olson (1963) for trees, shrubs, and herbaceous species:

$$Mt = e^{-kt},$$

where $Mt$ is the proportion of remaining biomass at time $t$ and $k$ is the decay rate,

and a double exponential model proposed by Bunnell et al. (1977) for herbaceous species:

$$Mt = A*e^{k1t} + (1 - A)*e^{k2t},$$

where $Mt$ is the proportion of remaining biomass at time $t$ and $A$ is a relatively easily decomposing fraction of litter, *(1-A)* is a more recalcitrant fraction, *k1* and *k2* are the decay constants for quickly and slowly decomposing fractions of the litter. The double exponential model is a development of the single exponential model which assumes that the litter substrate has two main substrate-quality components with different decomposition rates.

Based on this model and obtained $k$ values, we calculated the mean half decay time (*hd*) of each litter type:

$$hd = ln(0.50)*(-k)^{-1},$$

Next, we fitted a log-regression model and obtained the $k$ value for each species.

**Table 3**
The number of species-specific samples.

| Species | Functional group[1] | Number of experiment | Number of research plots | Number of samples on sample plot | Number of replicates | Collection number | Mean interval | Experiment period | Total number of samples | Date of start of the experiment |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Adoxa moschatellina*** | 1 | 1 | 4 | 3 | 12 | 11 | 7 | 119 | 132 | 10.08.2013 |
| ***Anemone nemorosa*** | 1 | 1 | 4 | 3 | 12 | 16 | 7 | 140 | 192 | 22.06.2013 |
| ***Convallaria majalis*** | 2 | 1 | 4 | 3 | 12 | 22 | 14 | 308 | 264 | 23.11.2013 |
| ***Corydalis cava*** | 1 | 1 | 4 | 3 | 12 | 16 | 7 | 140 | 192 | 22.06.2013 |
| ***Ficaria verna*** | 1 | 1 | 4 | 3 | 12 | 16 | 7 | 140 | 192 | 22.06.2013 |
| ***Galium aparine*** | 3 | 1 | 4 | 3 | 12 | 27 | 7 | 245 | 324 | 10.08.2013 |
| ***Galeobdolon luteum*** | 3 | 1 | 4 | 3 | 12 | 39 | 7 | 427 | 468 | 10.08.2013 |
| ***Impatiens parviflora*** | 2 | 1 | 4 | 3 | 12 | 22 | 14 | 308 | 264 | 23.11.2013 |
| ***Maianthemum bifolium*** | 3 | 1 | 4 | 3 | 12 | 22 | 14 | 308 | 264 | 23.11.2013 |
| ***Acer pseudoplatanus*** | 4 | 2 | 6 | 1 | 6 | 23 | 31 | 851 | 138 | 08.12.2012 |
| ***Aegopodium podagraria*** | 2 | 2 | 6 | 2 | 12 | 22 | 7 | 224 | 264 | 08.12.2012 |
| ***Carpinus betulus*** | 4 | 2 | 6 | 1 | 6 | 23 | 31 | 851 | 138 | 08.12.2012 |
| ***Corylus avellana*** | 4 | 2 | 6 | 1 | 6 | 23 | 31 | 851 | 138 | 08.12.2012 |
| ***Quercus robur*** | 4 | 2 | 6 | 1 | 6 | 23 | 31 | 851 | 138 | 08.12.2012 |
| ***Mercurialis perennis*** | 3 | 2 | 6 | 2 | 12 | 22 | 7 | 224 | 264 | 08.12.2012 |
| ***Stachys sylvatica*** | 2 | 2 | 6 | 2 | 12 | 22 | 7 | 224 | 264 | 08.12.2012 |
| ***Urtica dioica*** | 2 | 2 | 6 | 2 | 12 | 22 | 7 | 224 | 264 | 08.12.2012 |
| | | | | | | | | | **3900** | |

Collection number – number of collection dates for litter bags after field exposure; interval – time between harvests of litter bags after field exposure (days); experiment period – duration of the experiment (days);
[1]Functional group: 1 – spring ephemerals, 2 – summer-greens I, 3 – summer-greens II, 4 – trees and shrubs;

Statistical analyses of *k* and *hd* (multi-factor analysis of variance, ANOVA, with the *post hoc* Tukey HSD test) was done using log-transformed and standardized *k* values to normalize their distribution. To assess the correlations between plant traits and decomposition rates we used principal components analysis (PCA). All analyses were conducted in JMP Pro 14.0 (SAS Institute Inc. Cary, NC. USA; http://www.sas.com).

Nutrient remaining (*R*) was calculated according to Wang et al. (2009):

$$R\% = 100*(Mt*Rt)/(Mo*Ro),$$

where *Mo* (g) is the initial litter dry weight, *Mt* (g) is the dry weight of the remaining litter in the mesh bag when collected, *Ro* is the nutrient concentration (mg/g) of the initial litter, and *Rt* is the nutrient concentration (mg/g) of the remaining litter.

## 3. Results

### 3.1. Decomposition courses of all studies species

Multi-factor analysis of variance, ANOVA, with the *post hoc* Tukey HSD test showed that decomposition rates of leaf litter differed statistically significantly among species ($p < 0.0001$) and collection periods ($p < 0.0001$). Testing the effects of one factor independently from others, we obtained statistically significant differences in decomposition rates between particular species in all collection periods.

The values of regression coefficients show that the two-phase exponential decay model explains litter decomposition in all the plant species slightly better than the one-phase exponential model, although the fit was much better only for *G. luteum*, and for *G. aparine* (Table 4). This shows that litter decomposes uniformly and we did not observe slowing decomposition in later stages due to the occurrence of a harder-decomposable fraction of litter. Despite the fact that we observed marginal better fits for the double than the one-phase decay model, we decided to rely on k-values from the single exponential model, as these dominate the literature, and to address our hypotheses using single *k* value was more convenient.

In the one-phase decay model, the *k* constants ($yr^{-1}$) for litter decomposition of investigated species based on all experiments were arranged from highest to lowest as follows: *A. moschatellina* (11.25), *C. cava* (9.90), *F. verna* (9.27), *A. nemorosa* (6.71), *G. luteum* (6.08), *A. podagraria* (3.48), *G. aparine* (3.09), *M. perennis* (2.40), *M. bifolium* (2.25), *I. parviflora* (1.94), *U. dioica* (1.65), *C. majalis* (1.43), *S. sylvatica* (1.41), *C. betulus* (0.60), *A. pseudoplatanus* (0.54), *C. avellana* (0.47), *Q. robur* (0.33). We found statistically significant differences in the rates of litter decomposition among all species studied. Litter of spring ephemerals decomposed significantly faster (*A. moschatellina*, *C. cava*, *F. verna*) than *A. nemorosa* and *G. luteum* and other herbaceous and tree species litter (Table 4).

Decomposition rate was most strongly affected by species and functional group of plants. *A. moschatellina*, *C. cava* and *F. verna* litter was decomposed most quickly (*hd* from 22 to 26 days), while the decomposition of *A. nemorosa* and *G. aparine* litter was slightly slower (*hd*: 37 and 55 days respectively). *Hd* was much higher for *M. bifolium* (106 days) and *I. parviflora* (124 days). Litter decomposition was the slowest for *C. majalis* (*hd* – 179 days) (Table 4). The decomposition rate of *I. parviflora* (*hd* – 131) was comparable with native oak-hornbeam species senescing in the forest at the same time (*hd* in range: 22–179).

Litter from spring ephemerals decomposed the most quickly (mean *hd* – 27.8 days), while the decomposition of summer-green species and tree litter was significantly slower (mean *hd*: 117.1 and 552.3 days respectively).

Analysis of variance, ANOVA, with the *post hoc* Tukey HSD test showed that there were no statistically significant differences between decomposition rates of tree leaf litter and summer green species litter (Fig. 2, Table 4). Despite that, tree leaf litter decomposition rates (*k*) were much below 1 for all species, whereas the *k* rates for summer green species were higher than 1 (Table 4). In a compared group of plants (trees vs summer green species), *A. podagraria* decomposed the fastest (mean half decay time: 73 days), whereas *M. perennis*, *U. dioica*, and *S. sylvatica* decomposed slightly slower (mean half decay time from 106 to 179 days). The half decay time for tree leaf litter ranged from 420 days for *C. betulus* to 774 days for *Q. robur*. Tree leaf litter did not decompose significantly slower than *U. dioica* (*hd* = 153) or *S. sylvatica* litter (*hd* = 179).

### 3.2. N and C release from decomposing litter

Comparing all the species studied, the highest initial N concentrations (>3.0%) were found in *U. dioica* litter. Intermediate N concentrations (2.01–3.0%) occurred in *A. podagraria*, *C. cava*, *A. nemorosa*, *I. parviflora*, *F. verna*, *C. majalis*. Litter of *M. perennis*, *S. sylvatica*, *A. moschatellina*, *G. aparine*, *G. luteum*, *M. bifolium*, and *G. luteum* had the lowest N concentrations (1.01–2.0%; Table 2). The leaf litter N concentrations of trees were much differentiated and ranged from 1.12% for *Q. robur* leaf litter to 3.07% for *A. pseudoplatanus* leaf litter. Intermediate N concentrations were found in *C. betulus* and *C. avellana* leaf litter (2.72% and 2.48%, respectively).

The rates of N and C release in the entire group of species studied were affected by their decomposition rates. For C concentration of most

**Table 4**
Results of models describing decomposition in the field.

| | Single exponential model | | | | Double exponential model | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species** | **k** | **$R^2$** | **hd [days]** | **results of ANOVA** | **A** | **k1** | **k2** | **$R^2$** | **hd [days]** |
| ***Acer pseudoplatanus*** | 0.537 | 0.84 | 471 | h | 0.070 | 8.126 | 0.469 | 0.85 | 482 |
| ***Adoxa moschatellina*** | 11.245 | 0.70 | 22 | a | 0.997 | 11.567 | −9.574 | 0.70 | 22 |
| ***Aegopodium podagraria*** | 3.482 | 0.74 | 73 | c | 0.163 | 32.497 | 2.606 | 0.78 | 73 |
| ***Anemone nemorosa*** | 6.707 | 0.65 | 37 | b | 0.153 | 590.051 | 5.427 | 0.69 | 37 |
| ***Carpinus betulus*** | 0.602 | 0.86 | 420 | h | 0.961 | 0.602 | 0.605 | 0.86 | 420 |
| ***Convallaria majalis*** | 1.429 | 0.74 | 179 | defgh | 0.102 | 26.900 | 1.195 | 0.77 | 179 |
| ***Corylus avellana*** | 0.466 | 0.85 | 544 | h | 0.797 | 0.465 | 0.470 | 0.85 | 544 |
| ***Corydalis cava*** | 9.900 | 0.70 | 26 | a | 0.064 | −1.700 | 12.700 | 0.74 | 22 |
| ***Ficaria verna*** | 9.265 | 0.65 | 26 | a | 0.866 | 13.762 | −0.086 | 0.72 | 22 |
| ***Galium aparine*** | 3.090 | 0.34 | 80 | cdef | 0.572 | 11.760 | 0.402 | 0.76 | 55 |
| ***Galeobdolon luteum*** | 6.082 | 0.24 | 40 | b | 0.758 | 14.362 | 0.392 | 0.81 | 26 |
| ***Impatiens parviflora*** | 1.940 | 0.71 | 131 | cdefgh | 0.185 | 22.699 | 1.449 | 0.78 | 124 |
| ***Maianthemum bifolium*** | 2.254 | 0.84 | 113 | cdefgh | 0.153 | 13.458 | 1.853 | 0.86 | 106 |
| ***Mercurialis perennis*** | 2.398 | 0.85 | 106 | cdefg | 0.574 | 2.398 | 2.398 | 0.85 | 106 |
| ***Quercus robur*** | 0.327 | 0.77 | 774 | h | 0.415 | 0.327 | 0.327 | 0.77 | 774 |
| ***Stachys sylvatica*** | 1.411 | 0.83 | 179 | fgh | 0.046 | 77.178 | 1.255 | 0.84 | 186 |
| ***Urtica dioica*** | 1.654 | 0.80 | 153 | efgh | 0.238 | 1.654 | 1.654 | 0.80 | 153 |

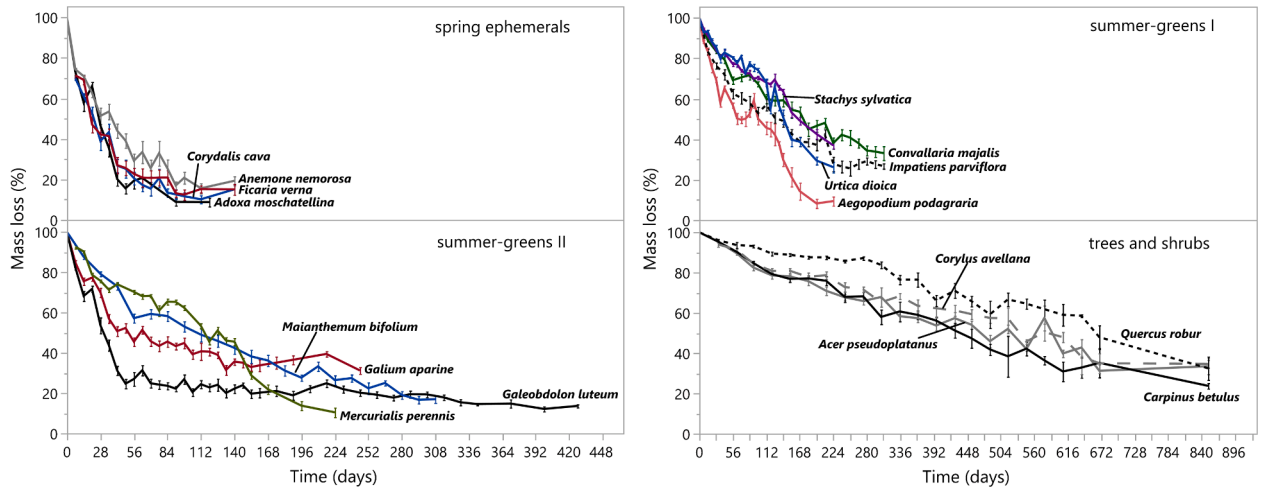


**Fig. 2.** Decomposition (percentage of initial mass loss) of studied species.

species, we found an exponential nutrient release right from the beginning of litter decomposition (Fig. 3a). For N, nutrient accumulation was found in the first month of decomposition for *A. moschatellina*, *G. aparine*, *G. luteum*, *M. bifolium*, *M. perennis*, and *S. sylvatica* and after the first year of decomposition for *Q. robur*; just after that, in the second month of the second year (in the case of *Q. robur*) of decomposition, a decrease started (Fig. 3b). In the other species, we found an exponential nutrient release right from the beginning of litter decomposition.

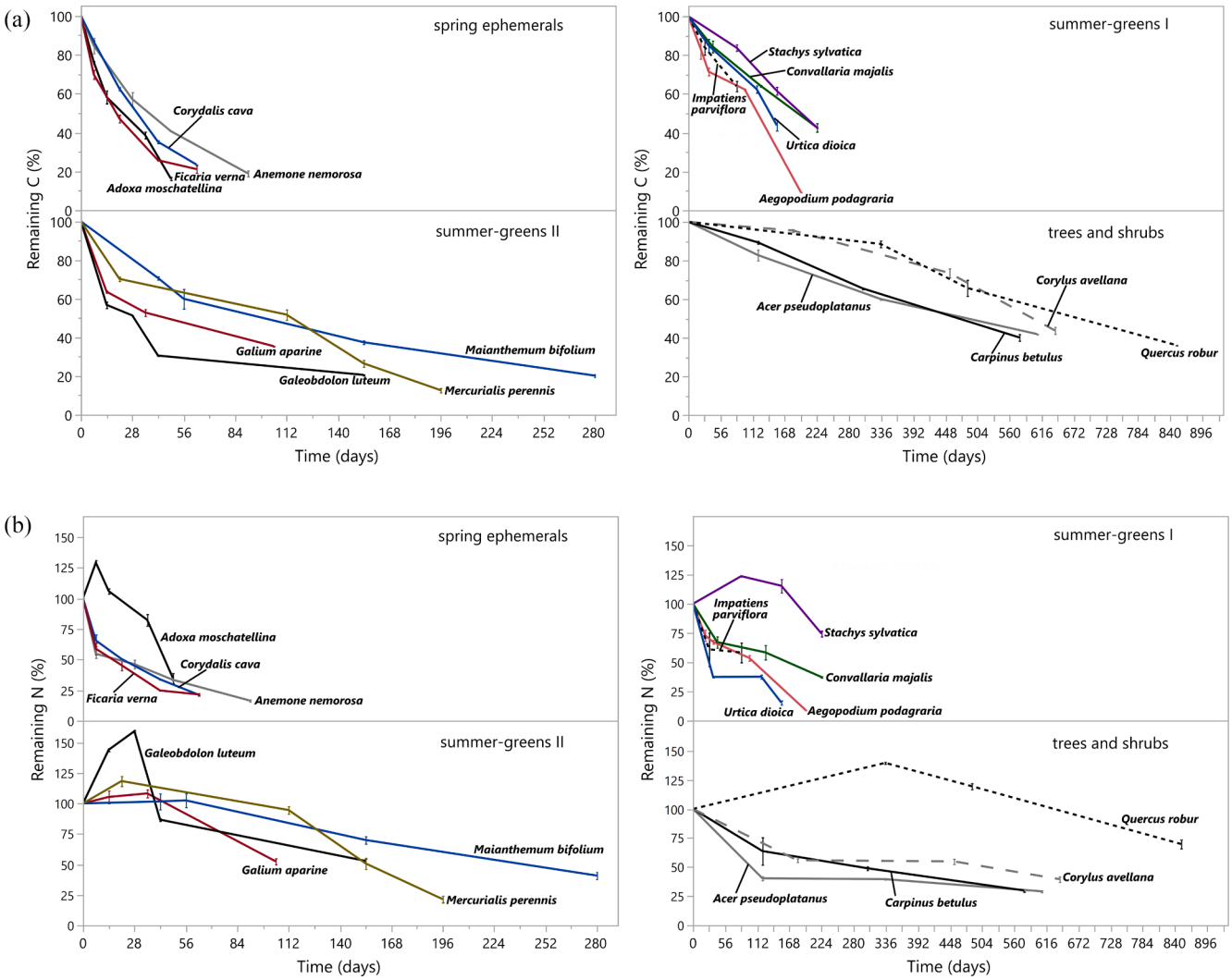


**Fig. 3.** Percent of mass remaining of nutrients: a) carbon (C) in decomposing litters, b) nitrogen (N) in decomposing litters.

### 3.3. Trait relationships across herbaceous species

PCA effectively captured the variations of traits included in the study. The principal ordination axis (PC1) accounted for 37.2% of the total trait variation, and together with the first two principal axes, accounted for 65.1% of the total trait variation (Fig. 4). LP, LCC, and C/N contributed to the first axis, whereas LDMC, and LNC also contributed to the first axis, but in the opposite direction. SLA, TAB, and TLA contributed to the second axis, whereas *k* and LMF contributed to the second axis, but in the opposite direction.

Correlation analyses revealed significant positive relationships between TLA and TAB as well as between C/N ratio and LCC and LP across all species, whereas a negative relationship was revealed between C/N ratio and LNC, LCC and LNC content, LMF and SLA. Decomposition rate was correlated statistically significantly negatively with TLA (Table 5).

## 4. Discussion

### 4.1. Decomposition courses of the species studied

Although the single exponential model proposed by Olson (1963) was the commonly used model in previous studies (Cornwell and Weedon, 2014), a double exponential model proposed by Bunnell et al. (1977) is recommended for herbaceous species litter, as it better covers the litters made up of different fractions. Labile compounds of litter which decomposed faster at the beginning of exposure in the field, differ from the more resistant fraction, resulting in a visible two-stage decomposition process. Results of our study indicate small differences in the fits of the single and double exponential models in the cases of most species studied. Only in the cases of two species (*G. luteum* and *G. aparine*) was the double exponential model a much better fit to the course of the decomposition process. Thus, in these two cases, decomposing material is made up of different fractions, decomposing at different rates. This is a bit surprising, as in most study species the material is a mix of leaves and shoots, which should differ in decomposition rates. These two species belonged to species with the smallest LMF, which can explain a big slowdown of the process after the first fast phase, when the leaf fraction is decomposed. However, it is still surprising that other species with similar biomass allocations (e.g. *I. parviflora*, *M. perennis*) did not show a clear differentiation of the decomposition process into two phases. Both *G. luteum* and *G. aparine* have hairy stems, which can enhance differences in decomposability of leaves and stems of these two plant species. It was proved that such structures, which increased protection of organs against herbivores, pathogens or the physical environment, simultaneously decreased their decomposability (Cornelissen et al. 2004; Bumb et al. 2018).

Generally, patterns of decomposition were similar to those obtained in our previous studies, connected with life strategies and functional traits (Rawlik et al. 2019; Rawlik et al. 2021), although in these studies we examined earlier stages of decomposition with a different pool of species and functional traits. Results of *k* obtained by a single exponential model were similar to results concerning the same species available in earlier publications. According to (Muller 2014), the decomposition rates of herbaceous species during 12 months of field exposure reached values in the range of 0.61–3.31. It is worth a reminder that lower k is equivalent to a slower decomposition rate. During our previous experiment (Rawlik et al. 2021) decomposition rates of six species included in the spring ephemeral group reached *k* values in the range of 4.7–6.9, while mid-summer senescing summer-green plants (three species) ranged from 0.2 to 1.4, autumn-senescing summer-green plants (four species) ranged from 0.9 to 3.2, and trees and shrubs ranged from 0.2 to 0.8. In the current studies, *k* was higher by about 0.5 for all of the repeated species studied (Table 4; Rawlik et al. 2021), which was contrary to our expectations. Previous studies were conducted in more rich and wet sites; thus, we expected higher values of decomposition rates in those sites. Explanation of this phenomenon can also be higher temperatures and precipitation during the currently described experiment (Table 2 and 3 in the Appendix ; Rawlik et al. 2021).

According to previous studies, the faster decomposition of herb litter than tree leaf biomass is one of the key certainties in decomposition in forest ecosystems (Halabuk and Gerhátová 2011; Mayer 2008; Muller 2014). Tree foliage has decomposition rates of $k < 1$, while for most herbaceous litter of $k > 1$. In our previous studies, we did not find significant differences between the decomposition of *F. excelsior* leaves and *A. podagraria* blooming shoots after six months of the study. This is in accordance with results obtained by Wang et al. (2021) in an old-growth temperate mixed deciduous forest in Belgium, which indicated that *F. excelsior* litter decomposed the fastest ($k = 1.68$) compared to four other tree species litter (*Fagus sylvatica*, *Q. robur*, *A. pseudoplatanus* and

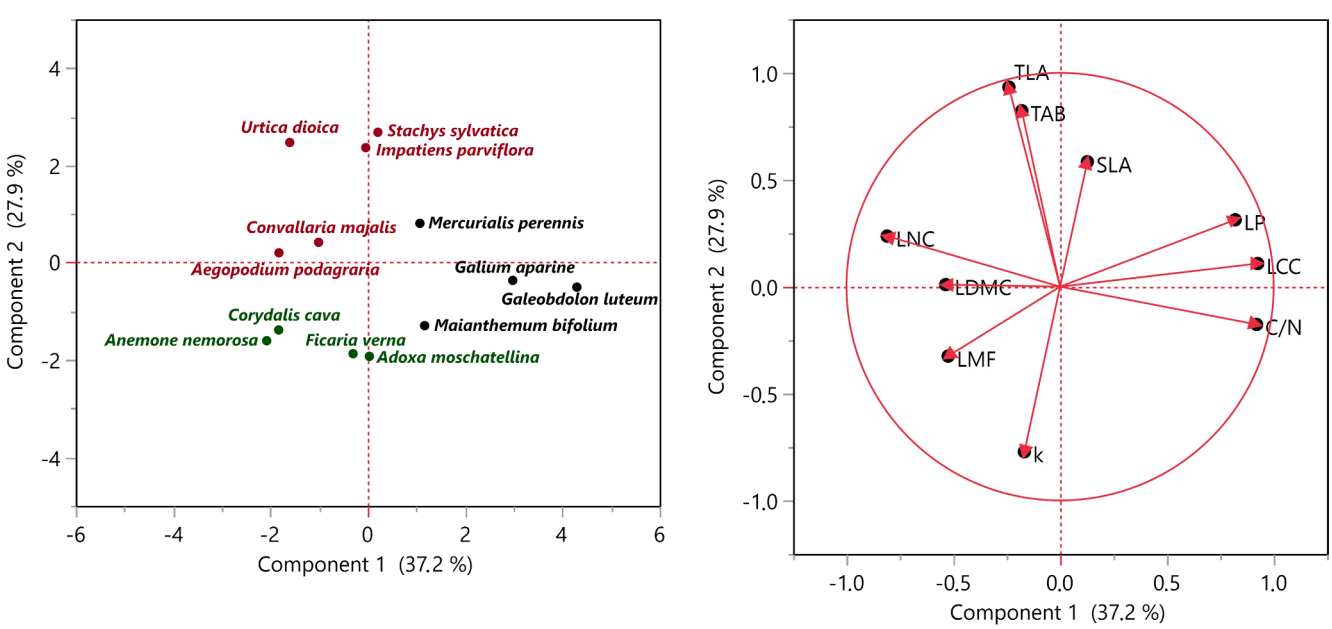


**Fig. 4.** Results of principal components analysis, including all herbaceous species. green dots – spring ephemerals; red dots – summer-greens I; black dots – summer-greens II; (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 5**
Correlation matrix of studied traits.

| Parameter | k | LDMC | C/N | LNC | LCC | LMF | TLA | TAB | SLA | LP |
|---|---|---|---|---|---|---|---|---|---|---|
| **k** | 1 | −0.2759 | −0.0804 | −0.0180 | −0.3170 | 0.0530 | **−0.6035** | −0.5167 | −0.3572 | −0.4690 |
| **LDMC** | | 1 | −0.3006 | 0.1792 | −0.3562 | 0.4734 | 0.1333 | 0.2101 | −0.4303 | −0.4643 |
| **C/N** | | | 1 | **−0.9527** | **0.8342** | −0.3230 | −0.3344 | −0.1881 | −0.1336 | **0.6388** |
| **LNC** | | | | 1 | **−0.6752** | 0.2872 | 0.3536 | 0.1710 | 0.1695 | −0.4390 |
| **LCC** | | | | | 1 | −0.3762 | −0.1177 | −0.0621 | 0.0378 | **0.8804** |
| **LMF** | | | | | | 1 | −0.1500 | −0.0644 | **−0.5739** | −0.3191 |
| **TLA** | | | | | | | 1 | **0.9335** | 0.3936 | 0.0724 |
| **TAB** | | | | | | | | 1 | 0.1356 | 0.0966 |
| **SLA** | | | | | | | | | 1 | 0.1231 |
| **LP** | | | | | | | | | | 1 |

litter decomposition rate (k); leaf dry matter content (LDMC); the ratio of C to N in senescent material; mean N content (%) in senescent material; mean C content (%) in senescent material; leaf mass fraction (LMF); total leaf area (TLA); total biomass (TAB); specific leaf area (SLA); leaf persistence (LP) – r values; significant correlations in bold;

*Tilia platyphyllos*), as it belongs to labile tree litter. In the current studies, we did not find significant differences between litter decomposition rates of trees and *U. dioica* and *S. sylvatica* litter, although tree leaf litter decomposed more slowly. This is in accordance with our previous studies and it shows that we should be careful to classify the plant litter into labile or non-labile fractions, as some parts of herbaceous plant materials (probably stems) can be categorized as more resistant to decomposition. The general concept of including herbaceous species litter in the labile fraction of litter was based on studies of leaf decomposition in this group of plants.

Several studies have compared litter decomposition between invasive alien species and natives, but no generalization about the comparison between decomposition of native and invasive species has arisen so far (Ehrenfeld 2003). According to the results of some studies, invasive species usually represent higher values of traits connected with size, growth rate, leaf-area allocation, and shoot allocation, connected with a strategy called 'try harder' (Dyderski and Jagodziński 2019; Van Kleunen et al. 2010). However, some of the previous results suggest that invasive species rather 'join the locals' – represent a similar life strategy to their most frequent competitors (Dyderski and Jagodziński 2019). Results of our studies show comparable decomposition rates of an alien invasive species (*I. parviflora*) and native oak-hornbeam herbaceous species.

### 4.2. N and C release from decomposing litter

According to previous studies, chemical elements differed in their release dynamics (Aponte et al. 2012; Berg and McClaugherty 2014). In general, some patterns in the dynamics of release of particular chemical elements are similar in various forest ecosystems and types of litter, while some patterns are highly specific (Aponte et al. 2012). We have observed N release-immobilization during the early phase of decomposition for *A. moschatellina*, leaves of *A. petiolata* and *G. aparine*, leaves and shoots of *G. luteum*, *M. bifolium*, *M. perennis*, *Q. robur*, and *S. sylvatica* litter. Similar trends were observed earlier (Jacob et al. 2010 or Kriiska et al. 2021) and were explained by rapid microbial growth which followed the initial leaching of soluble components. During this time nitrogen-enriched compounds are formed and N is immobilized in the detritus-microbe complex (Kriiska et al. 2021). Swift et al. (1979) described the phenomenon of synchronization of nutrients released from aboveground inputs and roots with plant growth demands. According to this conception the time of higher release of nutrients is synchronized with the time of other plants growth, thus peaks in N release from litter potentially give opportunities for maximum loss of N from the ecosystem. We did not observe such patterns for other species, as nutrient release in those cases was very rapid and an immobilization phase was not observed. In-depth studies of patterns of release of nutrients in herbaceous species of an oak-hornbeam forest are needed to understand these processes and their impact on ecosystem functioning.

### 4.3. Trait relationships across herbaceous species

Functional traits of leaves, as well as litter quality, are known to explain much of the variation in decomposition rates (Cornwell et al. 2008; Freschet et al. 2012; Pietsch et al. 2014; Weedon et al. 2009). This kind of studies has placed decomposition rates between traits characterizing the plant economic spectrum (Freschet et al. 2012; Wright et al. 2004), where species in the acquisitive side of the spectrum, with high SLA and nutrient concentrations, are associated with more rapid decomposition rates (Aerts 1997; Freschet et al. 2012; Pietsch et al. 2014), while species with conservative strategies, and traits such as high LDMC and low nutrient concentrations, decompose relatively slowly (Aponte et al. 2012; Cortez et al. 2007; Gallardo and Merino 1993). However, few studies have assessed the relationships between leaf and litter traits and decomposition rates in forest ecosystems (Jurkšienė et al. 2017; Horodecki and Jagodziński 2017, 2019), and they mainly focused on tree leaf litter. Our previous studies showed that functional traits of leaves of herbaceous plants were correlated with their decomposition, and the best predictor for decomposition rates was LDMC, before SLA and LNC (Rawlik et al. 2021). These results were similar to others (Freschet et al. 2012; Pietsch et al. 2014) indicating that economic traits such as SLA, LNC, LDMC were the best predictors of decomposition rates. In our previous studies, we did not include size traits in our analysis, as they are generally considered to have less influence on decomposition (Rawlik et al. 2021). Economics traits did not explain any parts of variability in decomposition rates in these studies, because the considered group of plants includes species with high SLA but also high contributions of stems to aboveground biomass (e.g. *A. petiolata* or blooming shoots of *A. podagraria*). Thus, we decided to include size traits (TAB, TLA, LMF) in our current study. As we suspected, these traits had an impact on the decomposition process of oak-hornbeam herbaceous species, but only the impact of TLA was statistically negatively significant. In the past, TLA was used as an explanation of the variability of aboveground biomass in a grassland ecosystem (Schumacher and Roscher 2009). Our results showed that TAB influenced decomposition, but this correlation was not statistically significant. Thus, we can make the simplification that within the studied group of species, big plants with big leaf area decompose relatively the slowest. The group of herbaceous species of temperate deciduous forests is diverse, consisting of plants with different phenological strategies. Within this group, we can distinguish two groups of plants, adapted to shade-stress differently: (a) small species with economically acquisitive strategies (spring ephemerals), (b) tall species with economically acquisitive strategies (summer and autumn species) (Jagodziński et al. 2016; Rawlik and Jagodziński 2020, 2021; Uemura 1994). Although spring ephemerals are fast growing species, their SLA is lower than summer-green species. This group of herbaceous plants grows in early spring, thereby avoiding shade, but at the same time must withstand frost. As noticed by Blondeel et al. (2020), it can be the result of a mass-investment trade-off, taking

into account the short leaf lifespan and stress-tolerance of these plants. Our results demonstrate that in this generally acquisitive group of plants (herbaceous plant species), size traits have a stronger impact on decomposition than economic traits. Studies of Funk and Cornwell (2013) and Messier et al. (2017) showed that correlations between SLA, photosynthetic rate, and leaf nitrogen concentration tend to be weak, when (a) the species pool consists of few growth forms, (b) leaf life span is constrained by climatic seasonality, and (c) variation in shade tolerance is low. Our results note limitations of generally accepted relationships between decomposition and functional traits, which can be explained similarly by a specific characteristic of the species pool. The other explanation of our surprising finding is the kind of materials included in studies, which is in our case mixed leaves and stems. Economic traits better explain leaf litter decomposition rate than other organs, which were described for roots and bark of trees (Pietsch et al. 2014).

## 5. Conclusions

1. The litter decomposition rate and C and N release were higher in spring ephemerals than summer green herbaceous species.
2. In herbaceous forest plant species, size traits have a stronger impact on decomposition than economic traits, as the plants with small total individual aboveground biomass (TAB) and small total leaf area (TLA) decomposed the fastest.
3. For almost all herbaceous forest species, the two-phase exponential decay model explains the course of herbaceous species litter decomposition only slightly better than the single exponential model.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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*Authors' contributions*

KR and AMJ conceived the ideas and designed methodology; KR, MN and MK collected the data; KR, MN, MK and AMJ analyzed the data; KR wrote the first draft of the manuscript; AMJ supervised. All authors contributed critically to the drafts and gave final approval for publication.

## Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120008.

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Table 1. General description of sample plots.

| N$^{o}$ of sample plot | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Tree stand age | 135 | 135 | 135 | 135 |
| Tree stand composition | *Quercus robur*, *Carpinus betulus* | *Quercus robur*, *Carpinus betulus* | *Quercus robur*, *Carpinus betulus* | *Quercus robur*, *Carpinus betulus* |
| Main plant communities | *Galio sylvatici-Carpinetum* (R.Tx. 1937) Oberd. 1957 *corydalidetosum* Oberd. 1957 | *Galio sylvatici-Carpinetum* (R.Tx. 1937) Oberd. 1957 *corydalidetosum* Oberd. 1957 | *Galio sylvatici-Carpinetum* (R.Tx. 1937) Oberd. 1957 *corydalidetosum* Oberd. 1957 | *Galio sylvatici-Carpinetum* (R.Tx. 1937) Oberd. 1957 *corydalidetosum* Oberd. 1957 |
| Soil type | Stagnic Gleyic Umbrisol (Arenic, Humic) | Brunic Gleyic Umbrisol (Arenic, Humic) | Stagnic Gleyic Gleysol (Arenic, Humic) | Stagnic Gleyic Umbrisol (Arenic, Humic) |
| LAI | 4.79 | 5.32 | 6.14 | 6.16 |

Table 2. Mean air temperature (°C) and monthly sum of precipitation (mm) during the growing seasons of 2010, 2011, 2012, 2013, 2014 and 2015.

| | Temperature (°C) | | | | | Precipitation (mm) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Month | 2011 | 2012 | 2013 | 2014 | 2015 | 2011 | 2012 | 2013 | 2014 | 2015 |
| January | 0.4 | 0.4 | -2.3 | -1.2 | 2.1 | 29.4 | 74.5 | 58.0 | 55.8 | 34.9 |
| February | -3.4 | -4.6 | 0.0 | 3.3 | 1.3 | 30.1 | 44.2 | 43.7 | 5.3 | 9.1 |
| March | 3.0 | 5.8 | -2.5 | 6.4 | 5.0 | 17.3 | 10.3 | 37.5 | 49.6 | 48.4 |
| April | 11.6 | 9.0 | 8.2 | 10.6 | 8.4 | 10.7 | 30.5 | 27.5 | 36.2 | 29.4 |
| May | 14.6 | 15.2 | 14.8 | 13.7 | 13.4 | 16.9 | 40.8 | 73.1 | 79.2 | 17.3 |
| June | 19.0 | 16.5 | 17.9 | 16.6 | 16.3 | 59.3 | 117.5 | 117.7 | 18.9 | 71.7 |
| July | 18.2 | 19.8 | 20.1 | 21.8 | 19.8 | 108.1 | 124.6 | 52.8 | 48.1 | 61.4 |
| August | 19.7 | 18.6 | 18.8 | 17.7 | 21.8 | 78.8 | 52.1 | 35.0 | 78.3 | 20.6 |
| September | 14.7 | 13.7 | 12.3 | 15.1 | 14.4 | 24.7 | 38.2 | 85.4 | 45.6 | 24.8 |
| October | 9.1 | 7.8 | 10.3 | 10.4 | 7.4 | 26.8 | 29.2 | 25.9 | 28.9 | 24.1 |
| November | 3.2 | 5.1 | 5.1 | 5.7 | 5.9 | 0.7 | 47.1 | 42.0 | 16.9 | 54.0 |
| December | 3.3 | -1.6 | 2.6 | 1.8 | 5.6 | 48.0 | 35.2 | 24.6 | 36.8 | 27.3 |

Table 3. Meteorological characteristics during the experiment. Ranges and mean values were given for 6 month periods from the beginning of the experiments, where leaf litter in litterbags was placed in the forest (4 terms)

| Date | Air temperature (°C) at the meteorological station | | | Ground temperature (°C) in the forest | | | Mean total daily precipitation (mm) at the meteorological station | | |
|---|---|---|---|---|---|---|---|---|---|
| | during 6 months | | | during 6 months | | | during 6 months | | |
| | Mean | SD | SE | Mean | SD | SE | Mean | SD | SE |
| 08.12.2012 | 3.50 | 8.08 | 0.60 | 4.67 | 6.45 | 0.10 | 2.16 | 3.28 | 0.29 |
| 22.06.2013 | 12.23 | 6.91 | 0.51 | 11.93 | 6.37 | 0.10 | 3.72 | 7.48 | 0.76 |
| 10.08.2013 | 8.74 | 5.64 | 0.46 | 7.70 | 5.77 | 0.09 | 2.58 | 4.48 | 0.49 |
| 23.11.2013 | 5.26 | 5.81 | 0.43 | 5.67 | 4.04 | 0.06 | 2.18 | 2.92 | 0.30 |

Table 4. Tree stand characteristics of the study plots.

| Sample plot N° | Tree species | Basal area ($m^2$ $ha^{-1}$) | Mean tree diameter (cm) | Mean tree height (m) | Trees density ($ha^{-1}$) |
|---|---|---|---|---|---|
| 1 | *Quercus robur* | 5.3 | 48.7 | 29.0 | 140 |
| | *Fraxinus excelsior* | 0.1 | 29.6 | 22.5 | 5 |
| | *Carpinus betulus* | 1.1 | 23.6 | 18.5 | 1215 |
| | *Padus serotina* | - | - | - | 5 |
| | *Acer pseudoplatanus* | - | - | - | 20 |
| | *Frangula alnus* | - | - | - | 25 |
| | *Corylus avellana* | 0.1 | 6.3 | - | 100 |
| 2 | *Quercus robur* | 4.0 | 29.7 | 33.0 | 126 |
| | *Fraxinus excelsior* | 0.2 | 30.9 | 25.5 | 74 |
| | *Carpinus betulus* | 1.1 | 24.8 | 19.3 | 1637 |
| | *Acer pseudoplatanus* | - | - | - | 393 |
| | *Frangula alnus* | - | - | - | 37 |
| | *Corylus avellana* | - | - | - | 15 |
| 3 | *Quercus robur* | 2.2 | 45.5 | 31.0 | 144 |
| | *Fraxinus excelsior* | 0.2 | 44.7 | 30.5 | 11 |
| | *Carpinus betulus* | 0.8 | 14.7 | 18.0 | 522 |
| 4 | *Quercus robur* | 2.6 | 41.6 | 29.0 | 200 |
| | *Fraxinus excelsior* | 0.03 | 20.0 | 20.5 | 11 |
| | *Carpinus betulus* | 0.6 | 15.7 | 19.0 | 422 |
| | *Corylus avellana* | 0.01 | 7.3 | - | 856 |

Table 5. Phytosociological descriptions of the sample plots.

| | | | | | |
|---|---|---|---|---|---|
| Succesive no. of relevé | | 1 | 2 | 3 | 4 |
| No. of sample plot | | P I | P II | P III | P IV |
| Date: d/m/y | | 17/04/2014 and 24/07/2014 | | | |
| Density of tree layer (a) in % | | 90 | 90 | 80 | 80 |
| Density of tree layer (a1) in % | | 60 | 60 | 40 | 60 |
| Density of tree layer (a2) in % | | 60 | 80 | 80 | 80 |
| Density of shrub layer (b) in % | | + | + | + | + |
| Cover of herb layer (c) in % | | 70 | 65 | 75 | 75 |
| Cover of moss layer (d) in % | | + | + | . | . |
| Area of relevé in $m^2$ | | 225 | 225 | 225 | 225 |
| No. of species | | 44 | 43 | 40 | 40 |
| **Ch. *Galio sylvatici-Carpinetum*** | | | | | |
| *Carpinus betulus* | a2 | 4 | 5 | 5 | 5 |
| *Carpinus betulus* | b | + | + | + | + |
| *Carpinus betulus* | c | 1 | + | 2 | 2 |
| *Dactylis polygama* | | . | + | + | . |
| *Tilia cordata* | c | . | . | + | + |
| *Cerasus avium* | c | . | . | . | + |
| **D. *G.s.-C. corydalidetosum*** | | | | | |
| *Corydalis cava* (*Fag*) | | + | +. | 2 | 2 |
| *Anemone ranunculoides* (*Fag*) | | + | + | 2 | + |
| *Ficaria verna* (*Fag*) | | + | + | 2 | + |
| *Gagea lutea* (*Fag*) | | . | + | + | . |
| **Ch. *Fagetalia sylvaticeae*** (*Fag*) | | | | | |
| *Acer pseudoplatanus* | b | + | + | . | + |
| *Acer pseudoplatanus* | c | . | + | + | + |
| *Acer platanoides* | c | + | . | + | + |
| *Padus avium* | b | . | + | . | . |
| *Padus avium* | c | + | . | + | + |
| *Fraxinus excelsior* | b | + | + | + | . |
| *Fraxinus excelsior* | c | 1 | 2 | 2 | 2 |
| *Galeobdolon luteum* | | 2 | 2 | 2 | 2 |
| *Asarum europaeum* | | + | . | + | + |
| *Polygonatum multiflorum* | | . | + | + | + |
| *Carex sylvatica* | | + | + | . | . |
| *Festuca gigantea* | | + | . | + | . |
| *Adoxa moschatellina* | | . | + | . | + |
| *Mercurialis perennis* | | . | . | + | + |
| *Lathyrus vernus* | | . | . | . | + |
| *Pulmonaria obscura* | | . | . | . | + |
| **Ch. *Querco-Fagetea*** | | | | | |
| *Corylus avellana* | b | + | . | + | . |
| *Corylus avellana* | c | + | . | + | + |
| *Euonymus europaeus* | b | r | . | . | . |
| *Euonymus europaeus* | c | + | + | + | . |
| *Anemone nemorosa* | | 4 | 4 | 4 | 4 |
| *Viola reichenbachiana* | | + | + | + | + |
| *Hepatica nobilis* | | + | + | + | + |
| *Milium effusum* | | + | + | + | + |

| | | | | | |
|---|---|---|---|---|---|
| *Brachypodium sylvaticum* | | 2 | + | . | + |
| *Scrophularia nodosa* | | + | . | + | . |
| *Viola riviniana* | | . | + | + | . |
| *Melica nutans* | | . | + | . | + |
| *Lilium martagon* | | . | . | . | r |
| *Poa nemoralis* | | + | . | . | . |
| *Epipactis helleborine* | | . | . | . | r |
| **Ch. *Artemisietea vulgaris*** | | | | | |
| *Moehringia trinervia* | | + | + | + | + |
| *Alliaria petiolata* | | + | + | + | + |
| *Galeopsis tetrahit* | | + | + | + | r |
| *Galium aparine* | | + | + | + | + |
| *Impatiens parviflora* | | 2 | 2 | 2 | . |
| *Aegopodium podagraria* | | + | + | + | . |
| *Fallopia dumetorum* | | r | r | . | r |
| *Chaerophyllum temulum* | | + | . | + | + |
| *Urtica dioica* | | + | + | . | . |
| *Geranium robertianum* | | + | . | + | . |
| *Geum urbanum* | | + | . | + | . |
| *Rubus caesius* | | + | . | . | . |
| **Others** | | | | | |
| *Quercus robur* | a1 | 4 | 4 | 3 | 4 |
| *Quercus robur* | c | + | + | + | + |
| *Sambucus nigra* | b | + | . | . | . |
| *Sambucus nigra* | c | + | . | + | . |
| *Padus serotina* | b | . | + | . | . |
| *Cornus sanguinea* | b | . | . | . | + |
| *Cornus sanguinea* | c | . | . | . | + |
| *Convallaria maialis* | | 2 | 2 | + | + |
| *Maianthemum bifolium* | | 2 | 2 | + | + |
| *Luzula pilosa* | | + | + | . | + |
| *Rubus idaeus* | | + | + | . | + |
| *Brachytheciastrum vellutinum* | d | + | + | . | . |
| *Carex spicata* | | + | + | . | . |
| *Hypnum cupressiforme* | d | + | + | . | . |
| *Padus serotina* | c | . | + | r | . |
| *Vicia sepium* | | . | + | + | . |
| *Pyrus pyraster* | c | + | . | . | . |
| *Dryopteris carthusiana* | | r | . | . | . |
| *Alnus glutinosa* | c | . | r | . | . |
| *Polytrichastrum formosum* | d | . | + | . | . |
| *Amblystegium serpens* | d | . | + | . | . |
| *Dryopteris dilatata* | | . | . | r | . |
| *Calamagrostis epigeios* | | . | . | . | + |
| *Rubus saxatilis* | | . | . | . | + |

Table 6. Properties of the soil on the sample plots.

| Sample plot No. | Soil horizon | Depth [cm] | Percentage content of fractions with particle diameter [mm] | | | Granulometric group | $C_{org}$ | $N_{tot}$ | C/N | Humus content | pH Reaction | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Sand (0.05-2 mm) | Silt (0.002-0.05 mm) | Clay (<0.002 mm) | | % | | | % | in $H_2O$ | in KCl |
| 1 | Ol | 2(3)-1 | - | - | - | - | 39.200 | 1.376 | 28.5 | 67.58 | 5.21 | 4.80 |
| | Ofh | 1-0 | - | - | - | - | 43.120 | 1.680 | 25.7 | 74.34 | 4.76 | 4.38 |
| | Au | 0-37 | 81 | 17 | 2 | LoSa | 1.597 | 0.135 | 11.8 | 2.75 | 3.82 | 3.48 |
| | AC | 37-47 | 85 | 12 | 3 | LoSa | 0.425 | 0.034 | 12.5 | 0.73 | 4.45 | 3.75 |
| | C1g | 47-78 | 93 | 6 | 1 | Sa | 0.152 | 0.012 | 12.6 | 0.26 | 6.96 | 6.43 |
| | C2g | 78-150 | 92 | 7 | 1 | Sa | 0.104 | 0.008 | 13.0 | 0.18 | 7.78 | 7.66 |
| 2 | Ol | 2(3)-1 | - | - | - | - | 39.200 | 2.026 | 19.3 | 67.58 | 5.22 | 4.78 |
| | Ofh | 1-0 | - | - | - | - | 35.031 | 1.800 | 19.5 | 60.39 | 5.02 | 4.68 |
| | Au | 0-30 | 76 | 20 | 4 | LoSa | 1.534 | 0.152 | 10.1 | 2.65 | 4.12 | 3.56 |
| | AB | 30-42 | 85 | 13 | 2 | LoSa | 0.424 | 0.039 | 10.9 | 0.73 | 5.39 | 4.56 |
| | BC | 42-59 | 81 | 13 | 6 | LoSa | 0.183 | 0.016 | 11.4 | 0.32 | 6.23 | 5.12 |
| | Cg | 59-150 | 92 | 5 | 3 | Sa | 0.078 | 0.007 | 11.1 | 0.13 | 6.70 | 5.53 |
| 3 | Ol | 2(3)-1 | - | - | - | - | 38.500 | 1.723 | 22.3 | 66.37 | 5.25 | 4.71 |
| | Ofh | 1-0 | - | - | - | - | 43.255 | 1.565 | 27.6 | 74.57 | 5.27 | 4.79 |
| | Au | 0-31 | 77 | 21 | 2 | LoSa | 1.962 | 0.182 | 10.8 | 3.38 | 4.48 | 3.95 |
| | AC | 31-51 | 62 | 35 | 3 | LoSa | 0.539 | 0.042 | 12.8 | 0.93 | 7.75 | 7.34 |
| | Cg | 51-120 | 95 | 4 | 1 | Sa | 0.082 | 0.006 | 13.7 | 0.14 | 7.99 | 7.71 |
| 4 | Ol | 2(3)-1 | - | - | - | - | 41.645 | 1.831 | 22.7 | 71.80 | 5.53 | 4.94 |
| | Ofh | 1-0 | - | - | - | - | 41.160 | 1.800 | 22.9 | 70.96 | 4.97 | 4.57 |
| | Au | 0-37 | 80 | 18 | 2 | LoSa | 1.875 | 0.151 | 12.4 | 3.23 | 4.43 | 3.51 |
| | AC | 37-50 | 91 | 7 | 2 | Sa | 0.329 | 0,031 | 10,6 | 0.57 | 5.67 | 4.40 |
| | C1g | 50-60 | 97 | 2 | 1 | Sa | 0.087 | 0.008 | 10.9 | 0.15 | 6.60 | 4.78 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| C2g | 60-82 | 90 | 7 | 3 | Sa | 0.087 | 0.007 | 12.4 | 0.15 | 6.77 | 5.34 |
| C3g | 82-150 | 90 | 8 | 2 | Sa | 0.067 | 0.006 | 11.2 | 0.12 | 6.81 | 5.24 |

Publikacja 4.

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ORIGINAL PAPER

# Differences in C and N release from *Alliaria petiolata* leaves and stems: consequences for nutrient cycling in forest ecosystems

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## Abstract

Garlic mustard (*Alliaria petiolata* (Bieb.) Cav. et Grande) is a widespread forest edge plant species in the European temperate zone and also one of the most invasive herbaceous species in North America. Studies of *A. petiolata* decomposition and nutrient release are relatively scarce. We know even less about the differences in decomposition of particular organs. Invasive species, by their impacts on litter quality, may have a large effect on ecosystem functioning. Therefore, we studied the decomposition process and N and C release patterns using the litterbag method. We determined decay constants ($k$), half decay rates and total decay rates of *A. petiolata* leaves and stems separately. We found statistically significant differences in the rate of litter decomposition both between organ types and collection times. During 126 days of the experiment, 87.3% of the leaves biomass of *A. petiolata* decomposed. At the same time, only 24.5% of the stem biomass of *A. petiolata* decomposed. During 532 days of the experiment, 55.4% of studied plant stems decomposed. Litter decomposition of *A. petiolata* leaves is 3.5 times faster than decomposition of *A. petiolata* stems. The patterns of N and C release were different for leaves and stems of *A. petiolata*. In the case of *A. petiolata* stems, we found N and C immobilization during decomposition. Our results support assumption that neglecting decomposition rates of stems leads to almost a fivefold (4.8) overestimation of whole-plant decomposition rate after six months of decomposition.

**Keywords** Ecosystem functioning · Total decay time · Herbaceous plants · Garlic mustard · Invasive species · Decomposition

## Introduction

*Alliaria petiolata* (Bieb.) Cav. et Grande (garlic mustard, Brassicaceae) is a tall, short-lived biennial, native to western Eurasia. Within its native range, *A. petiolata* is most common in habitats of relatively high air humidity. It prefers slightly shaded places beside rivers and at roadsides and tracks (British Isles; Grime 1988). *A. petiolata* was used as a culinary and medicinal herb, and because of this was probably introduced to North America in 1868 (Nuzzo 1999). Now *A. petiolata* is one of the most rapidly expanding invasive plants of woodland habitats in eastern North America. Meekins and McCarthy (2001) highlighted that *A. petiolata* can invade the forest understory in the absence of disturbance, thanks to shade tolerance. In North America, *A. petiolata* most frequently occurs in moist, shaded soils of river floodplains, forests, roadsides, edges of woods, forest openings and trails. Moreover, within its native range, this species is also considered an expansive species (Halabuk and Gerhátová 2011). Many aspects of *A. petiolata* ecology have been studied, but most of the studies were limited to its introduced range. Results of these studies show that *A. petiolata* impacts the diversity of native plant communities (McCarthy 1997; Stinson et al. 2007) and inhibits the growth of native plants (Meekins and McCarthy 1999; Prati and Bossdorf 2004). Moreover, *A. petiolata* negatively impacts the abundance of mycorrhizal fungi in the soil and on plant roots (Stinson et al. 2007) and impacts microbial activity (Hawkes et al. 2005).

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Despite the large effect of this species on biogeochemical cycles, only a few previous studies focused on *A. petiolata* litter decomposition. Rodgers et al. (2008) found that green rosette leaves of *A. petiolata* decomposed in about six months ($k$ close to 2) and senescent leaf litter of *A. petiolata* decomposed in about one year ($k$ close to 1) in a *Pinus strobus* plantation in North America. Halabuk and Gerhátová (2011), in South-West Slovakia, assessed the decomposition rate for leaves of *A. petiolata* ($k = 2.44$) during a 324 day experiment. In our previous studies in West Poland (Rawlik et al. 2021), we assessed the decomposition rate ($k = 0.9$) for litter of *A. petiolata* (mixed leaves and stems). Moreover, during the above-mentioned studies, we observed that after the first stage of decomposition of *Aegopodium podagraria* L. blooming shoots and *Alliaria petiolata* mixed litter, when leaves had already decomposed, the process slowed down, and rates of mass losses between dates of sample collection were stable or even decreased. Thus, we expected that stems and leaves differ in the way that they decompose (Rawlik et al. 2021).

Most studies of decomposition focused on decomposition rates of leaves (Hobbie 2015), overlooking that a large part of litter comes from stems or roots. Especially in forest ecosystems, studies of decomposition have focused on leaves of trees (Hobbie et al. 2006; Horodecki and Jagodziński 2017, 2019; Horodecki et al. 2019; Urbanowski et al. 2018, 2021a, b). Differences in structural and physiological traits between organs, connected with their different biological functions, might cause different decomposability, which must be connected with their different impacts on soil properties and ecosystem biogeochemistry (Freschet et al. 2012). The results of previous studies on different plant organ decomposability were not conclusive, as they were different for herbaceous and tree species. Bumb et al. (2018) showed the same leaf and shoot decomposability of 16 herbaceous Mediterranean rangeland species, whereas Zuo et al. (2018) stated that leaves generally decomposed faster than both twigs and branches, and twigs generally decomposed faster than branches in the case of eleven temperate woody species. Pietsch et al. (2014) estimated that wood decomposition rates were, in general, lower than leaf litter decomposition rates; however, Zanne et al. (2015) found weak coordination between decay rates across tissues (leaf, fine branch, and wood) in 21 woody species in a temperate deciduous oak-hickory forest in the USA. In our previous studies, we compared decomposition rates of leaves (only leaves) and blooming stems (mixed material dominated by stems) of *A. podagraria*, which indicated differences in decomposability of different organs of this herbaceous species (Rawlik et al. 2021).

Our primary objective was to compare decomposition rates of *A. petiolata* leaves and stems. We hypothesized that (1) decomposition rate and nutrient release of herb species leaves are much higher than that of herb species stems, as in previous studies of *A. podagraria* blooming shoots and *A. petiolata* mixed litter, we observed that the process slowed down after the first stage of decomposition, when leaves had already decomposed; (2) neglecting decomposition rates of stems leads to an overestimation of whole-plant decomposition rate.

## Materials and methods

### Experimental site

We set up our decomposition experiment in the Czmoń forest (in Central Wielkopolska in Poland; 52.1509° N, 17.0545° E). According to meteorological data from a nearby meteorological station (Institute of Dendrology, Polish Academy of Sciences, Kórnik; 52.2447° N, 17.1008° E; 10.5 km from the study area), the mean annual temperature in 1991–2010 was 8.7 °C and the mean annual precipitation was 553 mm, whereas during studies (2011–2015), the mean annual temperature was higher (9.5 °C) and the mean annual precipitation was lower (528 mm). The study area was located in a deciduous forest complex, in a 135 year-old stand dominated by *Quercus robur* L. in the main canopy and *Carpinus betulus* L. in the overstory, comprising the plant association of *Galio sylvatici-Carpinetum* (R.Tx. 1937) Oberd. 1957, subassociation *corydalidetosum* Oberd. 1957 with a rich, well-developed herbaceous layer. The soils were described as Stagnic Gleyic Gleysol (Arenic, Humic).

### Litterbag experiment

We harvested senescent *A. petiolata* from September to November 2013 in the close vicinity of the experimental plot. After transporting the collected biomass to the laboratory, we separated leaves from stems and dried the material in a dryer with forced air circulation at 65 °C to a constant mass. After that, we placed about 2.1 g of leaves or 3.0 g of stems inside the litterbags. These masses were different for different types of plant organs to avoid excessive compaction of material in litterbags (the amount of material was adjusted for each material type, to standardize litter densities and textures inside the bags). We used litterbags made of fiberglass netting (15 × 15 cm) with a mesh size of 1 mm. We chose this mesh size as it does not inhibit micro- and mesofauna from entering litterbags, and on the other hand, protects from material leaching out of the bags. In the end, we permanently closed and labelled litterbags.

We installed our experimental set of 224 samples (four samples of *A. petiolata* leaves and four samples of *A. petiolata* stems per harvest time) on 23 November 2013. We collected samples every week, for 168 and 532 days for

leaves and stems, respectively. We planned a longer period of exposition for *A. petiolata* stems, because previous studies suggested large differences in decomposition rate (Rawlik et al. 2021). We aimed to obtain as complete a level of stem decomposition as possible. The interval of sample collection was longer in the final stages of the decomposition experiment because we determined the mass loss of the plant material systematically during the experiment and we noticed that the decomposition rate was lower than previously assumed (Table 1). After drying at 65 °C, we removed litter from bags and cleaned it to remove sand, fungi, and roots, and then, we weighed it to determine the percent of the remaining initial litter mass.

### C and N determination

We determined nutrient contents in the initial litter material and at four times during the experiment for leaves (when around 20, 40, 60 and 80% of material decomposed) and two times for stems (when around 20 and 40% of material decomposed), during the experimental period. Contents of C and N were determined with an ECS CHNS – O 4010 Elemental Combustion System (Costech Instruments, Italy/USA).

### Statistical analysis

We assumed that the decomposition process over time will be described by a single exponential model proposed by Olson (1963; as the model that best describes decomposition of samples composed of one fraction of material):

$M_t = e^{-kt}$,where $M_t$ is the proportion of remaining biomass at time $t$ and $k$ is the decay rate.

Based on this model for both leaves and stems, we obtained:

(1) $k$ values:

$$k = -\ln M_t * (t)^{-1}$$

(2) mean half decay time (hd):

$$\mathrm{hd} = \ln(0.50) * (-k)^{-1}$$

and

(3) total decay time (td):

$$\mathrm{td} = \ln(1 - 0.95) * (-k)^{-1}$$

(4) Nutrient remaining ($R$) is calculated according to Wang et al. (2009):

$$R\% = 100 * \left(M_t * R_t\right) / \left(M_0 * R_0\right)$$

where $M_0$ (g) is the initial litter dry weight, $Mt$ (g) is the dry weight of the remaining litter in the litterbag when collected, $R_0$ is the nutrient concentration (mg/g) of the initial litter, and $Rt$ is the nutrient concentration (mg/g) of the remaining litter.

To verify our second hypothesis, based on $k$ rates obtained for leaves and stems in this study and for whole plants in the previous study (Rawlik et al. 2021), we calculated mass losses for each organ of *A. petiolata* separately and whole plants after 1, 2, 3, 4, 5, 6, and 24 months of decomposition. Differences in the rates of decomposition among the litter types studied in all sampling terms were assessed using Student's $t$ tests. We analysed the data using a mixed-effects linear model, describing differences in predicted mass loss as a function of the type of litter (fixed effect). To account for exposition time, we treated time as a random factor using random slope. All analyses were conducted in JMP Pro 15.0 (SAS Institute Inc. Cary, NC. USA; http://www.sas.com). For plot drawing, we use R software (R Core Team 2020) with ggplot2 package (Wickham 2016).

## Results

Decomposition rate of *A. petiolata* leaves biomass was faster than that for *A. petiolata* stems during the entire experimental period. We found statistically significant differences ($p = 0.0051$, $F = 22.5733$) during the first 7 days of the experiment. In this time, 14.03% (± 1.49) of *A. petiolata* leaf mass had decomposed, whereas only 5.38% (± 0.66) of *A. petiolata* stem biomass decomposed (Fig. 1; Table 1). We found statistically significant differences ($p < 0.0001$, $F = 1234.942$) during 126 days of the experiment, when 87.3% (± 1.44) of *A. petiolata* leaf mass had decomposed, whereas at the same time only 24.5% (± 0.80) of *A. petiolata* stem biomass decomposed. One year after that (at day 532 of the experiment), 55.4% (± 0.71) of *A. petiolata* stem mass had decomposed (Fig. 1; Table 1). *A. petiolata* leaves biomass decomposed faster ($k = 4.04$; hd = 62 days; td = 270 days), while the decomposition of *A. petiolata* stems was significantly slower ($k = 0.67$; hd = 380 days; td = 1635 days; Table 2; Fig. 1). We found statistically significant effects of type of plant organ (fixed effect; $p < 0.0001$, df = 182.7, $t = 727.518$) as well as time of exposition in the field (random effect; $p < 0.0001$) on decomposition rate (Table 3).

Stems of *A. petiolata* litter had higher initial N (2.76%) and C (35.24%) concentrations than *A. petiolata* leaf litter (N concentration = 2.09%, C concentration = 33.91%). For N, nutrient immobilization was found in the first month of the decomposition of *A. petiolata* leaves, while in the

**Table 1** Decomposition (percentage of initial mass remaining) during the time of the experiment

| Interval* | Date (day of the year) | Type of litter | Mean rest of litter (%) | SE (%) | p<br>F | N (%) in remaining mass | C (%) in remaining mass |
|---|---|---|---|---|---|---|---|
| 7 | 30.11.2013 (334) | Leaves | 85.97 | 1.49 | 0.0051 | | |
| | | Stems | 94.62 | 0.56 | 22.5733 | | |
| 14 | 07.12.2013 (341) | Leaves | 77.27 | 1.25 | < 0.0001 | 3.11945 | 41.6836 |
| | | Stems | 94.41 | 0.66 | 146.5598 | | |
| 21 | 14.12.2013 (348) | Leaves | 69.31 | 1.17 | < 0.0001 | | |
| | | Stems | 90.15 | 1.18 | 149.1871 | | |
| 28 | 21.12.2013 (355) | Leaves | 69.50 | 3.60 | 0.0026 | | |
| | | Stems | 93.23 | 0.53 | 30.6754 | | |
| 35 | 28.12.2013 (362) | Leaves | 66.62 | 3.00 | 0.0003 | | |
| | | Stems | 89.53 | 0.94 | 53.0345 | | |
| 42 | 04.01.2014 (4) | Leaves | 58.70 | 2.37 | 0.0001 | 3.3623 | 42.84755 |
| | | Stems | 85.48 | 2.00 | 74.7455 | | |
| 49 | 11.01.2014 (11) | Leaves | 45.83 | 3.48 | < 0.0001 | | |
| | | Stems | 81.26 | 1.07 | 94.6264 | | |
| 56 | 18.01.2014 (18) | Leaves | 42.96 | 0.96 | < 0.0001 | | |
| | | Stems | 80.73 | 1.96 | 297.6318 | | |
| 63 | 25.01.2014 (25) | Leaves | 50.23 | 2.18 | < 0.0001 | | |
| | | Stems | 79.26 | 1.19 | 137.1184 | 0.97645 | 45.92555 |
| 70 | 01.02.2014 (32) | Leaves | 44.91 | 0.46 | < 0.0001 | | |
| | | Stems | 80.41 | 1.98 | 306.1129 | | |
| 77 | 08.02.2014 (39) | Leaves | 46.41 | 1.33 | < 0.0001 | | |
| | | Stems | 80.03 | 1.17 | 360.4864 | | |
| 84 | 15.02.2014 (46) | Leaves | 45.66 | 1.88 | < 0.0001 | | |
| | | Stems | 81.12 | 1.26 | 244.7283 | | |
| 91 | 22.02.2014 (53) | Leaves | 37.36 | 1.73 | < 0.0001 | 3.41675 | 44.10545 |
| | | Stems | 80.14 | 0.97 | 464.0813 | | |
| 98 | 01.03.2014 (60) | Leaves | 37.50 | 2.21 | < 0.0001 | | |
| | | Stems | 78.96 | 1.09 | 283.1435 | | |
| 112 | 15.03.2014 (74) | Leaves | 44.78 | 6.08 | 0.0012 | | |
| | | Stems | 81.95 | 2.03 | 33.6258 | | |
| 119 | 22.03.2014 (81) | Leaves | 36.29 | 3.30 | < 0.0001 | | |
| | | Stems | 77.74 | 2.65 | 95.9430 | | |
| 126 | 29.03.2014 (88) | Leaves | 20.29 | 1.44 | < 0.0001 | | |
| | | Stems | 78.04 | 0.80 | 1234.942 | | |
| 154 | 26.04.2014 (116) | Leaves | 13.47 | 1.83 | < 0.0001 | | |
| | | Stems | 75.26 | 1.14 | 821.6968 | | |
| 168 | 10.05.2014 (130) | Leaves | 12.65 | 2.63 | < 0.0001 | 3.44505 | 45.9904 |
| | | Stems | 75.49 | 0.37 | 561.2341 | | |
| 182 | 24.05.2014 (144) | Stems | 72.08 | 1.90 | | | |
| 196 | 07.06.2014 (158) | Stems | 69.36 | 1.03 | | | |
| 210 | 21.06.2014 (172) | Stems | 69.51 | 1.83 | | | |
| 224 | 05.07.2014 (186) | Stems | 69.89 | 5.03 | | | |
| 238 | 19.07.2014 (200) | Stems | 67.49 | 3.26 | | | |
| 252 | 02.08.2014 (214) | Stems | 62.35 | – | | | |
| 266 | 16.08.2014 (228) | Stems | 58.71 | 1.45 | | 1.24665 | 46.9029 |
| 280 | 30.08.2014 (242) | Stems | 61.42 | 2.64 | | | |
| 294 | 13.09.2014 (256) | Stems | 56.46 | 1.94 | | | |
| 308 | 27.09.2014 (270) | Stems | 48.88 | 5.79 | | | |

**Table 1** (continued)

| Interval* | Date (day of the year) | Type of litter | Mean rest of litter (%) | SE (%) | p<br>F | N (%) in remaining mass | C (%) in remaining mass |
|---|---|---|---|---|---|---|---|
| 322 | 11.10.2014 (284) | Stems | 56.28 | 0.69 | | | |
| 336 | 25.10.2014 (298) | Stems | 57.21 | 2.92 | | | |
| 350 | 08.11.2014 (312) | Stems | 49.93 | 5.46 | | | |
| 364 | 22.11.2014 (326) | Stems | 55.05 | 0.50 | | | |
| 378 | 06.12.2014 (340) | Stems | 48.91 | 3.71 | | | |
| 416 | 19.01.2015 (19) | Stems | 50.53 | 3.94 | | | |
| 476 | 20.03.2015 (79) | Stems | 48.70 | 3.65 | | | |
| 532 | 15.05.2015 (135) | Stems | 44.56 | 0.71 | | | |

Interval* – in days means number of days from the beginning of the experiment

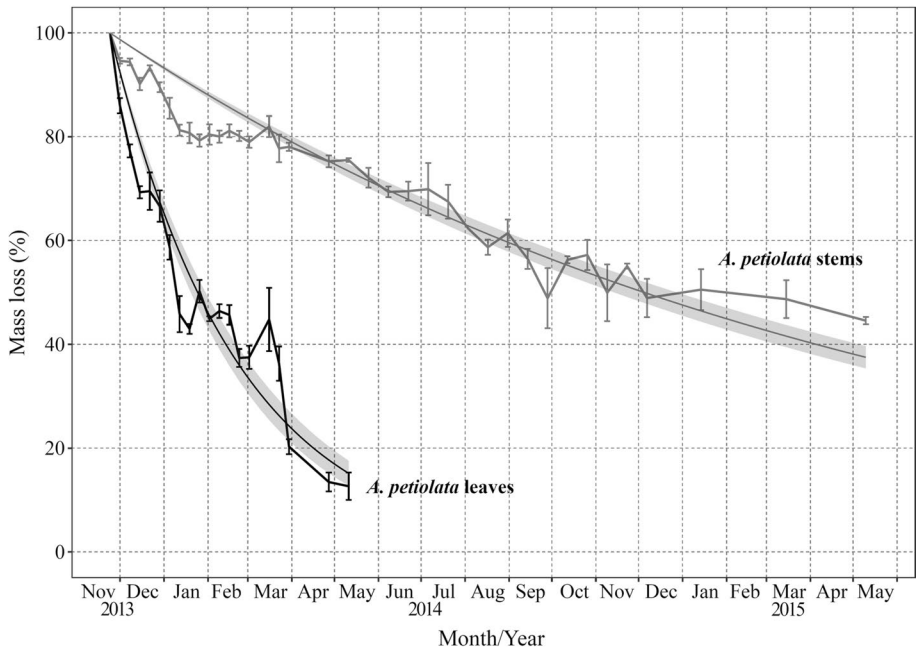


**Fig. 1** Decomposition (mean percentage of initial mass loss ± SE) of *A. petiolata* leaves and stems. We fitted exponential model using nonlinear fit with defined formula: $M_t = e^{-kt}$. The points represent mean values with error bars signifying ± SE (standard error). For 99% confidence intervals determination, we use propagate package (Spiess 2018) with predictNLS function

**Table 2** Results of the exponential decay model

| Parameter | *A. petiolata* leaves | *A. petiolata* stems |
|---|---|---|
| *k* (year) | 4.04 | 0.67 |
| $R^2$ | 0.83 | 0.82 |
| *hd* (days) | 62 | 380 |
| *td* (years) | 0.74 | 4.48 |

second month of the decomposition, it started decreasing (Fig. 2a). In the case of *A. petiolata* stems, we found an exponential nutrient release from the start to 50 days of the decomposition. After 50 days of the experiment, the release of N stopped and N content was almost unchanged through day 266 (Fig. 2a). For C, patterns of nutrient release were similar to N release patterns for leaves of *A. petiolata*. We observed C immobilization in the first month of the decomposition and fast release after that (Fig. 2b). For *A. petiolata* stems, we found a small C immobilization in the beginning of litter decomposition (first month) and slow release after that.

Leaf litter of *A. petiolata* had higher mass losses than whole plant litter during all compared terms of decomposition. The differences were bigger in the late stages than at the start of the process. After the first month of the experiment, leaf material mass loss was 130% higher than mass loss of whole plants, whereas after six months the difference was almost fivefold higher. After 24 months of study, leaf litter decomposition was 550-fold higher than decomposition of mixed litter (Table 4).

**Table 3** Linear mixed model analysis of organ-type effects on decomposition

| Fixed effect | | Prob > \|t\| | | DFDen | tRatio |
|---|---|---|---|---|---|
| Type of organ | | < 0.0001 | | 182.7 | 727.518 |
| Term | Estimate | SE | Prob > \|t\| | DFDen | tRatio |
| Intercept | 71.110 | 2.79 | < 0.0001 | 36.76 | 25.47 |
| Leaves | − 35.075 | 1.30 | < 0.0001 | 182.67 | − 26.97 |
| Random effect | Estimate | SE | Wald *p*-value | Mixed model parameters | |
| Time | 271.134 | 67.228 | < 0.0001 | $R^2$ | 0.87 |
| Residual | 62.729 | 6.654 | | AICc | 1631.434 |
| Total | 333.864 | 67.398 | | | |

Organ type was a fixed effect, whereas time of exposure in the field (duration of the experiment) was a random effect (random intercepts and slopes among types of litter) on the decay process

## Discussion

We found statistically significant differences in litter decomposition among the *A. petiolata* organs. Our study revealed that decomposition rate of this herb species leaf was six times higher than for stems. Moreover, we assessed that decomposition rates of *A. petiolata* leaves were more than fivefold higher than mixed material decomposition rate after a half year of decomposition. Thus, we can state that neglecting decomposition rates of stems of plants leads to an overestimation of whole-plant decomposition rate.

Most of the previous studies suggested that herbaceous plant litter material can be classified into the labile pool of material, whose decomposition is completed in less than a year ($k > 1$) (Muller 2014). Differences in estimated $k$ obtained in our experiment and the cited studies may be a result of poorer habitats, as climate conditions are comparable. Decomposition rates of *A. petiolata* have been studied only a few times so far. Halabuk and Gerhátová (2011) in SW Slovakia assessed $k = 2.44$ for *A. petiolata* leaves during a 324 day experiment. That experiment provided five plots in a gradient from forest clear-cut to closed forest, in an ecotone of the hornbeam-oak forest situated in a region with a mean annual temperature of 9.3 °C and total annual precipitation of 580 mm. Inferring from the composition of dominant species given by the authors, the described study occurred on a poorer habitat than that in our experiment. Site conditions impact decomposition rate of litter by the nature and abundance of decomposer organisms and microclimatic conditions (Coûteaux et al. 1995). Frouz et al. (2001) linked high biological activity of the soil and fast decomposition on richer sites. Higher site precipitation or temperature conditions can significantly impact decomposition rates (Coûteaux et al. 1995). The location of part of the plots outside a dense stand and a different habitat may cause differences in the estimated $k$. Rodgers et al. (2008) in Connecticut and Massachusetts in USA found that green rosette leaves of *A. petiolata* decomposed in about six months ($k$ close to 2) and senescent leaf litter of *A. petiolata* decomposed in about one year ($k$ close to 1) in a *Pinus strobus* plantation. The mean annual temperature was 7.0 °C, and the mean annual precipitation was 1330 mm. Moreover, studies of Rodgers et al. (2008) were conducted in areas where *A. petiolata* is an invasive species, where lack of specialized decomposer communities can decrease the decomposition process (according to the home-field advantage theory, e.g. Ayres et al. 2009; Horodecki and Jagodziński 2017; Horodecki et al. 2019; Fanin et al. 2021).

One of the problems in decomposition studies is a lack of data accounting for differences in decomposition rates of different plant organs, especially since morphological and chemical traits connected with decomposability for leaves and stems of the same plants are different. Moreover, it is needed to understand whether the decomposability of different organs is correlated and controlled by the same functional traits (Freschet et al. 2012; Hobbie 2015). This knowledge can help in predicting the role of plant litter inputs of different organs in forest biogeochemistry and carbon storage (Zuo et al. 2018). Previous studies on decomposability of different plant organs were not conclusive, as they were different for herbaceous and tree species (Bumb et al. 2018; Zuo et al. 2018). However, Bumb et al. (2018) showed the same leaf and shoot decomposability of fourteen herbaceous Mediterranean species in studies located on a limestone plateau in southern France, which is opposite to our results.

In general, it was assumed that stems decomposed on average almost threefold more slowly, than did leaf litter (Bardgett et al. 2014). In our study, *A. petiolata* leaves biomass decomposed sixfold faster (half decay time 62 days) than *A. petiolata* stems (half decay time 380 days). Thus, taking into account only decomposability of leaves provides a serious overestimation (4.8 times after half a year) of decomposition rates of whole plants. In our previous studies on the decomposition of mixed leaves and stems of *A.*

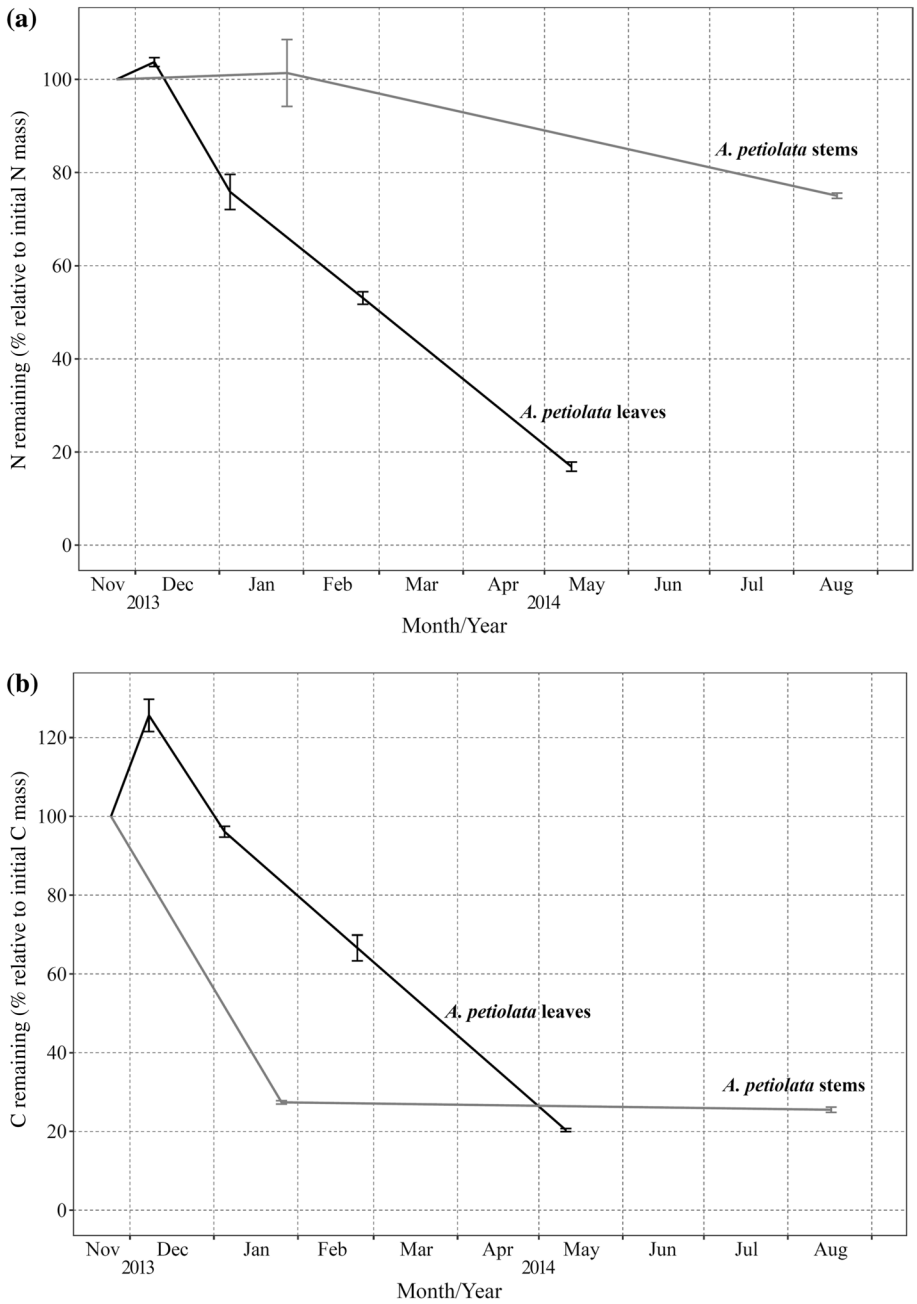


**Fig. 2** Mean percent of mass remaining of nutrients (% relative to initial mass): **a** nitrogen (N), **b** carbon (C) in decomposing leaves and stems of *A. petiolata* litter

**Table 4** Decomposition (percentage of initial mass remaining) during the time of the experiment

| Type of litter | *k* | Lmf* | Mass remaining from 100 g of litter after given number of months: | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | 4 | 5 | 6 | 24 |
| leaves | 4.04 | | 71.41 | 51.00 | 36.42 | 26.01 | 18.58 | 13.27 | 0.03 |
| stems | 0.67 | | 94.57 | 89.43 | 84.58 | 79.98 | 75.64 | 71.53 | 26.18 |
| mixed | 0.90 | 0.5276 | 92.77 | 86.07 | 79.85 | 74.08 | 68.73 | 63.08 | 16.5 |

*Source of data: Paź-Dyderska et al. (2020)

*petiolata*, we found a decomposition rate of about 0.9 (Rawlik et al. 2021). Our currently described results are different from all previous results, as we get a higher decomposition rate ($k = 4.04$) for *A. petiolata* leaves and a lower decomposition rate ($k = 0.67$) for *A. petiolata* stems. Also, comparison with our previous results (Rawlik et al. 2021) can support

a statement that neglecting decomposition rates of different parts of plants (other than leaves) leads to an overestimation of whole-plant decomposition rate.

In general, herb litter is considered as a labile pool of litter, which decomposes totally in the first year of the process (Muller 2014). Our previous studies in an oak-hornbeam forest (Rawlik et al. 2021, 2022) and in tree-stands of a post-mining heap (Rawlik et al. 2019) showed that this statement is not always true. Some parts of herbaceous species litter decompose at rates similar to leaves of trees. In these species, after the first stage of decomposition, the process slows down, and rates of mass losses between dates of sample collection are stable or even decrease. This phenomenon can be connected with biomass allocation to stems (Rawlik et al. 2021), as it was most visible in the cases of plant species which had the highest contributions of stems to aboveground biomass (Paź-Dyderska et al. 2020).

N and C litter concentration, as well as patterns of N and C release, were different for *A. petiolata* leaves and stems. For leaves of *A. petiolata*, we observed N immobilization during the early phase of decomposition, which can be connected with temporal changes in litter quality and decomposer requirements. This phenomenon was observed in previous studies (e.g. Rawlik et al. 2021) and was explained by the time of colonization of litter by bacteria (Jacob et al. 2009). According to Swift (1979), nutrients released can be synchronized with plant growth demands, as the time of higher release of nutrients is also the time during which other plants grow. Therefore, peaks in N release that potentially increase losses of N from the system may be blunted by the different timing of growth among plant species. In the case of stems of *A. petiolata*, we found C and N immobilization during the experiment. Mechanisms of N immobilization by plant traits during decomposition still need wider studies (Hobbie 2015), but in our case, it seems to be caused by a fraction of slowly cycling litter in stems. Deeper analyses of nutrient dynamics during stem decomposition are necessary to elucidate general patterns. Similar studies comparing nutrient dynamics of decomposing roots and leaf litter within species give no clear results (Hobbie 2015). Roots sometimes immobilized less (Wang et al. 2010) or more (Fujii and Takeda 2010) N than leaves.

Invasive plants, which can change the character, condition, form, or nature of ecosystems, are classified as 'transformers' (Richardson et al. 2000). One of the current tasks in the ecology of invasions is finding proper tools to measure the impact of singular species, which is important from the ecosystem managers' point of view (Parker et al. 1999). One of the most promising tools is the '*per capita*' effect, considered to be the response of invaded sites per invader's abundance or biomass unit (Barney et al. 2015). This effect cannot be assessed without properly counted decomposition rate, as input of litter with unique chemical properties (Ashton et al. 2005) is one of the ways invaders impact cycling of carbon and nutrients in ecosystems. According to our results, the leaves of *A. petiolata* decompose fivefold faster than whole plants, which means that they release elements faster than would be predicted from previously accepted models. This means that C and N pools embedded in leaf tissues return to ecosystems fast; in three months after leaf senescence, they are available for other plants in the same vegetation season. The same nutrients embedded in stem tissues can be immobilized much longer than one year, and further studies are needed to know the time of total decomposition. In other words, leaf litter belongs to the labile fraction of litter, but stems account for almost half of immobilized nutrients in *A. petiolata* biomass, making them unavailable for other organisms. Therefore, we should expect a larger '*per capita*' effect associated with decomposing leaves with high N content, which is rapidly released and may further affect elemental cycling, and the functioning of ecosystems, especially in the USA.

## Conclusions

Litter decomposition and N and C release of *A. petiolata* leaves are significantly faster than *A. petiolata* stems. Our results support assumption that neglecting decomposition rates of stems leads to almost a fivefold (4.8) overestimation of whole-plant decomposition rate after six months of decomposition. That led to the conclusion that whole plant litter decomposition rate should be taken into account in a '*per capita*' effect of invader assessment.

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**Author contribution** KR and AMJ conceived the ideas and designed the methodology; KR collected the data; KR and AMJ analysed the data; KR wrote the first draft of the manuscript; AMJ supervised.

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**Code availability** Not applicable.

## Declarations

**Conflict of interest** The authors have no conflict of interest to declare.

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

**Ethics approval** Not applicable.

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