



Benjamín Jarčuška

Is preformation of future shoots in *Fagus sylvatica* L. buds reflected in bud/sprouted shoot traits relationships?

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Abstract: The present study was aimed to find out whether the preformation of future shoot's organs within a bud is reflected in the bud size/shoot functional traits' size relationships. The survey attempts to evaluate whether relationships between the bud mass and stem mass, leaf mass, leaf area, total mass and number of leaves, respectively, of spring-shoot sprouted by the bud in *Fagus sylvatica* (L.) saplings are affected by parental bud location within shoot and parental shoot type. Dry mass of the terminal bud, the first and the last lateral buds placed on terminal and uppermost lateral shoots was estimated nondestructively for 58 beech saplings in December 2008. The shoots sprouted from the measured buds were sampled at the end of growing season, in August 2009. Bud mass, parental shoot type and bud location explained about 90% of shoot traits variability in full-factorial ANOVA. The leaf mass was the only shoot trait not affected by parental shoot type and bud location within shoot in scaling relationship with bud mass. There was not found differences among intercepts across parental shoot types and bud locations, however significant shift along common slope was observed among them. The presented findings could be viewed as a confirmation of the preformation and full development of leaf primordia within the European beech buds prior to bud burst.

Additional key words: European beech; bud mass; shoot functional traits; leaf mass; organ preformation

Address: Institute of Forest Ecology, Slovak Academy of Sciences, Štúrova 2, SK-960 53 Zvolen, Slovakia, e-mail: benjamin.jarcуска@gmail.com

Introduction

Preformation of a future shoot, as formation of its metamers and organs in its embryonic stage in a bud in the vegetation period preceding the shoot sprouting, is typical for rhythmic growth of permanent plants of the temperate and cold zone (Barthélémy and Caraglio 2007; Bell and Bryan 2008). The morphogenetic cycle of *Fagus sylvatica* (L.) bud was at first time described by Roloff (1987). According to this author, bud scales begin to form just towards the end of vegetation period two years before the bud burst; the leaf primordia at the beginning of the vegetation period in the preceding year. Eschrich et al.

(1989) have found in an experimental anatomical study that the sun- and shade-leaf differentiation in beech buds is triggered towards the end of July, so changes in light conditions occurring before July influence the structure of the leaves of the next season.

Based on findings of Roloff (1987) and Eschrich et al. (1989), concerning preformation of primordial organs in *Fagus sylvatica* trees, it could be expected that this process should be reflected also in the strength of correlation between the buds' mass and size of functional traits of shoots sprouted by these buds. Also, it could be hypothesized that the size of future shoot traits performed within the buds should not be affected neither by a location of paren-

tal buds within shoots, nor by a position of shoot within tree crown.

The present study investigated relationship between parental bud mass and future shoot traits of *Fagus sylvatica* saplings regarding to the parental bud location within shoot and parental shoot location within crown. The primary objective of the study is therefore to test whether the preformation of future shoot's organs within a bud is reflected in the bud size/shoot functional traits' size relationships with regard to parental bud location and parental shoot type.

Material and methods

Study localities

The dataset was assembled from *Fagus sylvatica* saplings originated from natural regeneration growing in three sites in central Slovakia (Western Carpathians Mts): in the Javorie Mts (J), the Nízke Tatry Mts (NT) and the Veľká Fatra Mts (VF). Forest stands on the study localities are mixed, and canopy layer consists mostly of European beech, with its dominance more than 70%. The study sites are situated between 680 and 740 m above the sea level. The mean sum of annual precipitation in years 2001–2009 was between 850 and 1010 mm (Table 1), the mean annual temperature ranged between 6 and 7°C (data from the closest meteorological stations, provided by the Slovak Hydrometeorological Institute, Bratislava). For more details about the study localities see Jarčuška and Barna (2011) and Jarčuška (2011).

Plant material and data collection

The beech saplings of approximately the same height but growing under different light conditions, with light supply ranging between 5 and 80% of the diffuse light availability (estimated by hemispherical photography analysis) were randomly selected. Selected were undamaged individuals, showing no symptoms of attack by pathogens. Current-year spring-shoots were randomly selected and tagged in December 2008: on each individual a terminal shoot and one uppermost first-order lateral shoot (lateral shoot hereafter) (Fig. 1). The terminal bud, the first lateral and the last lateral bud (counted from the from the shoot tip; Fig. 1) were sampled within every of the

selected shoots and their length and maximum diameter were measured. Dry mass of the measured buds (BM) was estimated in a nondestructive way, with using the log-log linear model developed concurrently (Jarčuška 2010), working with the bud length and maximum diameter. This model could explain 98.2% of bud mass variability with relative accuracy of 5.4% (at $P = 0.95$).

Terminal shoots had been protected mechanically against browsing by game, nevertheless, during win-

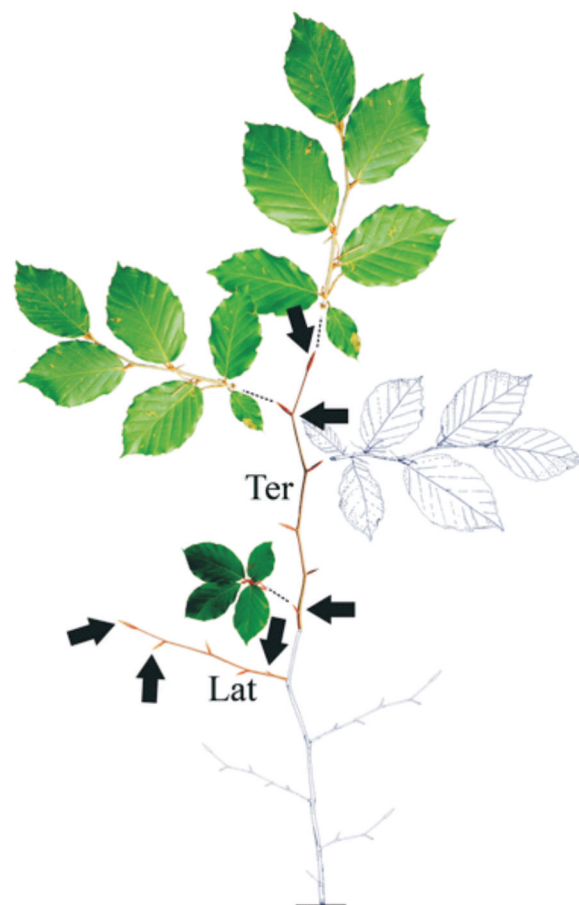


Fig. 1. Schematic representation of parental buds locations within parental shoots (Ter – terminal shoot, and Lat – lateral shoot) and of parental shoot within sapling's upper part of the crown. Measured parental buds are indicated by black arrows (terminal bud, the first lateral and the last lateral bud). Due to clarity, some of the future shoots, sprouted from the parental buds, are depicted only within terminal shoot. This figure is available in color in the online version of the paper

Table 1. General description of the study sites

Site	Latitude, longitude	MAP (mm)*	Parent rock [§]	Soil type [§]	pH (H ₂ O) [‡]
Javorie	48°30'13"N, 19°15'06"E	884 ± 124	andesite tuffaceous agglomerates	Dystic Cambisols	5.58 ± 0.40
Nízke Tatry	48°51'36"N, 19°25'38"E	852 ± 162	gneiss	Dystic Cambisols	5.13 ± 0.46
Veľká Fatra	48°50'41"N, 19°06'44"E	1010 ± 143	limestone	Eutric Cambisols	6.50 ± 0.52

(*) MAP – the mean annual precipitation over 2001–2009 (mean ± 1SD); (§) Miklós et al. (2002); (‡) samples from the upper soil layer (0–5 cm depth, mean ± 1SD): Javorie $n = 14$; Nízke Tatry $n = 18$; Veľká Fatra $n = 13$ soil samples from sites with broad light supply

ter 2008/2009 several individuals were damaged or deprived of shoot's tags by animals. The mechanically damaged individuals were discarded from further analyses. Height (measured as a vertical, perpendicular distance between the stem base and tip of main stem) of 58 sampled individuals used in the present study was (mean $\pm$ 1SD): 105.8 ± 24.0 cm ($n = 21$), 94.3 ± 24.7 cm ($n = 10$) and 96.0 ± 25.5 cm ($n = 27$) for J, NT and VF, respectively, and there were no significant differences neither in height of saplings among the localities (one-way ANOVA, $F_{2,55} = 1.1631$, $P = 0.320$), nor among the mean light environment of sampled individuals (one-way ANOVA, $F_{2,55} = 0.5990$, $P = 0.553$). The data from the three localities were pooled before the analysis.

Shoots sprouted from the parental buds ($n = 348$) were processed on the end of growing season, in August 2009. The number of leaves (NL) bearing by a shoot was counted in the field. Total shoot leaf area (LA) and total shoot leaf dry mass (LM) were estimated based on methods developed by Cicák (2003, 2008). These methods are based on knowledge about regularities in distribution of morphological traits in beech leaves growing on spring shoots, and they enable to determine the values of the total leaf area and total leaf mass of leaves on a shoot by measuring morphometric parameters on one single leaf and multiplying them by the corresponding calculation coefficient (corresponding to the number of leaves on the shoot). The calculation coefficients are defined as the ratio of the sum of the values of the relevant traits measured on all leaves on the shoot and the value of the trait of the given single leaf. The relative accuracy of estimated traits' values (i.e. LM and LA) ranges from 1.09 to 1.70% (at $P = 0.95$). The methods are applicable regardless of tree age and/or light energy supply during the tree growth (Cicák 2003, 2008). The sampled leaves were packed in plastic bags and stored in a transportable cooling box. In the laboratory, all the leaves (with leaf-stalks) were measured with an LI-3000A Portable Area Meter (LiCor, USA). Then, the material was dried for 48 hours at a temperature of 70°C and weighted (0.001 g) with a Mettler AE 200 (Mettler, Switzerland). The shoot stems were clipped and their dry mass (shoot stem mass, SM) (after drying to a constant mass at 70°C) was measured. If occurred, proleptic shoots were not taking into account. Total shoot mass (TM) was derived from the measurements as the sum of shoot stem mass (SM) and shoot leaf mass (LM).

Data analysis

All the data except the number of leaves per shoot were $\log_{10}$ -transformed to fit a normality, homoscedasticity and linearity prior to analysis. A hierarchical ANOVA with type I sum of squares was conducted on measured variables. It was shown that variance be-

tween parental buds' locations on the same shoot was strongly dominated over that between individuals (Table 2). Variability in measured traits of shoots sprouted from the parental buds was assessed with a model I full-factorial ANOVA working with parental bud location within parental shoot (three levels: terminal bud, the first lateral and the last lateral bud) and parental shoot type (two levels: terminal and lateral shoot) as the categorical factors and with the parental bud mass (BM) as the covariate. Adjusted, type II sum of squares was used because of non-orthogonal study design, i.e. the levels of categorical factors took different values of covariate – bud mass (Doncaster and Davey 2007).

As the research question was to test whether the relationships between parental bud mass and future shoot traits' size are affected by parental bud location and parental shoot type and therefore slopes and functional rather than predictive relationships were of particular interest, a model type II regression method was used instead of model type I linear regression (Sokal and Rohlf 1995; Warton et al. 2006). The slopes were calculated as standardised major axis (SMA), followed by methods of Warton and Weber (2002) to test the heterogeneity of regression slopes. If slopes did not differ among combinations of parental shoot types and bud locations, differences in the intercept of regression slopes and in shifting along the common slope were tested by Wald tests (Falster et al. 2006). These calculations were completed with freeware SMATR 2.0, kindly provided by Falster et al. (2006). Confidence intervals (95% CI) for the regressions' coefficients of determination were calculated according to Soper (2011).

In addition, two-way ANOVA followed by Tukey HSD post-hoc test were used to examine differences in the means of parental bud's and shoot's functional traits among parental bud locations and parental shoot types. Unless not stated otherwise, all the analyses were performed using software Statistica 7.0 (Statsoft, USA).

Table 2. Hierarchical ANOVA with type I sums of squares, converted to percentages at each level, for the functional traits of *Fagus sylvatica* saplings. Bud mass (BM; g), shoot stem mass (SM; g), shoot leaf mass (LM; g), shoot leaf area (LA; cm²), total shoot mass (TM; g) and number of leaves bearing by shoot (NL). All variables, except NL, were $\log_{10}$ -transformed prior to analysis

	Individuals	Shoots within individuals	Buds within shoots
BM	1.53	1.64	96.83
SM	1.03	1.80	97.18
LM	1.79	1.73	96.48
LA	1.02	1.57	97.40
TM	1.51	1.92	96.57
NL	1.47	1.47	97.06

Results

The outputs of ANOVAs (Table 3) revealed that bud location within parental shoot significantly affected shoot stem mass (SM), shoot total mass (TM) and number of leaves bearing by the shoot (NL). There was not found significant variation in shoot functional traits for two compared shoot types. Bud mass (BM) significantly affected all measured traits. There was significant bud location by shoot type interaction only for SM, the same hold for interaction of bud location with shoot type and BM. Effect of bud location interacted with BM also in SM, TM and NL. Shoot type by BM interaction did not affect any of the dependent variables. Shoot leaf mass and leaf area were traits affected only by BM. The presented models accounted for between 89 to 94% of shoot functional traits variance, while BM explaining the largest portion of it (see *F*-ratios in Table 3).

There were found significant differences in regression slopes of relationships between parental bud mass (BM) and shoot functional traits' size among six combinations of parental shoot types with bud locations within parental shoot for all shoot traits except shoot leaf mass (LM; $P = 0.515$) (Table 4). The common regression slope of the BM vs LM relationship was 1.261 (with 95% confidence intervals (CI) ranging from 1.188 to 1.338); 90% (CI = $\pm 2\%$; $P < 0.001$) of shoot leaf mass variation across shoot types and bud locations could be accounted for by the variation in parental bud mass (Fig. 2). Moreover, there were not detected neither differences among intercepts of scaling relationships between BM and LM across parental shoot types and bud locations (Wald = 8.582, *df* = 5, $P = 0.127$), however, there was found significant shift along common slope for them (Wald = 746.18, *df* = 5, $P < 0.001$), with shoots sprouted from terminal buds on terminal shoots having the largest leaf mass (Table 5). These results

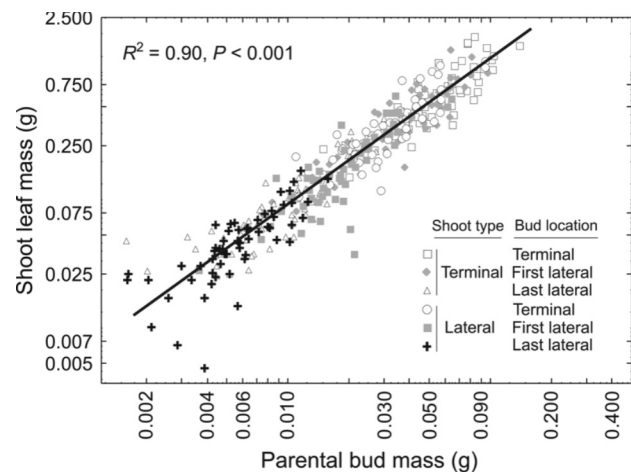


Fig. 2. The scaling relationship between parental bud mass and future shoot leaf mass for six parental shoot type by parental bud location combinations. All individual slopes were non-heterogenous, no significant differences in intercepts were found among the groups, significant shift along common slope was observed across parental shoot types and bud locations. See *Results* for more information

could suggest that LM is the only shoot trait not affected neither by location of parental bud within parental shoot nor by shoot type. In others traits, BM accounted for between 33 to 88% of shoot traits' variability (Table 4). Besides the above mentioned differences among regression slopes in the rest of shoot traits, the significant differences were also observed among their means across combinations of parental shoot types and bud locations (Table 5).

Discussion

In accordance with the stated hypothesis, there have been found the significant effect of parental bud mass (BM) on variability of functional traits of shoots emerged from these buds (Table 3); BM, also, ex-

Table 3. Summary of a full-factorial ANOVA with type II sum of squares to assess the variance in sprouted shoot stem mass (SM), shoot leaf mass (LM), shoot leaf area (LA), total shoot mass (TM), and number of leaves (NL), respectively, explained by parental bud location within shoot (Bud), parental shoot type (Shoot), bud mass (BM), and their interactions. Presented are the results of *F*-test with associated *P* values, error mean square and overall model R^2 . All variables, except NL, were $\log_{10}$ -transformed prior to analysis. For parental shoot and bud locations see Fig. 1. $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***), non-significant (^{ns})

Effect	df	SM	LM	LA	TM	NL
(1) Bud	2	2.3663***	0.923 ^{ns}	0.008 ^{ns}	14.565***	75.26***
(2) Shoot	1	0.0021 ^{ns}	0.466 ^{ns}	0.027 ^{ns}	0.499 ^{ns}	0.48 ^{ns}
(3) BM	1	52.3066***	746.326***	11.183***	1014.393***	601.83***
1×2	2	0.1991*	0.053 ^{ns}	0.003 ^{ns}	0.387 ^{ns}	0.79 ^{ns}
1×3	2	1.7294***	0.461 ^{ns}	0.004 ^{ns}	11.026***	71.38***
2×3	1	0.0165 ^{ns}	1.042 ^{ns}	0.067 ^{ns}	0.001 ^{ns}	0.39 ^{ns}
1×2×3	2	0.2495*	0.049 ^{ns}	0.001 ^{ns}	0.283 ^{ns}	0.70 ^{ns}
Error MS	336	0.0558	0.0250	0.0220	0.0268	0.7440
Model R^2		0.94***	0.90***	0.90***	0.93***	0.89***

Table 4. Standardised major axis regression slopes and 95% confidence intervals (CIs) of linear relationships between parental bud mass and functional traits of shoots sprouted from three parental bud locations and two parental shoot types. Rows within a trait followed by the same letters are not significantly different at $P < 0.05$. All variables, except NL, were $\log_{10}$ -transformed prior to analysis. For traits explanations see Table 2, for parental shoot types and bud locations within these shoots see Fig. 1. All the relationships were highly significant at $P < 0.001$

	Shoot type	Bud location	$R^2 (\pm \text{CI})$	Slope	Slope CIs	
SM	Terminal	Terminal	0.75 (± 0.11)	2.095	(1.832, 2.397)	bcd
		First lateral	0.88 (± 0.06)	2.256	(2.055, 2.477)	cd
		Last lateral	0.58 (± 0.16)	1.698	(1.430, 2.017)	abc
	Lateral	Terminal	0.80 (± 0.09)	2.695	(2.390, 3.039)	de
		First lateral	0.76 (± 0.10)	2.462	(2.158, 2.808)	cde
		Last lateral	0.57 (± 0.16)	1.349	(1.133, 1.606)	ab
LM	Terminal	Terminal	0.70 (± 0.12)	1.247	(1.076, 1.445)	a
		First lateral	0.78 (± 0.10)	1.203	(1.059, 1.365)	a
		Last lateral	0.69 (± 0.13)	1.153	(0.994, 1.338)	a
	Lateral	Terminal	0.72 (± 0.12)	1.283	(1.113, 1.479)	a
		First lateral	0.70 (± 0.12)	1.356	(1.171, 1.570)	a
		Last lateral	0.59 (± 0.15)	1.385	(1.168, 1.642)	a
LA	Terminal	Terminal	0.65 (± 0.14)	0.916	(0.782, 1.074)	abcd
		First lateral	0.71 (± 0.12)	0.899	(0.779, 1.039)	abc
		Last lateral	0.63 (± 0.15)	0.967	(0.821, 1.138)	abc
	Lateral	Terminal	0.64 (± 0.14)	1.048	(0.893, 1.230)	abcde
		First lateral	0.59 (± 0.15)	1.140	(0.960, 1.353)	bcd
		Last lateral	0.51 (± 0.17)	1.286	(1.068, 1.548)	cde
TM	Terminal	Terminal	0.74 (± 0.11)	1.626	(1.420, 1.861)	bcd
		First lateral	0.85 (± 0.07)	1.577	(1.422, 1.748)	bcd
		Last lateral	0.71 (± 0.12)	1.209	(1.046, 1.397)	ab
	Lateral	Terminal	0.80 (± 0.09)	1.625	(1.440, 1.834)	cd
		First lateral	0.76 (± 0.10)	1.572	(1.379, 1.792)	bcd
		Last lateral	0.63 (± 0.15)	1.331	(1.131, 1.566)	abc
NL	Terminal	Terminal	0.74 (± 0.11)	8.460	(7.382, 9.697)	a
		First lateral	0.76 (± 0.10)	8.125	(7.133, 9.255)	a
		Last lateral	0.41 (± 0.19)	3.498	(2.851, 4.290)	b
	Lateral	Terminal	0.77 (± 0.10)	8.917	(7.852, 10.126)	a
		First lateral	0.62 (± 0.15)	8.300	(7.039, 9.786)	a
		Last lateral	0.33 (± 0.19)	2.896	(2.332, 3.597)	b

Table 5. Means with associated 95% confidence intervals of functional traits of *Fagus sylvatica* saplings' parental buds and the shoots sprouted from them. The differences among the parental shoot types and bud locations were determined with using two-way ANOVA followed by Tukey HSD post-hoc test. The means with the same letters are not significantly different at $P > 0.05$. All variables, except NL, were $\log_{10}$ -transformed prior to analysis. Presented values are back-transformed by antilogarithms (Sokal and Rohlf 1995). For traits explanations see Table 2, for parental shoot types and bud locations within these shoots see Fig. 1

Trait	Terminal shoot			Lateral shoot		
	Terminal bud	First lateral bud	Last lateral bud	Terminal bud	First lateral bud	Last lateral bud
BM	0.054 a (0.047, 0.062)	0.038 b (0.033, 0.043)	0.009 c (0.008, 0.010)	0.031 b (0.027, 0.035)	0.018 d (0.016, 0.021)	0.006 e (0.005, 0.006)
SM	0.700 a (0.529, 0.924)	0.330 b (0.250, 0.436)	0.008 c (0.006, 0.011)	0.147 d (0.111, 0.194)	0.041 e (0.031, 0.055)	0.004 f (0.003, 0.006)
LM	0.588 a (0.498, 0.696)	0.391 b (0.331, 0.462)	0.074 c (0.063, 0.088)	0.328 b (0.278, 0.388)	0.154 d (0.130, 0.182)	0.041 e (0.035, 0.049)
LA	164.22 a (142.94, 188.66)	110.10 b (95.83, 126.48)	24.06 c (20.94, 27.64)	99.01 b (86.18, 113.74)	48.42 d (42.14, 55.65)	13.95 e (12.14, 16.03)
TM	1.324 a (1.089, 1.608)	0.754 b (0.621, 0.916)	0.084 c (0.069, 0.102)	0.503 d (0.414, 0.611)	0.205 e (0.169, 0.249)	0.046 f (0.038, 0.056)
NL	8.21 a (7.81, 8.60)	7.14 b (6.74, 7.53)	2.95 c (2.55, 3.34)	6.24 d (5.85, 6.64)	4.67 e (4.28, 5.07)	2.53 c (2.14, 2.93)

plained up to 88% of shoot traits' variance in the scaling relationships (Table 4). The linear association between parental bud mass and shoot leaf mass (LM) was the strongest one (Fig. 2), accounting for 90% of the leaf mass variability. Cochard et al. (2005) reported 94% of leaf primordia dry mass variability estimated by fresh bud mass. However, besides above stated strength of association between BM and shoot traits, further hypothesized postulate concerned with non-significant effects of a location of parental bud within shoot and of a position of shoot within tree crown should be fulfilled to provide indirect corroboration of preformation of future shoot organs within winter bud of *Fagus sylvatica*.

The LM was the only shoot trait which was not affected neither by the bud position within the shoot, nor by the parental shoot position within the crown: there were not found significant differences in regression slopes among shoot type by bud location groups for the BM vs LM relationship (Table 4, Fig. 2). This could be explained by preformation of leaves within the bud before its burst (Roloff 1987). Eschrich et al. (1989) have found in an anatomical experimental study, in accordance with Roloff (1987), that differentiation into sun- and shade-leaf primordia takes place at the beginning of August in the year before the bud flushing. Fully developed leaves enclosed within a protecting bud have acquired their final shape, mostly by cell multiplication, but not yet reached their final size, which will mostly due to the cell enlargement after the flushing (Bell and Bryan 2008). Leaf preformation and full development of leaf primordia within buds is also reflected in delayed morphological and anatomical response of beech leaves to canopy release/removal and subsequent enhancement of light availability (e.g. Reynolds and Frochot 2003). The allometric common slope of the relationship between BM and LM was higher than unity (Fig. 2), what might suggests size-dependency of biomass partitioning within the bud among future leaves (i.e. leaf primordia), other future shoot organs and protective bud scales.

The ANOVA revealed that besides LM, shoot leaf area (LA) was another trait independent of the shoot type and parental bud location within shoot (Table 3). This discrepancy between ANOVA outputs and results of standardised major axis (SMA) regression are due to differences in the direction in which errors from the fitted line are measured (see Warton et al. 2006). By definition, LA can be viewed as the ratio of LM to leaf mass per unit area (LMA, g m^{-2}), therefore observed differences in regression slopes of BM vs LA relationships among combinations of shoot types and bud locations could be explained by differences in LMA among those factors' groups. LMA was found to be significantly lower in shoots sprouted from the last lateral parental buds (full-factorial two-way ANOVA: $F_{2, 342} = 10.984$, $P < 0.001$), and from lateral parental

shoot ($F_{1, 342} = 8.901$, $P = 0.003$) in comparison with others bud locations and terminal parental shoot, respectively. Moreover, leaf mass per area is plastic in response to the increasing light supply, i.e. the sunny leaves have larger mass at a given area compared to the shaded ones (e.g. Masarovičová 1988; Valladares 2003; Jarčuška 2011), positive effect of increasing LA on LMA had been also observed (Milla et al. 2008).

Thickening of stems and roots by means of secondary growth is typical for gymnosperms and most angiosperms (Evert 2006). The product of secondary thickening is an increase of the volume of conducting tissues essential for hydraulic transport of water to foliage, and of supportive and protective tissues essential for supporting an aerial canopy (Lambers et al. 2008). It is also well known that the growth of plant biomass is closely associated with light environment (e.g. Canham 1988). These could explain the significant positive effect of increasing bud mass on stem mass (SM) of shoots sprouted by the parental buds (Table 3) with scaling slopes larger than unity (Table 4). This indicates that shoot stem growth is more intense in the shoots sprouted from larger buds. Besides this, shoot stem's growth may depend on the branch position within the crown (Goulet et al. 2000; Suzuki and Suzuki 2009) and on the shoot type, i.e. long and short shoots (Yagi 2006), which have been confirmed by a significant effects of the parental shoot type, bud location and their interactions with BM on stem mass in the present study (SM, Table 3).

The significant effect of parental bud location by BM interaction on number of leaves supported by shoot (NL; Table 3), altogether with non-heterogeneous slopes of BM vs LM relationships among parental shoot types and bud locations (Fig. 2, Table 4), indicates that partitioning of the shoot leaf size (i.e. mass or area) among the single leaves within a shoot, i.e. shoot mean leaf size, is affected by location of the shoot within parental shoot and by parental bud mass.

Summarizing, performance of leaf primordia enclosed within bud before it burst can be approved indirectly by observed non-heterogeneity of regression slopes of relationships between parental bud mass and shoot leaf mass across shoots sprouted from the buds differently located within two shoot types. This indicates full development of leaf primordia within bud. On the other hand, the size of others shoot's mass-based traits, i.e. shoot stem mass and subsequently total shoot mass, was influenced by location of parental bud within shoot and of parental shoot within crown, suggesting secondary growth of woody tissues.

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