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Allometry varies among related families of Norway spruce

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Abstract

· **Key message** Slopes and intercepts of allometric equations for organs' biomass varied among half-sib families of Norway spruce and between age categories in a family-dependent manner. Genetic variation should be accounted for when applying allometric analysis to mixtures of genetic groups.

· **Context** Genetic variation in relationships among plant biomass components was rarely addressed in trees, though depending on deployment strategies in tree improvement programs, variation among genetic groups in plant organs' growth rates, and thus biomass allocation, would affect forest growth and carbon balance.

· **Aims** We investigated growth and biomass distribution in Norway spruce (*Picea abies* [L.] H. Karst) half-sib families. We assumed invariance among families in allometric relationships, and stability in growth rates of different organs between

ages 2 and 8 years in the subset of those families. We also tested for ontogenetic trend in allometry using the independent dataset of biomass at age 21 years.

· **Methods** We analyzed allometric relationships among plant components using standardized major axis regression.

· **Results** Slopes and intercepts of allometric relationships varied among families, indicating variation in both organs' growth rates and biomass partitioning at a given plant size. Variation in scaling exponents between age categories was also dependent on the family and plant organ considered.

· **Conclusion** Variation in slopes of allometric relationships indicates that a single scaling coefficient should not be applied when different genetic groups are compared. For the interpretation of age effect on biomass partitioning, both slopes and intercepts of allometric relationships should be examined.

Keywords Allocation · Biomass · Distribution · Growth · Partitioning · *Picea abies*

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1 Introduction

Studies of biomass partitioning in plants are a way to explore inherent growth patterns and to examine how those growth patterns and biomass allocation vary in response to environmental stimuli. The general models of scaling relationships between plant parts have been developed that span several orders of magnitude in size from herbaceous plants to mature trees (Enquist 2002; Enquist and Niklas 2002; Niklas 2004). Yet, the generality of those models has just begun to be tested in the context of genetic variation in growth, biomass allocation, and physiology observed within the species (Vasseur et al. 2012).

Functions relating the biomass of an organ to the biomass of the whole plant or inter-relating biomass of different organs (components) are often approximated with the "allometric

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equation": $Y = aX^b$. Here, Y and X are the biomass of different components (or X is the whole plant mass), a is an allometric constant, and b is an allometric (scaling) exponent. When b takes the value of 1, it implies isometry, i.e., direct proportionality between plant parts. The allometric equation is more conveniently used with the log-transformed data: $\log Y = \log a + b \log X$, where $\log a$ becomes the Y intercept and b becomes the slope of the log-log relationship. The latter equation often takes a linear form and its parameters may be estimated using the appropriate line-fitting procedure (Warton et al. 2006; Smith 2009). A useful feature of the allometric approach to biomass partitioning is that it implicitly accounts for differences in plant size. The other approach to biomass partitioning is based on taking the fractions of total plant mass constituted by particular organs—leaves (LMF—leaf mass fraction), stem (SMF—stem mass fraction), and roots (RMF—root mass fraction). Because the strength of the allometric relationships (R^2) depends on the range of plant sizes compared, it has been advocated to combine both approaches in studies of plant biomass partitioning (Poorter and Sack 2012; Poorter et al. 2015).

Genetic variation in parameters of relationships among plant biomass components was rarely addressed in trees (Stovall et al. 2012; Aspinwall et al. 2013; Stovall et al. 2013). However, the observed genetic variation in biomass allocation patterns in various tree species (Oleksyn et al. 1992; Oleksyn et al. 1999; Retzlaff et al. 2001; Chmura et al. 2007; Aranda et al. 2010; Sanchez-Gomez et al. 2010; Chmura et al. 2013; Cheng et al. 2014) implies that variation in allometry may also exist at the intra-species level. Comparing half-sib families or any other genetic groups using allometric relationships may reveal genetic effects on plant growth and biomass partitioning. When intercepts but not slopes of the allometric relationships vary, it reflects variation in biomass distribution at a given plant size, but not in growth rates. In contrast, variation in slopes may reflect genetic differences in growth rate of an organ relative to the other or to total plant mass. If slope differences among genetic groups persist throughout the years, it will lead to contrasting patterns of variation in biomass partitioning as plants grow in size (Warton, Wright et al. 2006; Smith 2009). When data for genetic groups fall into different portions of the same regression line, it reflects genetic differences in size, but not in biomass distribution.

An important question remains whether the biomass scaling persists fixed through ontogeny in genetically identified groups or whether the allometric exponents vary with plant age and size. A different question is whether the observed biomass scaling relationships conform to apparently fixed values that were grounded on the theoretical assumptions regarding vascular networks in plants (Enquist and Niklas 2002; Niklas 2004). The validity of such fixed scaling exponents for plant organs' mass has been debated based on the data

spanning >10 orders of magnitude in plant size (Poorter et al. 2015). However, the interpretation of the allometric analysis at the intraspecific level (ontogenetic trends) can differ significantly from the broad interspecific biomass allocation patterns (Weiner 2004; Niklas 2006), and thus, these two types of comparisons should not be confused.

In this study, we investigated growth and biomass distribution in half-sib families of Norway spruce (*Picea abies* [L.] H. Karst). This is an important commercial tree species in Europe and subject to tree improvement programs. Differences in biomass partitioning into particular organs among genetic groups would affect forest growth and carbon balance, depending on the deployment strategies of improved material. We hypothesized that half-sib families within a single population would vary in biomass partitioning at 2 years of age. We expected this variation to result from differences among families in distribution of biomass into plant components at the same plant size (intercepts), rather than from variation in slopes of allometric relationships between biomass components and the whole plant. Alternatively, if slopes were to differ, we assumed that those differences in growth rates in the nursery would be correlated with height growth performance of these same families in the field at age 5 years. We also hypothesized that growth rates (allometric slopes) for different organs would be maintained in the subset of the same families at age 8 years. To test for intraspecific ontogenetic trend in biomass partitioning, we compared allometric relationships obtained across the examined families at ages 2 and 8 years with the independent dataset of Norway spruce biomass at age 21 years. In contrast to the ontogenetic variability of slopes found in the interspecific comparisons (Poorter et al. 2015), we hypothesized that the scaling exponent would be maintained throughout ontogeny in our intraspecific dataset and that biomass partitioning would vary between age categories as a consequence of variation in allometric constants (intercepts).

2 Materials and methods

2.1 Plant material

The study material consisted of Norway spruce seedlings, saplings, and trees. Most of the seeds were obtained from the restitution seed orchard of the Norway spruce population "Kolonowskie" (Giertych 1993; Chałupka et al. 2008). That population was selected based on its superior adaptability and growth performance in the IUFRO 1964-68 provenance experimental series (Giertych 1978). The seed orchard was established in 1981 in the experimental forest "Zwierzyniec" of the Institute of Dendrology in Kórnik, Poland (52° 14′ N, 17° 04′ E, 80 m a.s.l.) with 109 clones and six grafts per clone.

During the winter of 2006/2007, cones were collected from 70 clones in the orchard and seeds were extracted separately

by clone. Thus, each set of seeds comprised the open-pollinated maternal half-sib progeny. In addition, the two open-pollinated half-sib families from Zawadzkie Forest District (representing the supposed vicinity of the "Kolonowskie" population origin) and three families from the Szczebra Forest District were also included in the experimental series.

Seeds were sown into large containers in spring 2007, and shortly after germination, the seedlings were re-planted into open nursery beds with unconstrained soil volume. After two growing seasons, in March 2009, the seedlings were planted at three common garden sites in forest districts Zawadzkie (50° 36′ N, 18° 30′ E), Jarocin (51° 58′ N, 17° 26′ E), and Szczebra (53° 56′ N, 22° 58′ E) in a randomized complete block design with three blocks (replications) at each site. At tree age 5 years, the height of all 23,080 live trees was measured in the field in all three sites. Survival at that time varied from 62% at the Jarocin site to 64% in Szczebra and 88% in Zawadzkie (Table S1).

In order to test for age effect in biomass distribution, we sampled 49 trees in total from the four families at the site in Jarocin at age 8 years (see below). Three of those families were sampled earlier at the seedling stage. We also sampled 18 trees at age 21 years in the separate experiment to test for generality of age trends in biomass distribution within the species. These trees were sampled from the experimental site with Norway spruce populations from the Beskidy Mountains, growing in the "Zwierzyniec" Experimental Forest near Kórnik, Poland (52° 15′ N, 17° 04′ E, 70 m a.s.l.) (Chmura 2006).

2.2 Biomass sampling

During the time when the seedlings were lifted for planting at field sites in spring 2009, 11 families of seed orchard trees were randomly selected and one family from Zawadzkie Forest District (no. 4135) was sampled for detailed biomass study. Fifty seedlings from each of those families were randomly taken and their leader shoot length was measured. Subsequently, the seedlings were divided into aboveground and belowground parts. Root systems were thoroughly washed with tap water. All seedling components were dried at 65 °C to a constant weight and weighted on a laboratory scale. Foliage was separated from the aboveground part after drying, and weighted separately. Total plant dry mass (PM) was determined as a sum of dry masses of all components—stem, including the main axis and branches (SM), leaf (LM), and roots (RM). The aboveground biomass was calculated as the sum of stem and leaf biomass (AG = SM + LM). The fractions of stem mass (SMF), leaf mass (LMF), and root mass (RMF) were calculated as a fraction of total plant biomass constituted by each component.

At age 8 years, we measured again tree heights at the site of Jarocin. The mean tree height was 160.3 ± 0.83 cm then and varied from 7 to 402 cm among individual trees. Subsequently, we selected in total 49 model trees from the four families to represent the distribution of tree heights within a stand. Each family was represented by 12 trees (one family by 13 trees). The trees were felled on a tarp, and the aboveground part was divided into components—stem and branches, and weighted in the field. The roots were excavated from the 1.5×1.5 m pit centered around the stem to the depth of 50 cm (shallower if the roots did not extend below that depth). All roots extending from the root collar were extracted from the pit, and all roots protruding beyond the pit margins were marked and followed to their ends (most of those roots were in the upper organic layer of the soil). All the plant parts were packed into paper bags and transported into the laboratory, and the procedure was followed as described above to obtain dry mass of trees and their components.

At the separate experimental site with Norway spruce, we measured tree diameters at age 21 years. The mean diameter at breast height was 15.4 ± 0.07 cm and varied from 1.0 to 27.5 cm among individual trees. Eighteen model trees were selected that represented the distribution of diameter classes within the stand. The diameter of model trees varied between 4.4 and 24 cm, and height varied between 5.03 and 15.37 m. The procedure of field sampling was similar to that described above. Fresh mass of all components was weighted on site, and stratified samples (about 10% of fresh mass) were taken for branches (dead, live without needles, live with needles). Stems were cut into 1-m-long sections and weighted. From each section, a 10-cm-thick central part was sampled for dry mass estimation. The whole root systems of nine trees were excavated from the 2.0×2.0 m pits centered around the tree to the depth of 50 cm. Below this depth, only coarse roots were extracted. All roots protruding beyond the pit margins were marked and followed to their ends. Stratified samples of roots were taken for dry mass measurements. Field samples were dried as above and total dry mass of each biomass component was calculated from the ratio of fresh to dry mass established on the samples. Trees at this site represent various populations. However, during the sampling of the trees, we did not take into account their population identity, and therefore, they were treated as a single population for the purpose of this study.

2.3 Allometric analysis

The allometric relationships between biomass components were analyzed using the standardized (reduced) major axis method (Niklas 2004; Niklas 2005; Warton et al. 2006; Smith 2009) in the *smatr* package version 3.4-3 (Warton et al. 2012) available in R (R Core Team 2015).

Based on the log 10-transformed data, we analyzed linear relationships between the biomass of plant components and total plant biomass. We also analyzed the relationships between leaf and stem (LM vs SM—including stem and branches), leaf and root (LM vs RM), between stem and root (SM vs RM), and between root and aboveground biomass (RM vs AG).

For each allometric relationship, several comparisons were conducted. First, we tested for differences among families, i.e., family effect, at age 2 years (12 families), and separately at age 8 years (4 families). Secondly, within each of the three families sampled at both ages, we tested for differences between years, i.e., age effect within family. Subsequently, for the entire dataset including all data—all families sampled at ages 2 and 8 years and all trees sampled at 21 years—we tested for differences among years, i.e., age trend.

In each relationship at the same age (2 or 8 years), we first tested for slope differences among compared groups (test 1). When significant differences were found in test 1, the slope values were compared with Sidak correction (when more than two groups were compared). In those cases where the slopes did not differ statistically, we tested for significance of a shift in the intercept (elevation; test 2) and a shift along the common slope (test 3) (Warton et al. 2006). Statistical significance of these tests among compared groups was claimed at the probability value $P = 0.05$.

2.4 Statistical analysis

For all the 75 families in the field, the plot-level mean data on tree height at age 5 years from three sites were subjected to analysis of variance according to the following model:

$$Y_{ijk} = S_i + B_{j(i)} + F_k + FS_{ik} + e_{(ijk)} \qquad (1)$$

where Y_{ijk} is the plot level mean, S_i is the effect of the ith site ($i = 1,\ldots, 3$), $B_{j(i)}$ is the effect of the jth block within the ith site ($j = 1,\ldots, 3$), F_k is the effect of the kth family ($k = 1,\ldots, 75$), FS_{ik} is the effect of interaction of the kth family with the ith site, and $e_{(ijk)}$ is the error term.

Separate ANOVAs were also performed for each site, with the model involving family, block, and error effects at each site. Comparison of means was performed with Tukey's HSD test.

For the 12 families examined at the nursery, one-way ANOVA was performed to estimate family effect on examined seedling traits. For those same families, the Pearson correlation analysis was performed among seedling traits based on family means, and the correlation between seedling traits at the nursery and tree height at age 5 at the three experimental sites. For the root and stem biomass, where significant differences in slopes of allometric relationships were found among families, the correlation analysis was also performed between the slope value and the tree height in the field. Statistical

analyses were performed using the JMP 9.0.0 statistical package (SAS Institute Inc., Cary, NC, USA).

3 Results

3.1 Biomass partitioning in the nursery and at the field site

Significant variation was found among 12 families for all seedling traits examined in the nursery (leader length, SM, LM, RM, PM, SMF, LMF, and RMF, all $P \leq 0.0001$). For most families, the majority of biomass was allocated into foliage (Fig. 1). On average, family 4106 had the greatest biomass of all components and SMF (Table 1, Fig. 1). The two families with the lowest biomass—4057 and 4135—had among the lowest SMF, but the greatest RMF. In contrast, families 4060, 4068, and 4124 with comparatively low SMF compensated it with a greater LMF rather than RMF (Fig. 1).

At age 8 years, significant variation among the four families was found in SMF and LMF (Fig. 1). For the three families examined at both age categories, the SMF significantly increased between ages 2 and 8 years, whereas LMF and RMF decreased, except for RMF in family 4066 (Fig. 1).

3.2 Allometric analysis

3.2.1 Family effect

The analysis of bivariate relationships between biomass components at age 2 years revealed significant differences among families in slopes of allometric relationships for SM and RM vs PM, SM vs RM and RM vs AG (Table 2, Table S2, Fig. 2). For the other four relationships, the slope differences were not statistically significant among families (test 1), but both the shifts in the intercepts (test 2) and shifts along a common regression line (test 3) were significant (Table 2). Thus, those latter relationships, mostly involving aboveground components, reflected family differences in size of biomass pools and in biomass distribution at a given plant size, but not in growth rates.

At age 8 years, the significant differences among families in slopes of allometric relationships were found for LM vs PM and LM vs RM (test 1; Table 2, Fig. 3). The shifts in the intercepts (test 2) were significant among families for SM vs PM, SM vs RM, and LM vs SM (Table 2, Fig. S1). Because trees at age 8 years were selected to represent the whole range of tree sizes (heights) within a family, the shifts along a common regression line (test 3) were not significant for those latter relationships (Table 2).

3.2.2 Age effect within the half-sib families

The age effect in allometric relationships showed contrasting patterns within the examined families (Table 3, Table S3).
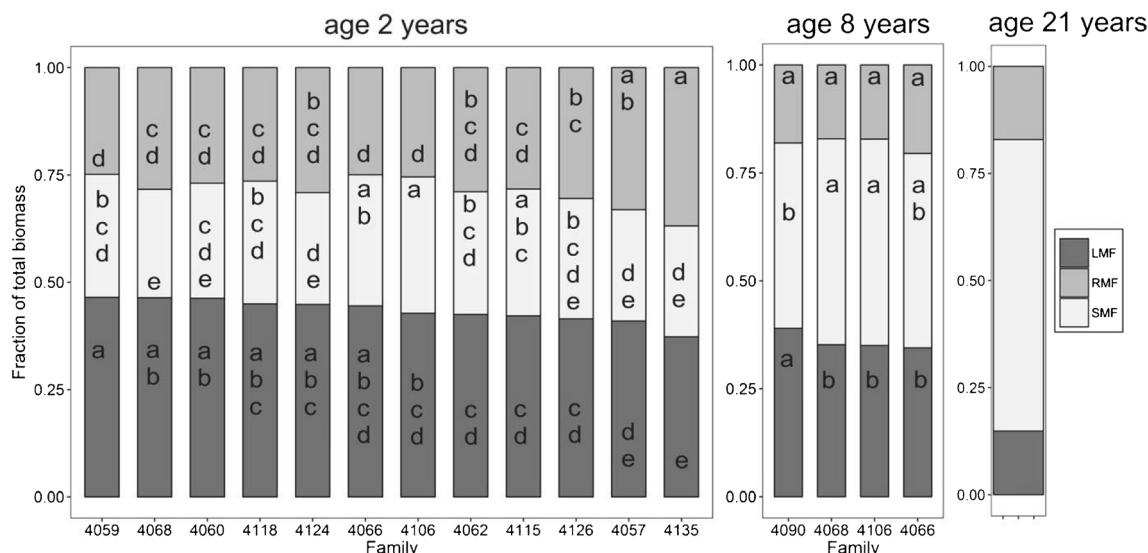
Fig. 1 Mean values of leaf (*LMF*), stem (*SMF*), and root mass fraction (*RMF*) for the 12 half-sib families of Norway spruce examined at age 2 years (*n* = 50 per family, except family 4059 with *n* = 49) and four families examined at age 8 years (*n* = 12 per family, except family 4090 with *n* = 13). Data from the independent study at age 21 are also included (*n* = 9). At each age, values were ordered according to decreasing LMF. *Bars* of a given trait sharing the *same lowercase letter* were not significantly different in the Tukey-Kramer HSD test at the α = 0.05 level

Between the measurements at ages 2 and 8 years, the slopes differed (test 1) for all the relationships involving root mass in family 4066, and for SM and AG vs PM relationships in family 4106 (Fig. S2), whereas slopes did not vary between ages in family 4068 (Table 3, Table S3). In families 4066 and 4068 for most of the relationships where slopes did not vary, a significant variation was found in the intercepts between two age categories (test 2), in contrast to family 4106. In all families, test 3 was significant because tree sizes obviously varied between age

categories, and thus, when the regression lines shared a common slope, the values fell onto different portions of the regression line (Table S3). For the same reason, a direct comparison of intercepts is problematic, because there was virtually no overlap in plant mass between the ages 2 and 8 years (e.g., Fig. S2).

The allometric age effect between 2 and 8 years was consistent with relative biomass partitioning when both intercepts and slopes for all components were considered. For example, in family 4106, a lower slope of SM vs PM relationship at age 8 than 2 years (Table 3) would indicate that SMF should be decreasing with age and size, whereas the opposite was observed (Fig. 1). This apparent contradiction is resolved by the observation that although the rate of SM growth in relation to the whole plant mass decreased from age 2 to 8 years, the relative partitioning into SM was still greater (slope $\geq$ 1) than for LM and RM, which both had slopes <1.0 (Table 3). Moreover, the intercept values, although not statistically different between the two age categories, would indicate a decreasing partitioning into leaf and root biomass with age in this family. In family 4066, we found lower biomass partitioning into leaves and greater into stem mass in relation to plant mass, and a decreasing rate of root mass growth in relation to other components with age (Table 3, Fig. S2). In contrast, in family 4068, biomass allocation at a given plant size, but not growth rate, differed between age categories (Table 3).

3.2.3 Age trend

For the purpose of analysis of ontogenetic trend in allometry, we ignored family variation found above and fitted the SMA regression lines by age category, including data from a separate experiment at age 21 years. We found significant differences in slopes

Table 1 Mean values (and standard deviations) of foliage, stem, and root biomass for seedlings of the 12 half-sib families of Norway spruce examined in a nursery (*n* = 50 within a family, except for fam. 4059, *n* = 49)

Family	Foliage biomass[a] [g]			Stem biomass [g]			Root biomass [g]		
4106	2.9	(1.02)	a	2.2	(0.89)	a	1.7	(0.55)	a
4060	2.3	(0.96)	b	1.3	(0.67)	bc	1.3	(0.53)	b
4118	2.2	(0.90)	b	1.4	(0.69)	b	1.3	(0.55)	b
4115	2.0	(0.89)	b	1.5	(0.76)	b	1.3	(0.65)	ab
4059	2.0	(0.89)	b	1.3	(0.57)	bc	1.1	(0.54)	bc
4068	1.9	(0.73)	b	1.0	(0.42)	cde	1.1	(0.50)	bc
4124	1.9	(0.84)	b	1.2	(0.59)	bcd	1.2	(0.55)	b
4066	1.8	(0.77)	b	1.3	(0.54)	bc	1.1	(0.62)	bc
4126	1.8	(0.72)	b	1.3	(0.67)	bc	1.4	(0.78)	ab
4062	1.7	(0.99)	b	1.2	(0.64)	bcd	1.1	(0.57)	bc
4135	1.2	(0.49)	c	0.8	(0.48)	de	1.1	(0.52)	bc
4057	1.0	(0.55)	c	0.7	(0.35)	e	0.8	(0.45)	c
Mean	1.9	(0.94)		1.3	(0.72)		1.2	(0.60)	

[a] Families were ordered according to decreasing values of foliage biomass. Values connected with the same letter for each trait are not significantly different at α = 0.05 (Tukey-Kramer HSD test)

Table 2   Results of the allometric analysis (*P* values) testing differences among half-sib families of Norway spruce at age 2 years (12 families) and 8 years (4 families). Test 1 is for differences in slopes among families, test 2 is for the shifts in the intercepts, and test 3 is for the shifts along a common regression line. The range of slope values (min. to max.) among families is given when test 1 was significant or a single slope value otherwise

Variable 1 biomass vs	Variable 2 biomass	Family effect at age 2 years			Slope	Family effect at age 8 years			Slope
		Test 1 "Slope"	Test 2 "Intercept"	Test 3 "Shift"		Test 1 "Slope"	Test 2 "Intercept"	Test 3 "Shift"	
Leaf	Plant	0.5840	<0.0001	<0.0001	1.020	*0.0147*			0.940–1.006
Stem	Plant	*0.0135*			1.021–1.241	0.6854	<0.0001	0.8091	1.021
Abovegr.	Plant	0.0984	<0.0001	<0.0001	1.041	0.1575	0.0839	0.7802	1.006
Root	Plant	*0.0112*			0.975–1.438	0.1388	0.0627	0.7832	0.981
Leaf	Stem	0.1115	<0.0001	<0.0001	0.898	0.1092	<0.0001	0.7712	0.968
Leaf	Root	0.0545	<0.0001	<0.0001	0.934	*0.0451*			0.868–1.058
Stem	Root	*0.0019*			0.847–1.207	0.3394	*0.0291*	0.8119	1.036
Root	Abovegr.	*0.0157*			0.920–1.488	0.1412	0.0662	0.7837	0.975

among compared age categories for most of examined allometric relationships, except for SM vs RM and RM vs AG (Table 4, Fig. 4, Fig. S3). In the RM vs PM relationship, however, test 1 indicated significant variation in slopes, but the multiple comparison test failed to distinguish significantly different slopes (Fig. 4). The SMF increased, but RMF and especially LMF decreased with increasing plant age and size (Fig. 1, Fig. S4).

3.2.4 Correlation analysis of seedlings in the nursery and saplings in the field

In seedlings at the nursery, the leader length was strongly positively correlated with biomass of all components and with total seedling biomass. However, when component biomass was expressed as a fraction of total biomass, significant

Fig. 2   Relationships between biomass components which showed significant variation in slopes (test 1) among 12 families of Norway spruce examined in a nursery at age 2 years. *Points* show data for individual seedlings; *lines* show SMA regression fitted by family (*n* = 50 per family, except one with *n* = 49)
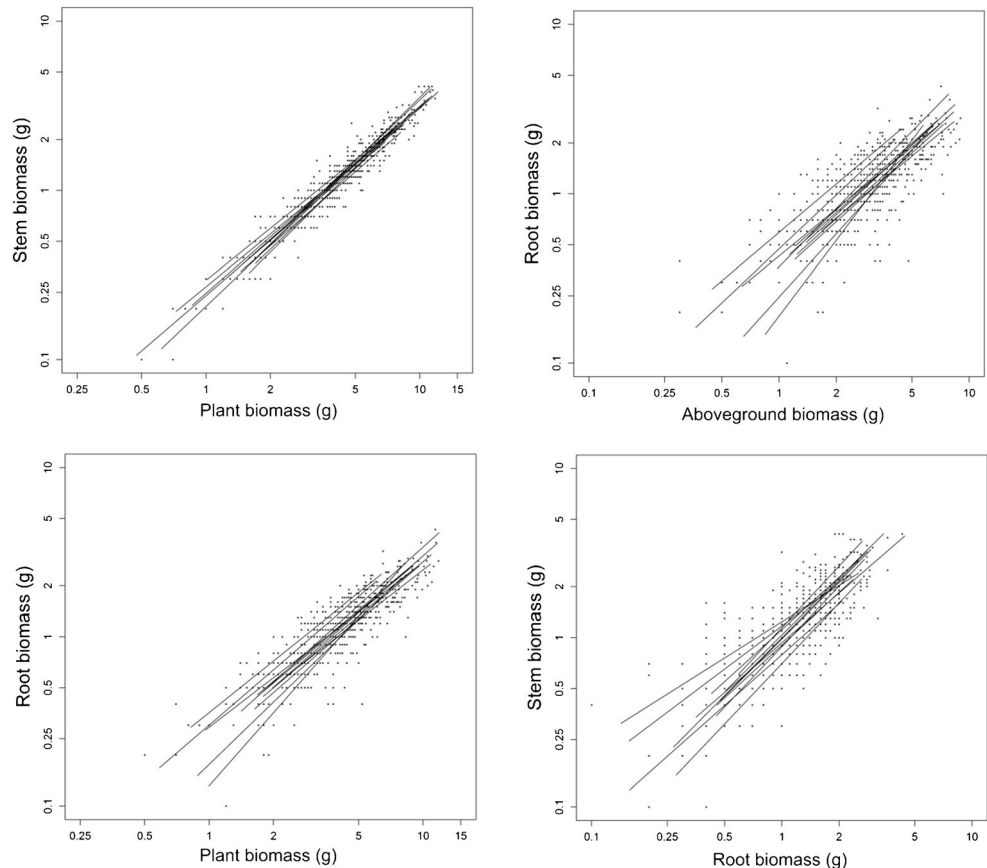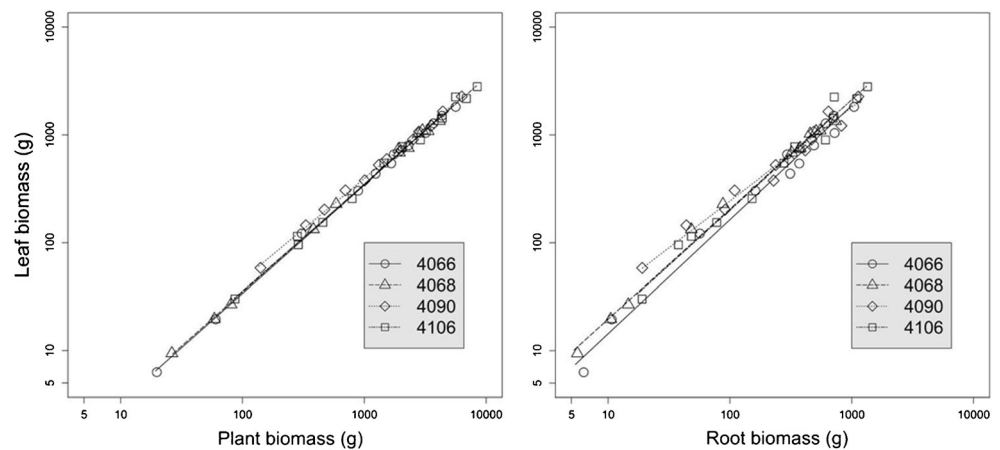
Fig. 3 Relationships between biomass components for which significant variation in slopes (test 1) was found between families of Norway spruce examined at age 8 years. *Points* show data for individual trees, and *lines* show SMA regression fitted by family (n = 12 per family, except family 4090 with n = 13)

correlations of leader length were found only for SMF (positive) and RMF (negative; Table S4).

At age 5 years in the field, all sources of variation were statistically significant (P < 0.0001) in the analysis of tree height, except for the family × site interaction term (P = 0.0572). The mean tree height varied among three sites by 20% (Table S1). Variation among all 75 families was significant at the sites in Zawadzkie and Jarocin, where the differences in tree height between extreme values reached 39 and 46%, respectively (Table S1). When analyzed across three test sites, tree height at age 5 years was positively correlated with leader length, LM, PM, and LMF at the nursery, and negatively correlated with RMF (Table S4). However, although statistically significant, the strength of these correlations was rather weak.

For the SM and RM that showed slope variation among families at age 2 years, no correlation was found between the slope value for the family and tree height at age 5 years (r = 0.12, P = 0.4966 for SM and r = −0.18, P = 0.3002 for RM).

4 Discussion

To further our understanding of allometric relationships governing biomass partitioning in trees, we investigated growth and biomass distribution among half-sib families within a single population of Norway spruce. We hypothesized that families would differ in biomass distribution at the same plant size (allometric intercepts), but not in slopes of allometric relationships relating biomass of different plant components. Our hypothesis was partially supported, as we found significant variation among families in both intercepts and slopes of allometric relationships at the seedling stage in the nursery and at age 8 years in the field.

The allometric approach used in this study directly accounts for plant size in biomass partitioning. For testing relationships between plant components, test 1 ("slope test") is the most meaningful (Warton et al. 2006), because it helps to determine whether scaling between plant parts is isometric

or allometric. However, for testing differences among families in biomass partitioning, both tests for slope homogeneity (test 1) and for intercept homogeneity (test 2) are meaningful. When the compared groups share a common slope, it indicates that they have similar growth trajectories, and thus similar biomass distribution, even if the groups differ in plant size. Such a situation would be equivalent to the significance of test 3 only ("shift test") where groups occupy different portions of the same regression line. On the other hand, the significance of test 2 only points to variation in biomass partitioning among groups independent of plant size. Both tests 2 and 3 were significant for LM vs other components and AG vs PM at age 2 years, reflecting variation among families in plant size (or component biomass) and in biomass partitioning at a common plant size, rather than allocation patterns changing in relation to plant size. Similarly, at age 8 years, families varied in biomass partitioning between LM and SM, and SM and RM at a common plant size. In contrast, slope differences found for SM and RM vs PM, for RM vs AG and SM at age 2 years and for LM vs PM, and LM vs RM at age 8 years indicated that biomass distribution to these components varied among families depending on plant size. Genetic variation in slopes of allometric equations relating branch, stem, and tap-root biomass to total plant mass was also found among clones of loblolly pine (*Pinus taeda* L.) beyond a seedling stage (Stovall et al. 2012; Stovall et al. 2013). In this same species, the slopes and intercepts varied for the fine root vs total biomass relationship among genotypes, and for the stem mass vs foliage relationship among genetic groups including clones, half-sibs, and full-sibs (Aspinwall et al. 2013). Together, these results suggest that stem and root growth rates may be under tight genetic control. Genetic variation in slopes of allometric relationships indicates that a single scaling (allometric) coefficient should not be applied for these relationships when examining a mixture of different genetic groups.

If variation in slopes at the seedling stage continues through time, differences in biomass partitioning would compound and affect tree growth patterns at later ages.

Table 3 Estimates and their lower and upper 95% confidence limits of intercepts and slopes of allometric relationships at ages 2 and 8 years in three open-pollinated half-sib families of Norway spruce

Variable 1 biomass vs	Variable 2 biomass		Family 4066				Family 4068				Family 4106			
			Intercept 2 years	Intercept 8 years	Slope 2 years	Slope 8 years	Intercept 2 years	Intercept 8 years	Slope 2 years	Slope 8 years	Intercept 2 years	Intercept 8 years	Slope 2 years	Slope 8 years
Leaf	Plant	Estimate[a]	−0.3588	−0.4776	1.0045	1.0045	−0.3397	−0.4722	1.0061	1.0061	−0.3685	−0.4467	0.9964	0.9964
		L95%	−0.3812	−0.5572	0.9780	0.9780	−0.3590	−0.5461	0.9839	0.9839	−0.4004	−0.5737	0.9611	0.9611
		U95%	−0.3364	−0.3980	1.0290	1.0290	−0.3205	−0.3983	1.0345	1.0345	−0.3366	−0.3198	1.0388	1.0388
Stem	Plant	Estimate	−0.5365	−0.4334	1.0287	1.0287	*−0.6090*	*−0.3617*	1.0139	1.0139	−0.6523	*−0.3969*	*1.1874*	*1.0242*
		L95%	−0.5624	−0.5315	0.9976	0.9976	−0.6300	−0.4415	0.9903	0.9903	−0.7256	−0.5056	1.1016	0.9906
		U95%	−0.5106	−0.3354	1.0598	1.0598	−0.5880	−0.2819	1.0460	1.0460	−0.5791	−0.2882	1.2798	1.0589
Abovegr.	Plant	Estimate	−0.1357	−0.1455	1.0151	1.0151	*−0.1499*	*−0.0995*	1.0063	1.0063	−0.1846	*−0.1090*	*1.0693*	*1.0087*
		L95%	−0.1524	−0.2053	0.9934	0.9934	−0.1615	−0.1290	0.9970	0.9970	−0.2281	−0.1566	1.0177	0.9938
		U95%	−0.1190	−0.0857	1.0327	1.0327	−0.1383	−0.0700	1.0171	1.0171	−0.1410	−0.0615	1.1235	1.0237
Root	Plant	Estimate	−0.8815	−0.5505	*1.4376*	*0.9510*	−0.5494	−0.7334	0.9869	0.9869	−0.5783	−0.6776	0.9702	0.9702
		L95%	−1.0100	−0.7662	1.2443	0.8836	−0.5860	−0.8797	0.9428	0.9428	−0.6335	−0.8941	0.9080	0.9080
		U95%	−0.7529	−0.3347	1.6611	1.0237	−0.5127	−0.5871	1.0412	1.0412	−0.5231	−0.4612	1.0390	1.0390
Leaf	Stem	Estimate	*0.1651*	*−0.0527*	0.9759	0.9759	*0.2646*	*−0.1106*	0.9913	0.9913	0.1457	0.0105	0.9475	0.9475
		L95%	0.1384	−0.1710	0.9337	0.9337	0.2428	−0.2336	0.9461	0.9461	0.1181	−0.1669	0.8776	0.8776
		U95%	0.1919	0.0655	1.0176	1.0176	0.2864	0.0125	1.0358	1.0358	0.1732	0.1879	1.0019	1.0019
Leaf	Root	Estimate	0.2561	0.0990	*0.6782*	*1.0583*	0.2203	0.2725	1.0210	1.0210	0.2256	0.2509	1.0263	1.0263
		L95%	0.2116	−0.1225	0.5540	0.9699	0.1806	0.1486	0.9670	0.9670	0.1863	0.0220	0.9411	0.9411
		U95%	0.3006	0.3206	0.8303	1.1547	0.2600	0.3963	1.0767	1.0767	0.2649	0.4798	1.1225	1.1225
Stem	Root	Estimate	0.0940	0.1603	*0.7100*	*1.0823*	*−0.0447*	*0.3886*	1.0289	1.0289	0.0853	0.2646	1.0786	1.0786
		L95%	0.0493	−0.1027	0.5840	0.9782	−0.0817	0.2285	0.9618	0.9618	0.0451	0.0334	0.9982	0.9982
		U95%	0.1386	0.4233	0.8632	1.1975	−0.0076	0.5486	1.1015	1.1015	0.1255	0.4958	1.1896	1.1896
Root	Abovegr.	Estimate	−0.7216	−0.4055	*1.4876*	*0.9339*	−0.4010	−0.6265	0.9773	0.9773	−0.4428	−0.5499	0.9543	0.9543
		L95%	−0.8666	−0.6649	1.2255	0.8510	−0.4438	−0.7952	0.9228	0.9228	−0.5016	−0.7993	0.8773	0.8773
		U95%	−0.5766	−0.1461	1.8058	1.0248	−0.3582	−0.4579	1.0376	1.0376	−0.3841	−0.3006	1.0321	1.0321

Italicized values show pairs of intercepts or slopes that were significantly different between two age categories ($P \leq 0.05$)

[a] Estimates for slopes differ in cases when test 1 ("slope test") showed significant differences between age categories. Otherwise, the common slope was fitted to both age categories and test 2 ("intercept test") for intercept variation was applied

Table 4 Results of the allometric analysis (*P* values) testing differences among the three age categories of Norway spruce. Test 1 is for differences in slopes among age categories, test 2 is for the shifts in the intercepts, and test 3 is for the shifts along a common regression line

Variable 1 biomass vs	Variable 2 biomass	Age trend among three age categories		
		Test 1 "Slope"	Test 2 "Intercept"	Test 3 "Shift"
Leaf	Plant	*0.0001*		
Stem	Plant	*<0.0001*		
Abovegr.	Plant	*<0.0001*		
Root	Plant	*0.0372*	*<0.0001*	*<0.0001*
Leaf	Stem	*<0.0001*		
Leaf	Root	*0.0186*		
Stem	Root	0.16345	*<0.0001*	*<0.0001*
Root	Abovegr.	0.54579	*<0.0001*	*<0.0001*

Accordingly, we hypothesized that different growth rates of particular organs in the nursery would be correlated with height growth performance of these same families in the field at age 5 years. Contrary to the hypothesis, we did not find a significant correlation between the slopes of SM and RM vs TM relationships at age 2 years and tree height in the field. Further, no correlation was found between SMF of 12 families at the nursery and field tree height at age 5 years. This lack of correlation may partially result from including biomass of side shoots into the calculation of stem mass and SMF at the nursery, whereas tree height in the field reflects growth of main axis only. The other reason may be the narrow, although statistically significant, range of variation in slopes among families, especially for SM. Perhaps some of those slopes varied with age, which has caused differences in biomass partitioning in the field compared to what was observed in the nursery (see below). Yet another reason may be different environmental influence of nursery than field conditions. Typically, correlations of tree growth at such an early age as in our experiment with growth at later ages are weak or even negative (Lambeth 1980; Namkoong and Kang 1990; Nilsson 1991), and even the age 5 years would be too early to make convincing predictions of future performance.

We hypothesized that growth rates (allometric slopes) for different organs would be maintained between ages 2 and 8 years in the subset of examined families. This hypothesis was only partially supported, and whether the scaling exponent was maintained between age categories depended on the family and plant organ considered. However, there is also some indication that variation in slopes found among families at the seedling stage has caused differences in biomass partitioning at a later age. Namely, for family 4066, the slope of SM vs PM was the lowest and of RM vs PM was the highest among examined families at the nursery (Table S2), indicating the decreasing biomass distribution to stem and

increasing to root mass as plants increased in size. This is consistent with the relative biomass partitioning of this family at age 8 years, as it had slightly lower SMF and greater RMF compared to the other two families that were also examined at age 2 years (Fig. 1), despite it having a lower slope of RM vs PM at age 8 than 2 years (Table 3). This findings strengthen our conclusion that genetic variation in allometric relationships should not be ignored. Furthermore, for the interpretation of age effect on biomass partitioning, both slopes and intercepts of allometric relationships should be examined.

Another question we explored was whether the scaling exponent would be maintained throughout ontogeny in our intraspecific dataset. For that purpose, we ignored genetic variation in allometric slopes found at ages 2 and 8 years, which obviously violates our conclusions given above. This violation seems particularly serious for data at age 2 years, because for the majority of families the individual slope values were outside the 95% confidence limits of regression line fitted across the entire dataset at that age. The regression line had a very poor fit especially for seedlings' root biomass ($R^2 \leq 0.75$, Fig. 4, Fig. S3). Nonetheless, our hypothesis was not supported, and for majority of relationships, especially those involving leaf biomass, we found significant variation in slopes of allometric relationships among age categories.

The slope values for relationships between LM and SM or RM obtained with our data at age 2 years were very close to those obtained by Poorter et al. (2015) for the similar range of plant sizes, by Niklas (2004) based on a dataset for small-sized herbaceous and juvenile woody plants, and by Cheng et al. (2014) for seedlings of five tree species. This indicates that in tree seedlings that accumulated little secondary tissues the slope values for those relationships are close to those obtained in our study. In contrast, at ages 8 and 21 years, our slope estimates for the LM vs SM and RM differed markedly from those of the interspecific allometries at the similar plant size range. Whereas Poorter et al. (2015) found that for these relationships slopes decreased with increasing plant size, we found that slopes increased from the younger, and thus smaller saplings, to the older and larger trees. Also, slope values for the SM vs RM relationships in these two age categories were smaller than those reported by Poorter et al. (2015). It confirms that intraspecific ontogenetic trends in growth and biomass distribution may differ significantly from the interspecific allometric comparisons, and this variation likely contributes to the "noise" in those broad comparisons (Niklas 2006). However, the relationships we found between relative biomass fractions and total plant mass followed strikingly well the trends described in a large multi-species dataset (Poorter et al. 2015).

Our findings have at least two important implications. First, variation among families in allometric relationships may guard a population against the risks associated with multiple resource limitations. Plants allocate carbon and biomass into
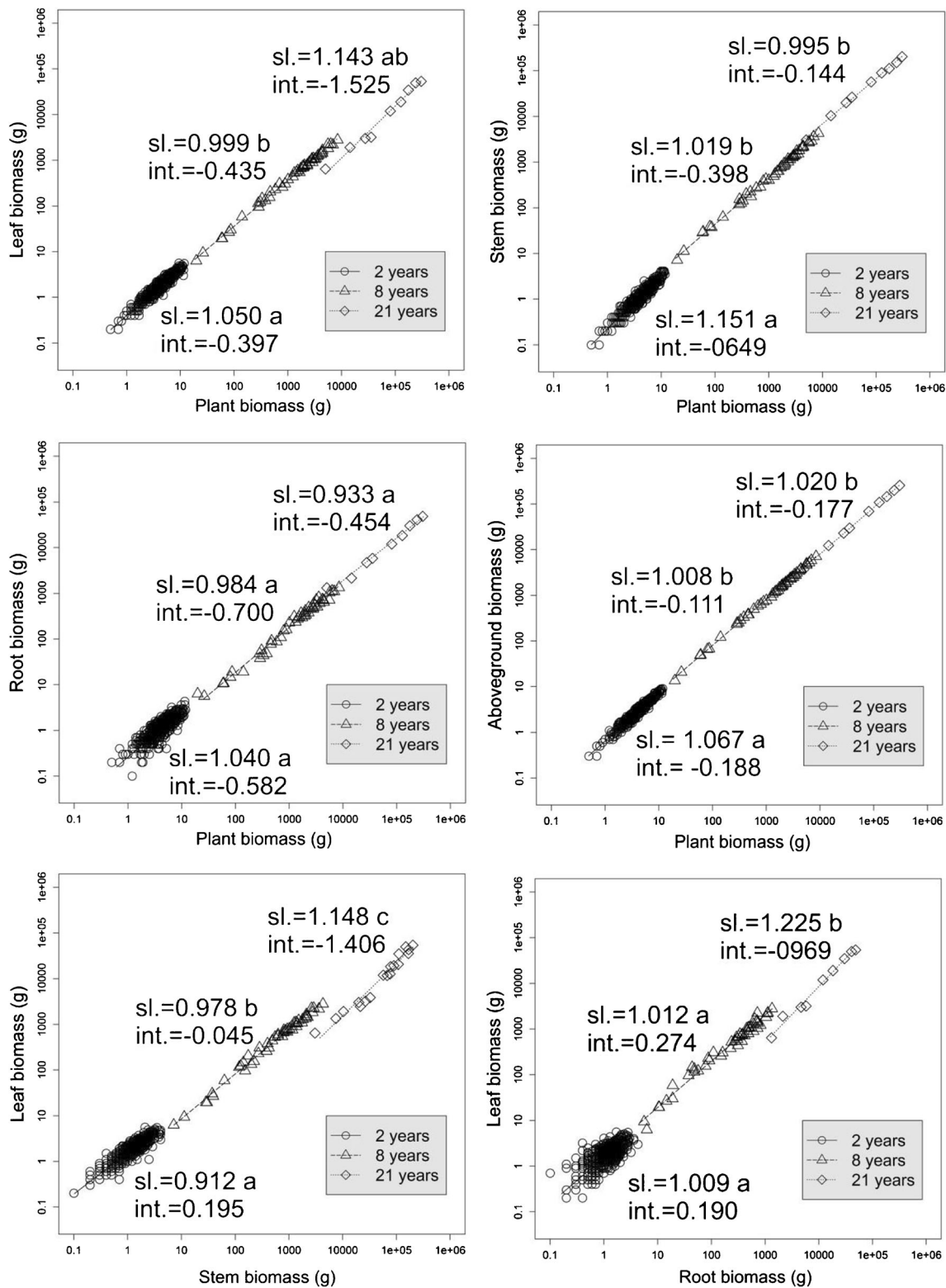
Fig. 4 Age trend in the SMA relationships which showed significant variation in slopes (*sl.*) across the compared age categories of Norway spruce. *Slope values* followed with the *same lowercase letter* did not differ at the $P \leq 0.05$ level; intercept (*int.*) is also given for each relationship; $n = 599$ at age 2 years, 49 at age 8 years. At age 21 years, $n = 18$ for leaf and stem biomass, and 9 for other components

components responsible for uptake of most limiting environmental resources (Bloom et al. 1985; Poorter et al. 2012).

Hence, representation of multiple biomass allocation strategies within a single population makes it less vulnerable to

various environmental limitations, thus increasing its fitness. Second, different allometric relationships leading to variable biomass distribution lay at the base of tree ideotype development in tree breeding (Dickmann 1985; Martin et al. 2001). Depending on deployment strategies, families representing various ideotypes may be planted to fulfill specific breeding goals or to match particular sites. Nevertheless, whether variation we found at a young age would lead to differences that may be relevant to above implications at later ages remains to be seen.

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Compliance with ethical standards

Conflict of interest   The authors declare that they have no conflict of interest.

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