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Scaling allometric relationships in pure, crowded, even-aged stands: do tree shade-tolerance, reproductive mode and wood productivity matter?

D. Gafta, F. Crișan

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Abstract. Tree allometric relationships are likely to be influenced by species tolerance to shade, nutrient availability and plant ontogenetic origin. The aim of this paper was to test to what extent these factors affect the scaling exponents of two allometric relationships in pure, even-aged, canopy-closed forest stands: stem diameter (D) versus stem height (H) and versus stem density (N). Data were collected by tree species (*Betula pendula, Fagus sylvatica* and *Quercus petraea*), wood productivity class and reproductive mode (seed origin and sprouting stands) from published forest yield tables. Reduced major axis analysis was used to estimate the slopes of regression lines in the log-log space of H-D and D-N. The scaling exponent of the H-D relationship was significantly larger in birch than in beech stands (0.897 versus 0.745), and in low productivity, beech stands as compared with their high productivity counterparts (0.876 versus 0.745). However, no significant difference was detected between high stands and coppices of durmast oak. The scaling exponent of the D-N relationship was significantly larger in birch than in beech stands (-0.690 versus -0.558), in low than in high productivity beech stands (-0.694 versus -0.558), and in seed origin than in sprouting stands of durmast oak (-0.609 versus -0.580). We explained these results in terms of plant stem growth strategies and resource availability from a biomechanical perspective. Contrary to certain studies that have reported an invariant scaling relation between stem diameter and density across tree species and communities, but in accordance with other recent studies, we have brought new evidence on species-specific allometric scaling under self-thinning. In addition, we have revealed within-species variance of the scaling exponent of stem diameter-density relationship.
Keywords: beech, birch, diameter-density relationship, durmast oak, forest yield tables, height-diameter relationship, resource availability, scaling exponent, self-thinning, stem biomechanical safety.

Author. Dan Gafta (dan.gafta@ubbcluj.ro), Florin Crişan - Department of Taxonomy and Ecology, Babeş-Bolyai University, Republic Street 42, 400015 Cluj-Napoca, Romania.
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Introduction

The primary functions of stems to support the foliage efficiently, to overtop the adjacent competitors and to carry water and nutrients, require some constraints on adaptations for energy capture: (i) mechanical stability and safety, (ii) photosynthetic efficiency, (iii) whole plant growth and (iv) competitive ability (Givnish 1986, 1995). The allometric constraints on resource use and stem size should easily be revealed under self-thinning conditions. The peculiarities of space sequestration under crowded conditions are a benchmark for the competitive ability of a tree species in closed-canopy forest stands.

Tree architecture is a strong determinant of the biomechanical safety factor (Sterck et al. 2001, Poorter et al. 2003, van Gelder et al. 2006). Stems must at least be able to resist buckling from self-loading, which imposes a maximum height that can be reached by a tree of given diameter (McMahon 1973). Thus, the elastic-stability model predicts that tree maximum height (H_{max}) should scale as the 2/3 power of basal stem diameter (D):

$$H_{\max} \sim k \times D^{2/3}$$

where k is a function of wood stiffness and density, and stem shape (Niklas & Spatz 2004). This formula gives values for H_{max} that exceed those observed in real trees, the differences between measured and estimated heights being ascribed to safety factors against elastic toppling in still air (King 1981, 1986, 1990). The relationship between H and D is log-log nonlinear across small values of D, gradually changes to a log-log linear relationship, and converges on a line with a slope of 2/3 as D becomes very large (Niklas & Spatz 2004). Henry & Aarssen (1999) also showed that the diameter-height relationship in the log-log space becomes non-linear for uneven-aged or cohort-structured populations, with height increasing faster than diameter in the youngest cohorts (trees) and vice versa. The observed values of the scaling exponent are expected to vary across and within species due to the adaptive allometric adjustments of trees to different environmental conditions.

The growth dynamics of tree stems in a particular ecological context is set by some trade-offs, with a balance between safety, growth and resource availability. This arises because stems with a higher margin of biomechanical safety do have higher rates of survival following disturbances or can withstand greater stresses, but at the cost of greater allocation to stem tissue at a given height (Givnish 1995). Therefore, shade-intolerant, fast-growing tree species should have slender stems (lower biomechanical safety margins) than shade-tolerant species of comparable stature, because the former tend to allocate proportionally more to vertical stem growth in order to capture more light. On the other hand, trees on fertile sites do have enough resources to invest in stem safety (radial growth), whereas their conspecific counterparts from poor sites should allocate proportionally less to unproductive, support tissue. The same reasoning should apply to regenerating shoots and saplings, as the former benefit from accessing a larger amount of resources stored in the roots of their mother trees. Consequently, trees growing on low fertility sites or originated from seed should have more slender stems than their conspecific individuals developed on rich habitats or through producing shoots, respectively.

The mean stem diameter ($\overline{D}$) in even-aged, unthinned forest stands can be theoretically expressed as a function of tree density (N) on a simple geometric basis. Since the mean growing area ($\overline{A}$) occupied by a tree is proportional to the square of mean stem diameter (i.e., $\overline{A} \sim \overline{D}^{2}$), and since N is the quotient of the total area occupied by all trees (ΣA_i) and the area occupied by an average tree in a stand (i.e., $N = \Sigma A_i / \overline{A}$), the tree density will scale as the -2 power of average stem diameter (Pretzsch 2006): $N \sim \overline{D}^{-2}$ (equation 1) or equivalently, $\overline{D} \sim N^{-1/2}$ (equation 2). Values equal or close to -2 or -0.5 of the scaling exponent (as in the equations 1 and 2, respectively) were found by analysing either continental or worldwide allometric data sets encompassing a broad spectrum of ecologically and taxonomically diverse forest communities (Enquist & Niklas 2001, Niklas et al. 2003). Lower outliers of the scaling exponent in the equation 1 (up to -2.5) were found only in some tropical and subtropical communities, whereas higher values (up to -0.5) are common worldwide but especially in temperate and conifer forests. Pretzsch (2006) brought evidences against an invariant scaling relationship between stem size and frequency by finding values of the scaling exponent in equation 1 significantly higher than -2 and also different across tree species in pure, even-aged, unthinned stands. A further confirmation of such a hypothesis may come by comparing the scaling exponents between stands formed of tree species with contrasting requirements with respect to light, which is the most limiting resource in crowded populations located on moist, nutrient-rich sites. Despite Pretzch (2006) not finding significant differences between conspecific, unthinned stands, the comparison of such communities located on sites with contrasting productivity could reveal higher rates of tree survival and/or stem growth on fertile habitats.

In this paper we address two questions related to allometric relationships in pure, even-aged, canopy-closed forests: (i) to what extent are these affected by the differences in shade-tolerance between tree species and (ii) is there any within-species differentiation between stands of contrasting productivity and reproductive mode (seeding versus sprouting)? In particular, we attempted to test the following hypotheses: (i) the slope of the log(height)-log(diameter) relationship varies between contrasting stands as follows: shade-intolerant > shade-tolerant (between-species), low > high productivity and seed origin > sprouting (within-species); (ii) the slope of the log(diameter)-log(density) relationship differs between contrasting stands as follows: shade-intolerant > shade-tolerant (between-species), low > high productivity and seed origin > sprouting (within-species). These working hypotheses are summarised and graphically illustrated in Fig. 1.

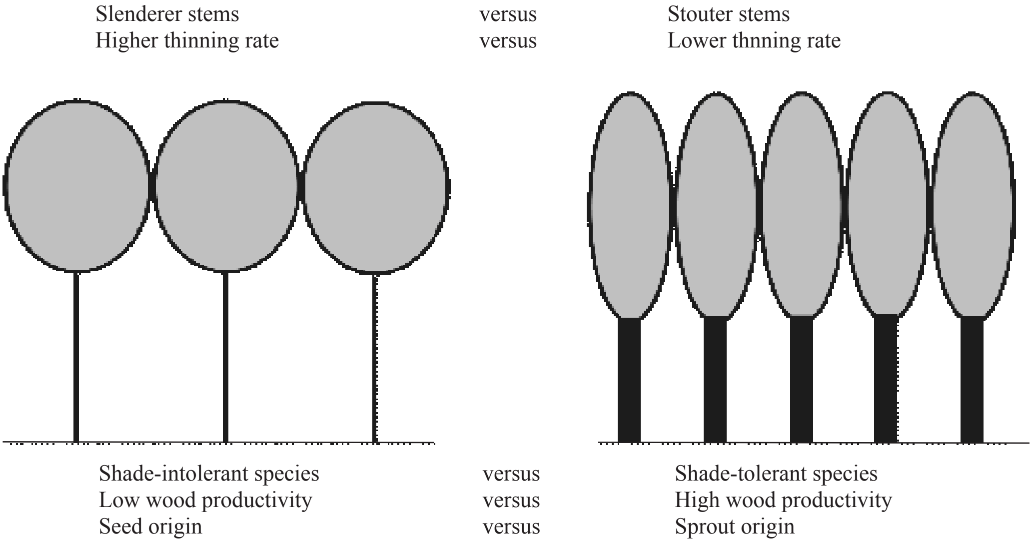

Figure 1 Outline of hypotheses on stem slenderness and density (upper) in contrasting types of pure, even-aged, canopy-closed stands (lower).

Materials and methods

Data collection

The data used in this paper come exclusively from published forest yield tables that were designed specifically for the pure, even-aged, canopy-closed stands of Romania (Armăşescu 1972). These tables were designed by species, stand origin and wood productivity class, the latter being distinguished by reference to the relationship between tree age and mean height.

The main entries in the yield tables are average dendrometric, allometric and timber cubage estimates at stand level, whose margin of error does not exceed ± 10% within 95% confidence interval. The main advantages of these tabulated data are: (i) the inclusion of a series of five-year lag cohorts (from saplings to mature trees); and (ii) their level of representation for a large range of site conditions. On the other hand, such data cannot be analysed through standard numerical methods, as they are not direct measurements but statistical estimates. Given the aim of this study, three tree species with well-known life-history traits were selected for testing the above hypotheses: European beech - *Fagus sylvatica* L. (shade-tolerant), European silver birch - *Betula pendula* Roth (shade-intolerant), and durmast or sessile oak - *Quercus petraea* (Matt.) Liebl. (for which extensive data on both high stands and coppices exist).

The following dendrometric and density data were extracted by tree species, wood productivity class (from I - the highest to V – the lowest) and stand origin (seed and sprout): mean stem height (H), mean stem diameter at breast height (D) and total number of trees per hectare (N). These data were available for stand ages of 10 (15) to 60 (140) years old, depending on species and regeneration mode.

Data analysis

All data were $\log_{10}$-transformed in order to reduce the power-law allometric relationships to handier, linear models. The transformed data fulfilled the assumptions of linear regression analysis such as normal distributions of residuals, homoscedasticity and independence of residuals.

The scaling exponents and allometric constants were computed by reduced major axis (RMA) regression, also known as Model Type II regression. This procedure is preferred to ordinary least square regression when the variables of interest are biologically interdependent, subject to unknown measurement error, and when functional rather than predictive relationships are sought (Sokal & Rohlf 1981, Niklas 1994). In addition, Zeide (1987) and Niklas (1994) claim that RMA regression represents the ‘‘true relationship’’ between variables, as RMA slope of X on Y is exactly the inverse of that of Y on X. Confidence intervals of slope estimates were calculated by bootstrapping (100,000 resamples with replacement). The whole regression procedure was carried out using RMA software (Bohonak & van der Linde 2004).

Results

Stem height-diameter scaling

The slope of the H-D relationship was significantly larger (steeper) in birch than in beech stands of high productivity and originated from seed (Table 1 and Fig. 2a), confirming the differences in tree architecture between shade-tolerant and shade-intolerant species. The regression slope was also significantly steeper in low productivity, seed origin, beech stands as compared with their high productivity counterparts (Table 1 and Fig. 2a), suggesting within-species variation of growth traits as a response to contrasting levels of soil resource availability. On the other hand, no significant difference was detected between the regression slopes of high stands and coppices of durmast oak at the same level (intermediate) of productivity (Ta-

Table 1 Slopes of the allometric relationships estimated through log-log RMA regression analysis in pure, even-aged, canopy-closed stands of contrasting tree species, productivity and reproductive origin (Roman numbers refer to wood productivity class; sd – seed origin; st – shoot origin)

Tree species, stand productivity & origin	Estimated slope (z)	Bootstrap 99% confidence interval		Coefficient of determination (r^2)
		Lower limit	Upper limit	
Stem height-diameter fitting: *log(H) = k + z × log(D)*				
Birch_I (sd)	0.8967	0.8006	0.9405	0.9966
Beech_I (sd)	0.7455	0.6386	0.7766	0.9922
Beech_V (sd)	0.8756	0.7793	0.9112	0.9941
Oak_III (sd)	0.7558	0.6394	0.7985	0.9908
Oak_III (st)	0.7192	0.6215	0.7499	0.9940
Stem diameter-density fitting: *log(D) = k + z × log(N)*				
Birch_I (sd)	-0.6901	-0.7426	-0.6177	0.9937
Beech_I (sd)	-0.5577	-0.5654	-0.5536	0.9999
Beech_V (sd)	-0.6945	-0.7883	-0.5940	0.9771
Oak_III (sd)	-0.6094	-0.6279	-0.5973	0.9993
Oak_III (st)	-0.5805	-0.5956	-0.5678	0.9993

ble 1 and Fig. 2a), which may be the consequence of an ecophysiological compensation.

Stem diameter-density scaling

The slope of the D-N relationship was significantly larger in birch than in beech stands of high productivity and originated from seed (Table 1 and Fig. 2b), suggesting that shade-tolerant species are able to reach the same stem size as shade-intolerant species but under more crowded populations. Within the same species, the regression slopes of both high productivity beech stands and sprouting durmast oak stands were significantly lower than their conspecific stands of low productivity and seed origin, respectively (Table 1 and Fig. 2b). The lower self-thinning rates detected on fertile sites and in coppices seem to be related to higher resource availability at plant level.

Discussion

Stem height-diameter scaling

The scaling exponents of modelled H-D relationships are all higher than 2/3, which is certainly related to the lack of large values of D in our data. Significant upward departures from the 2/3 reference were also found by Price et al. (2009), who estimated a mean scaling exponent of 0.768. Exponent values close to 1 were reported by Niklas (2003) for conifer communities. Moreover, in newly established, crowded plantations of *Pinus radiata*, Watt et al. (2006) estimated a very large H-D slope (1.63), which supports the 'age-dependency' feature of the allometric scaling exponent (Whittaker & Woodwell 1968, King & Loucks 1978, Niklas 1995). On the other hand, Russo et al. (2007) and Dietze et al. (2008) found mean values of the scaling exponent that are lower than 2/3 (i.e., 0.45 and 0.61, respectively). Unfortunately, reliable comparisons between these outcomes and our findings are not possible, because the former were derived from heterogeneous data-sets, partly including mixed and/or uneven-aged stands. Another potential bias could arise from the different light conditions in which the compared tree populations established, i.e. in forest gaps or in an open area (Henry & Aarssen 1999). Theoretically the slope of height-diameter relationship should be steeper in the latter case, but probably this differentiation is detectable only in

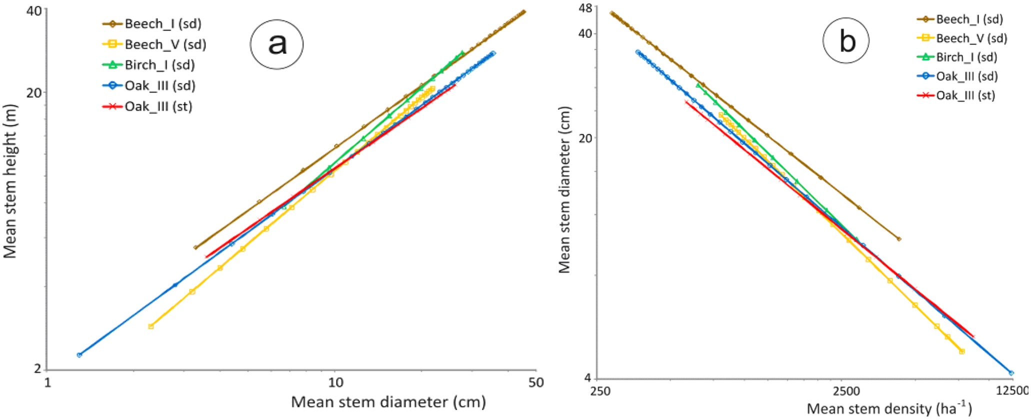

Figure 2 Log-scale adjusted allometric relationships in pure, even-aged, canopy-closed stands of contrasting tree species, productivity and reproductive origin (a - stem height versus diameter; b – stem diameter versus density). Abbreviations as in Table 1

young populations and disappears among old stands. Last but not least, stem allometry is influenced by the growth pattern response of trees to mechanical stresses caused, for instance, by wind or snow load (Jaffe 1973, Cordero et al. 2007).

As predicted, the regression slope is significantly larger for birch than for beech stands. A decline in the scaling exponent or H:D ratio with an increase in shade-tolerance was also observed in other studies (King 1996, Poorter et al. 2003, Gratzer et al. 2004, van Gelder et al. 2006, Dietze et al. 2008). These findings are consistent with the theory according to which the safety factors against buckling decrease with increasing species light requirements (van Gelder et al. 2006). Thus, shade-intolerant species favour height growth over diameter growth at all costs (including lower density wood production) to overtop neighbourhood competitors, whereas shade-tolerant species form stouter stems (Claussen & Maycock 1995, Poorter et al. 2005, 2006).

Consistent with our hypothesis, low productivity beech stands have a larger scaling exponent than their conspecific high productivity stands. This outcome confirms that stem architecture and its biomechanical characteristics are highly specific to the ecological context in which any tree is living and, also demonstrate certain plasticity (Henry & Aarssen 1999, Niklas & Spatz 2004, Read & Stokes 2006, Watt et al. 2006). However, to our knowledge, there are no similar studies addressing this specific issue, i.e. the effect of stand productivity (habitat fertility) on tree stem slenderness.

Contrary to our prediction, the scaling exponents do not differ significantly between sprouting and seed origin stands of durmast oak. One plausible explanation would be that the detection of distinct regression slopes is possible only between very young sapling and sprout stands, when the roots of the former are much less developed than those of stumps or mother trees from which shoots grow. Another possible explanation is that trees developed from seed are capable to enhance their radial growth by producing a less dense wood. Since we are not aware of any study or theoretical model dealing with the influence of reproductive mode on stem allometric relationships, the validity of our initial hypothesis remains questionable.

In addition to confirm the effect of species-specific tolerance to shade on stem slenderness (height:diameter ratio), we brought some evidence on the importance that habitat fertility might have on tree stem allometry from a biomechanical perspective. Further investigations are needed to assess a causal relationship between habitat fertility and stem slenderness, given the possible confounding effects of other environmental factors (e.g., mechanical stress, steepness of terrain) and the influence of tree stand age on stem growth architecture.

Stem diameter-density scaling

The scaling exponent of N with respect to D in all our models is always lower than -1/2, which is consistent with the space occupancy-based theory and other studies performed in temperate and boreal forests (Niklas et al. 2003, Pretzsch & Biber 2005, Zeide 2005, Pretzsch 2006). Surprisingly low values of the scaling exponent as in the equation 1 (up to -2.5) were found by Enquist & Niklas (2001), but only in some tropical and subtropical communities (<30° N or S latitude), probably because of the mixed, uneven-aged (multi-layered) structure of tree stands, composed of highly specialised species.

As predicted, the log-log regression line corresponding to birch stands is steeper than the one associated with beech stands. This logically means that at equal diameters, a larger number of trees of shade-tolerant species can grow per unit area as compared with trees of shade-intolerant species. Pretzsch & Biber (2005) also found significantly differences in scaling exponent between beech stands and those of relatively shade-intolerant species (*Pinus sylvestris, Picea abies* and *Quercus petraea*).

In accordance with our hypotheses, high productivity tree stands show a gentler self-thinning slope than their conspecific but low productivity stands. Assuming a positive relationship between stand productivity and overall habitat fertility, this implies a sensible eco-physiological response of trees developed on rich sites that consists in mustering additional resources to compensate for light deficit. Morphologically, such plasticity may be expressed in the development of shade foliage, increasing shoot-root ratio or crown flattening (Horn 1971, Takahashi 1996, Zeide 2005).

At the same level of woody biomass productivity, coppices display a lower rate of self-thinning than stands formed of conspecific trees but originating from seed, which conforms to our prediction. A plausible explanation of this outcome is based - as above - on the difference in amount of resources available to counterbalance the effects of light deficit. Unlike seedlings, regenerating shoots obtain benefit from the extensive, residual root system and the substantial storage of metabolites in the remaining parts of the parent tree (Boring et al. 1988, Brown 1994, Negrelle 1995, Lloret et al. 2004). Such differentiation reflects the competitive advantages of shoots over seedlings, e.g. higher rates of survival (Arthur et al. 1997, Ceccon et al. 2004).

Our results contradict some previous studies that reported an invariant scaling relation between stem diameter and density across tree species and communities (Enquist & Niklas 2001, Niklas et al. 2003). On the other hand, there is some evidence on species-specific allometric scaling under self-thinning conditions (Pretzsch & Biber 2005, Zeide 2005, Pretzsch 2006) to call into question any claim of a universal allometric law. The exponent value of -1/2 (as in equation 2) seems to be rather an upper threshold that corresponds to the mildest slope a self-thinning line may have in pure, even-aged and fully-stocked stands. Apart from this, we revealed within-species variance of the scaling exponent of stem diameter-density relationship that is related to differences in terms of stand productivity and regeneration mode of trees. This outcome needs to be validated by future analyses in many different tree communities.

Practical implications and conclusions

Apart from the lack of evidence for significantly different slopes of log(H) - log(D) relationship between conspecific stands originated from seeds and sprouts, all the intial hypotheses were confirmed. This could have important implications for silvicultural practices that aim to maximise the wood quality and timber production. First, selective cuttings exceeding the self-thinning rate applied in pure, even-aged plantations of shade-intolerant tree species on low productive sites could enhance the growth of stem diameter and consequently, the stem resistance to strong winds and heavy snow. Second, an overall increase of timber production in low fertility sites could be achieved by a near optimal space occupancy model built in a mixed, two-layer tree canopy: an upper, low-density tree layer formed of a shade-intolerant (fast-growing) species and a lower, high-density tree layer composed of a shade-tolerant (slow-growing) species.

The present study is, to our knowledge, the first to address explicitly how stand productivity and reproductive mode of trees affect the scaling of allometric relationships in pure, even-aged, canopy-closed stands. However, these hypotheses should be further validated by employing real field data from many stands of different tree species.

Much of the work done on allometric scaling in trees is not readily usable for comparisons or meta-analyses. This is because many authors did not report: (i) essential data on forest stand structure (tree species composition, age distribution, regeneration mode, etc.), and/or (ii) used dendrometric data from partly mixed, uneven-aged forest stands.

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