LINK BETWEEN THE SELF-THINNING RULES FOR HERBACEOUS AND WOODY PLANTS

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Self-thinning rules assume allometry between mean plant body mass $\overline{w}$ and plant number N in fully stocked unmanaged stands of herbaceous or woody plants, thus $\overline{w} \propto N^b$. Scaling exponent b reflects the relation between size and requirement of growing space. Generalized exponents b, posed by Reineke, Yoda and West, Brown and Enquist, still our propensity to reduce complexity. However, numerous publications reveal for herbaceous and woody plants a considerable variation of b. The question, whether unified rules of self-thinning for herbaceous and woody plants exist, is still open for debate. This paper addresses a special trait of trees, which frequently has been overlooked when searching for unified self-thinning slopes. Unlike herbaceous plants, many tree species develop a stem with a core of inert heartwood which can come to a considerable proportion of a tree's total biomass and might flaw b. In order to separate between dead and living tissue, functions for estimation of biomass and sapwood area, and a stereometric model for distinction between a stem's sapwood and dead heartwood are developed for European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and European oak (*Quercus petraea*). Founded on unthinned experimental plots, which are under survey for over 130 years, self-thinning lines were evaluated for both total biomass $\overline{w}$ and living biomass $\overline{w}'$ ($\overline{w} \propto N^b$ and $\overline{w}' \propto N^{b'}$, respectively). For $\overline{w} \propto N^b$ OLS regression yielded $b = -1.403, -1.614, -1.575$ and -1.592 for European beech, Norway spruce, Scots pine, and European oak, i.e., Norway spruce < European oak < Scots pine < European beech. However, the differences between the species vanish, when the evaluation is carried out for $\overline{w}' \propto N^{b'}$. The corresponding values are $b' = -1.396$, $-1.365, -1.447$, and -1.369, respectively. ANOVA reveals significant differences between b and self-thinning slopes b'. Comparison with the geometrical scaling exponent $b = -3/2$ postulated by Yoda and fractal scaling slopes $b = -4/3$ expected by West and Enquist show that observed slopes b deviate considerably from the generalized exponents. However, values for b' show that the elimination of inert heartwood shifts allometry remarkably towards fractal scaling. The heartwood's elimination yields a less biased slope b', improves comparability between woody and herbaceous plants' scaling rules and paves the way for a general usability of self-thinning slopes for density estimation, density control, and growth prediction.

self-thinning; allometry; geometrical scaling, fractal scaling; sapwood; inert heartwood; European beech; Norway spruce; Scots pine; European oak

INTRODUCTION

Self-thinning rules describe the relation between the increase of average body weight $\overline{w}$ and the decrease of plant number N in even-aged, fully stocked plant stands as $w \propto N^b$, with negative exponent b. Plotted on the ln-ln scale, the $\overline{w}$-N-trajectories are supposed to follow a descending straight line with slope b and intercept a (ln $\overline{w}$ = $a + b$ ln N). Slope b reflects the plants' pattern of resource allocation when it copes with crowding. Intercept a is determined by growth form and environment. Parameters a an b give shape to metabolic processes and, although not elucidated in detail, they make the processes' results applicable for density control, growth prediction, and linkages between organismal and ecosystem level.

A considerable string of publications, e.g., from R e i n e k e (1933), Y o d a et al. (1963), W e l l e r (1987), N i k l a s (1994), P r e t z s c h (2002), W e s t et al. (1997), and E n q u i s t et al. (1998), reflects the hunting for a species-invariant self-thinning slope b. Y o d a et al. (1963), H a r p e r (1977), W h i t e (1981) and L o n g, S m i t h (1984) strongly argued for a general exponent of $b = -3/2$, founded on Euclidian geometry. G a d o w (1986), P r e t z s c h (2005), W e l l e r (1987,

1990) and Z e i d e (1987) offer strong evidence against general self-thinning rules; they interprete b as a species-specific trait of space occupation. Recently W e s t et al. (1997, 1999) and E n q u i s t et al. (1998, 1999, 2001) presented a model which considers plants as fractal objects and postulate the generality of quarter-power scaling. The model describes the supply of the plant volume by a space-filling fractal network of tubes. In this way they explain that the metabolic rate of individual plants scale as the 3/4 power of body mass and predict from their model in particular $b = -4/3$. As previously geometrical scaling, also generalization of $b = -4/3$ came under fire (W h i t e f i e l d, 2001). After scrutiny, K o z l o w s k i and K o n a r z e w s k i (2004) criticize West, Brown and Enquist's model as neither mathematically correct nor universal. They claim for more biological realism and analysis, and exactly that is the objective of my paper.

This paper addresses a special trait of trees, which frequently has been overlooked when searching for unified self-thinning slopes and might be behind trees' deviations from generalized scaling rules. Unlike herbaceous plants, many tree species develop inert heartwood in the course of ontogenesis. Although physiological inactive, this tissue is rarely excluded when self-thinning slopes

are evaluated. Portion of heartwood usually increases with tree dimension and comes to considerable portions: Trendelenburg and Mayer-Wegelin (1955, pp. 472–474) report volume portions of dead heartwood up to 36, 60, 53, 74% for European beech, Norway spruce, Scots pine, and European oak, respectively. Knigge and Schulz (1966, p. 109) report up to 50 and 75% for Scots pine and European oak, respectively. Lohmann (1992, p. 46) found up to 78% of inert wood for Norway spruce. However, as long as self-thinning rules do not consider the portion of inert heartwood they are hardly comparable with analogue relationships for herbaceous plants. Self-thinning slopes probably would become considerably flatter by substraction of deadwood portion.

In the sequel, stands of European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and European oak (*Quercus petraea*) in Germany, growing under self-thinning conditions and surveyed for over 130 years, are used for scrutiny of the subsequent hypotheses:

H1: Stand of European beech, Norway spruce, Scots pine, and European oak do not differ with respect to slope b of the self-thinning line $\overline{w} \infty N^b$.

H2: Any difference between the species' slopes b disappear or at least diminish when portion of inert heartwood is excluded and the analysis is based on $\overline{w}' \infty N^{b'}$.

H3: Conventionally evaluated slopes b and adjusted slopes b' are equal.

H4: After elimination of inert heartwood, b' of $\overline{w}' \infty N^{b'}$ approximates to generalized geometrical or fractal self-thinning slopes.

MATERIAL AND METHODS

Long-term experimental plots

This paper follows a study, which revealed species-specific slopes b of $\overline{w} \infty N^b$ for European beech, Norway spruce, Scots pine and European oak on the basis of unthinned, fully stocked, even aged long-term experimental plots (Pretzsch, Biber, 2005). The oldest of these experiments are under observation since the mid-19th century. Table 1 reports the essentials for these plots. More background information is reported elsewhere (Pretzsch, 2005).

Separate biomass functions for leaves, branches and stem wood

Unlike herbaceous plants, biomass of trees or stands can hardly be measured completely, rather it is estimated in dependence on tree diameter. In order to develop estimation functions, biomass analyses were carried out on experimental plots with sampling techniques reported by Grote et al. (2003). All together 90 beeches, 235 spruces, 48 pines, and 30 oaks were included, covering approximately the diameter range of the unthinned plots (Table 2). In the sequel biomass of leaves w_l, branches w_b, and stem wood w_s is estimated in dependence on stem diameter d by Formula (1) and by parameters reported in Table 2.

$$\ln w_x = c + d \cdot \ln d \qquad (1)$$

Table 1. Essentials of the underlying thinning trials for European beech, Norway spruce, Scots pine, and European oak

Characteristics	European beech	Norway spruce	Scots pine	European oak
Number of experiments	5	6	5	4
Name of experiments	ELM 20, FAB 15, HAI 27, MIS 25, ROT 26	EGL 72, EGL 73, PB 697, SAC 03, SAC 67, SAC 68	SLU 50, SNA 57, WAS 234, BUL 240, HED 243	WAL 88/2, WAL 88/5, ROH 90, ROH 620
Longitude (degree E)	07°55'07"–10°34'16"	08°52'08"–11°51'13"	10°53'02"–12°20'30"	07°52'34"–09°25'18"
Latitude (degree N)	49°23'27"–50°11'42"	47°50'03"–51°36'06"	49°10'11"–50°00'31"	49°22'44"–49°53'43"
Elevation (m)	400–505	340–840	320–530	430–470
Mean ann. temp. (C)	7.0–8.0	6.2–8.0	5.9–8.4	7.0–8.0
Sum ann. precip. (mm a^{-1})	780–1080	830–1200	540–690	780–1120
First–last survey (cal. year)	1870–1994	1882–1999	1899–1999	1934–2001
Aver. num. succ. surveys	14	14	10	8
Age span (years)	38–162	33–131	26–138	48–132
Mean height age 100 (m)	23.1–31.8	30.1–36.4	17.8–26.5	23.4–30.8
Mean diameter (cm)	5.7–43.6	8.6–50.7	7.8–32.1	13.3–32.5
Stem number (N ha^{-1})	11,242–269	7,428–443	5,104–456	1,671–352
Total biomass (kg tree^{-1})	10.8–1,598.3	16.4–1,776.1	10.6–363.6	95.2–710.7
Living biomass (kg tree^{-1})	10.7–1,551.5	14.5–772.1	10.5–278.1	62.0–350.8

Abbreviations, preceeding the experiments' number, refer to nearby place names: ELM – Elmstein, FAB – Fabrikschleichach, HAI – Hain, MIS – Mittelsinn, ROT – Rothenbuch, EGL – Eglharting, PB – Paderborn, SAC – Sachsenried, SLU – Schlüsselfeld, SNA – Schnaittenbach, WAS – Waldsassen, BUL – Burglengenfeld, HED – Heideck, WAL – Waldleiningen, ROH – Rohrbrunn

Table 2. Scaling functions for above ground biomass in dependence of stem diameter. Estimates ± (SE) for c and d of the model $\ln w = c + d \ln d$ [w = weight (kg) of leaves, branches and stem wood, respectively; d = diameter at breast height (cm), c, d = regression coefficients]. For each estimation function n = number of harvested sample trees, $d_{min} - d_{max}$ = minimum to maximum diameter of sample trees (cm), and r^2 = coefficient of determination are reported

Biomass component	European beech	Norway spruce	Scots pine	European oak
Leaves				
n	61	235	25	25
$d_{min} - d_{max}$	10.0–67.0	7.0–98.2	11.8–58.0	9.8–77.1
$c_l \pm$ SE	−5.479 ± 0.356	−3.118 ± 0.148	−3.251 ± 0.433	−8.045 ± 0.483
$d_l \pm$ SE	2.181 ± 0.105	1.840 ± 0.049	1.523 ± 0.127	2.742 ± 0.132
r^2	0.88	0.86	0.86	0.95
Branches				
n	90	215	48	30
$d_{min} - d_{max}$	6.5–67.0	3.8–98.2	9.0–58.0	19.2–77.1
$c_b \pm$ SE	−1.588 ± 0.232	−2.427 ± 0.168	−2.917 ± 0.428	−4.933 ± 0.600
$d_b \pm$ SE	1.778 ± 0.075	1.763 ± 0.054	1.891 ± 0.129	2.773 ± 0.172
r^2	0.87	0.83	0.82	0.90
Stem				
n	80	51	48	30
$d_{min} - d_{max}$	3.0–67.0	7.0–56.8	9.0–58.0	19.2–77.1
$c_s \pm$ SE	−2.856 ± 0.144	−3.839 ± 0.227	−3.581 ± 0.204	−1.179 ± 0.222
$d_s \pm$ SE	2.678 ± 0.044	2.861 ± 0.069	2.693 ± 0.062	2.173 ± 0.064
r^2	0.98	0.97	0.98	0.98

Table 3. Species-specific parameters for the estimation of a stem's portion of sapwood area (pbas) at ground level in dependence on tree diameter d and threshold diameter d_{lc} (pbas $= e^{(e \ln(1+d-d_{lc})+f(d-d_{lc}))}$) [n = number of analysed cross-sections, d_{lc} = threshold stem diameter, from which on dead heartwood occurs, e, f = regression coefficients]

Characteristic	European beech	Norway spruce	Scots pine	European oak
n	14	17	399	502
d_{lc} (cm)	2.22	3.54	7.31	4.77
$e \pm$ SE	−0.009 ± 0.001	−0.104 ± 0.032	−0.034 ± 0.007	−0.238 ± 0.014
$f \pm$ SE	–	−0.012 ± 0.005	−0.009 ± 0.001	−0.006 ± 0.001
r^2	0.78	0.96	0.74	0.79

All allometric coefficients and exponents are set in italics in this paper.

Determination of species specific sapwood area

Computertomograph SIEMENS Somatom AR.HP was applied for differentiation between the sample tree's sapwood and dead heartwood. For attributes of the analysed trees, see Table 3. At 6 different heights above ground level we cut out stem discs for cross-section analyses. From each disc we took three CT shots, which cover a layer of 1 mm and were carried out with an acceleration voltage of 130 kV. The different power of absorption of wet sapwood and dry core wood results in CT images on which living and dead tissue was distinguished and quantified by software Photoshop™,

version 7.0. Unlike conventional staining methods, which detect contents of starch and ph-value, CT indicates water content, which is closely correlated with physiological activity.

Results of CT-analyses were utilized to parameterize the model

$$pbas = \begin{cases} e^{(e \ln(1+d-d_{lc})+f(d-d_{lc}))}, & d \geq d_{lc} \\ 1, & d < d_{lc} \end{cases} \quad (2)$$

It formulates the dependency between the portion of sapwood area at ground level pbas, the tree diameter d and a species-specific threshold diameter d_{lc}. The latter represents the diameter, up to which stems completely consist of sapwood (pbas = 1.0). If a tree's diameter $d \geq d_{lc}$ pbas results the exponential model in Formula (2) which is flexible enough to describe, inter alia,
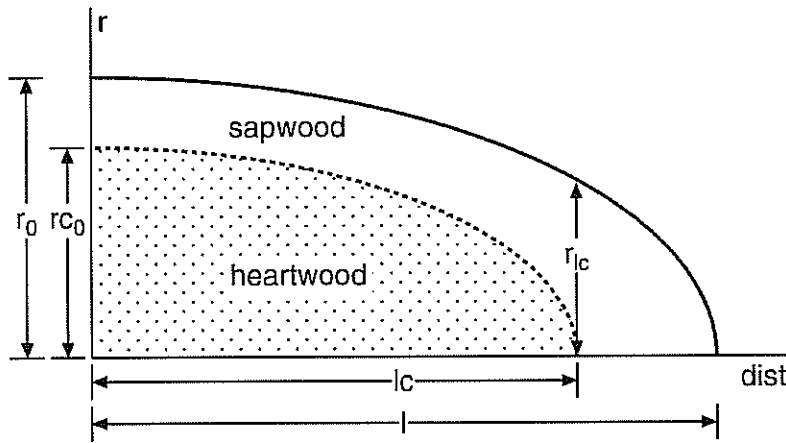
Fig.1. Stem form (continous black line) and border between sapwood and core wood (broken line) are approximated by a paraboloid (r_0 = stem radius at ground level, l = stem length, rc_0 = radius of dead heartwood at ground level, lc = length of core wood zone, r_{lc} = stem radius at position lc, where sapwood portion is 1.0)

degressive, linear, and exponential decrease of sapwood portion with growing tree diameter. In order to extract species specific threshold diameters d_{lc}, all available value pairs of stem diameter d and heartwood core diameter dc were used to fit a straight line dc = h + id. Intersection of this straight line with the x-axis yields d_{lc}, i.e., the diameter up to which pbas = 1.0. Parameters e and f in Formula (2) were fitted by nonlinear regression, using the same dataset and the previously determined d_{lc}. Summand 1.0 in the first term of the exponent provides $e \ln(1 + d - d_{lc}) = 0$ and $e^{e \ln(1 + d - d_{lc}) + f(d - d_{lc})} = 1$, respectively, if d = d_{lc}.

From sapwood area to sapwood weight. Model approach

Portion of sapwood volume (pvs) and weight (pws) of a stem are to be estimated in dependence on sapwood basal area $pbas_0$ at ground level. In order to keep the model simple, we assume an identical specific gravity of sapwood and heartwood, so that pvs = pws. I developed a simple stereometric model (Fig. 1), which assumes that the stem and its core of dead wood resemble a paraboloid (P r o d a n , 1965, pp. 50–59). In that case the stem basal area ba decreases proportionally with distance dist from ground level

$$ba_{dist} = r_{dist}^2 \pi = p (1 - dist),$$ (3)

with ba_{dist} = stem basal area at a given distance dist from ground level, r_{dist} = stem radius at a given distance dist from ground level, p = stem shape parameter, l = total stem length, and dist = distance from ground level. Insertion of dist = 0 and rearrangement of Formula (3) yields shape parameter p = $r_0^2 \pi/l$. Substitution of $r_0^2 \pi/l$ for p in Formula (3) results in

$$r_{dist}^2 \pi = (r_0^2 \pi/l) (l - dist) = r_0^2 \pi (1 - dist/l).$$ (4)

On the basis of latter function I calculate the solid of revolution around the x-axes from 0...l

$$v = \pi \int_0^l r_0^2 (1 - \frac{dist}{l}) ddist = \pi r_0^2 \int_0^l 1 - \frac{dist}{l} ddist =$$ (5)

$$= \pi r_0^2 \left[dist - \frac{dist^2}{2l} \right]_0^l = \frac{r_0^2 \pi l}{2}$$

and get the volume v of the whole paraboloid. Analogously, when core wood radius is rc_0 and core wood emerges at distance lc (Fig. 1), the volume of the stem's core wood amounts to

$$vc = \frac{rc_0^2 \pi lc}{2}.$$ (6)

Thus, sapwood volume is vs = v − vc, and portion of sapwood volume

$$pvs = \frac{v - vc}{v} = \frac{r_0^2 \pi l - rc_0^2 \pi lc}{2} \frac{2}{r_0^2 \pi l} = 1 - \frac{rc_0^2 lc}{r_0^2 l}.$$ (7)

In this equation, lc can be replaced by $l(1 - d_{lc}^2/d_0^2)$, as according to Formula (2),
$r_{lc}^2 \pi = (r_0^2 \pi/l)(1 - lc) = r_0^2 \pi (1 - lc/l)$. Solution of the latter equation with respect to lc yields

$$lc = l(1 - \frac{r_{lc}^2}{r_0^2}) = l(1 - \frac{d_{lc}^2}{d_0^2})$$ (8)

In addition, the quotient rc_0^2/r_0^2 in Equation (7) can be replaced by the portion of inert heardwood area pbac (pbac = 1 − pbas). Through these substitutions, Equation (7) becomes

$$pvs = 1 - \frac{rc_0^2 \pi l (1 - \frac{d_{lc}^2}{d_0^2})}{r_0^2 \pi l} = 1 - pbac (1 - \frac{d_{lc}^2}{d_0^2}) =$$ (9)

$$= 1 - pbac + pbac \frac{d_{lc}^2}{d_0^2} = pbas + pbac \frac{d_{lc}^2}{d_0^2}.$$

Equation (9) reflects that pvs is determined just by the portion of sapwood area at ground level pbas [cf. Equation (2)], and the species-specific squared quotient of threshold diameter d_{lc}/diameter at ground level d_0. Concerning d_{lc} three cases are distinguished

$$pvs = \begin{cases} pbas, & d_{lc} = 0 \\ pbas + pbac \ d_{lc}^2/d_0^2, & \text{if } 0 < d_{lc} < d_0 . \\ 1, & d_{lc} = d_0 \end{cases}$$ (10)

If d_{lc} = 0, pvs is equal to pbas, as pbac dc_0^2/d_0^2 = 0. In this case corewood appears simultaneously with stem growth. If 0 < d_{lc} < d_0, the portion of sapwood volume is by pbac dc_0^2/d_0^2 higher than the portion of sapwood area, due to the bold's top, consisting entirely of sapwood. If d_{lc} = d_0, a stem completely consists out of sapwood.

Regression algorithm

For all calculations I used SPSS (Version 11.5). After ln-ln-transformation most of the data sets fulfilled the assumptions of linear regression analysis such as normal distributions of residuals, homoscedasticity and independence of residuals. Exponents and scaling coefficients of ln $\overline{w}$ *vs* ln N and ln $\overline{w}'$ *vs* ln N were computed by both, Model I (ordinary least square regression, OLS) and Model II (reduced major axis regression, RMA). Zeide (1987) and Niklas (1994) argue that only RMA regression (Model 2) represents the "true relationship" between the variables, as RMA slopes of x on y are exactly the inverse of those of y on x. However, Sackville Hamilton et al. (1995) showed that slope estimates of both algorithm converge with increasing r^2. As the fitting of self-thinning lines yielded always $r^2 > 0.90$, the differences between OLS and RMA were negligible. I restrict my report on OLS-slopes, in order to keep comparable with the cited studies, which are mostly based on OLS regression.

RESULTS

For scrutiny of H1 to H4 scaling functions for biomass [Table 2, Equation (1)], functions for estimation of sapwood area pbas [Table 3, Equation (2)], and the stereometric model for a stem's sapwood and heartwood portion [Formula (10)] are applied. Estimates of all individual trees' biomass w and w' enables calculation of $\overline{w}$ and $\overline{w}'$. On the basis of value pairs $\overline{w}$, N and $\overline{w}'$, N OLS regression yielded slopes b and   for the subsequent analyses.

Estimation of biomass and distinction between living and dead stem wood

The range of diameter of the sample trees, substantiating the scaling functions (Table 2, $d_{min} - d_{max}$), reaches considerably beyond the diameter spectrum of the experimental plots (Table 1, mean diameter), so that the functions are appropriate for biomass estimation on the experimental plots. Depending on tree species and stand age, total shoot biomass (w = $w_l + w_b + w_s$) of individual trees range between 10.6 and 1,776.1 kg tree^{-1} (Table 1, total biomass). Estimates of all individual trees' above ground biomass w enables calculation of $\overline{w}$ and depiction of the ln $\overline{w}$-trajectories for the considered tree species (Fig. 2). The total above ground biomass W amounts to 110–445, 109–787, 46–200, and 154–346 tons ha^{-1} for European beech, Norway spruce, Scots pine, and European oak, respectively.

Fig. 3 and Table 2 display the species-specific relationships between tree diameter and portion of sapwood area pbas at ground level, which underlie the subsequent evaluation of portion of sapwood volume pvs and sapwood weight pws. Species differ in threshold diameter d_{tc} for heartwood formation (European beech < Norway

spruce < European oak < Scots pine) (cf. Table 2), as well as in the decrease of sapwood portion with increasing stem diameter (European beech < Scots pine < Norway spruce < European oak). European beech and European oak, respectively, outline the upper and lower limit of sapwood portion within the concerned size range of trees, whereas Scots pine and Norway spruce lie in between (Fig. 3).

Portion pbas is needed for estimation of pvs and pws via Equation (10) and for estimation of weight of sapwood (w_{sap} = w_s pvs). So, biomass of living tissue w' (w'= $w_l + w_b + w_{sap}$) can be calculated and compared with total biomass w (w = $w_l + w_b + w_s$) (cf. Table 1, total *vs* living biomass). The total above ground living biomass W' amounts to 109–433, 96–342, 45–153, and 93–171 tons ha^{-1} for European beech, Norway spruce, Scots pine, and European oak, respectively. So, in adult stands of the considered species, the dead heartwood biomass amounts to 3, 56, 23, and 51%, respectively, of the total biomass.

Scrutiny of hypotheses H1 to H4

H1: For each of the 20 plots I estimated slope b for the relation ln $\overline{w}$ *vs* ln N by OLS regression. The regression ln $\overline{w}$ *vs* ln N yielded r^2-values from 0.909 to 0.999. In average (min. to max.) slopes b were −1.403 (−1.439 to −1.305) for European beech, −1.614 (−1.650 to −1.567) for Norway spruce, −1.575 (−1.751 to −1.476) for Scots pine, and −1.592 (−1.778 to −1.352) for European oak. ANOVA was applied for detection of differences between the species' scaling exponents. Variance analysis included all 20 plots and was carried out for slopes b, estimated by OLS. Levene's statistic proved homogeneity of variances for the four species ($p < 0.05$). The hypothesis that the slope b of the relation ln $\overline{w}$ *vs* ln N is equal for all four considered species can be rejected (F = 4.638, df = 3, p = 0.016, n = 20). The mean slopes (± standard error) were b = −1.403 (± 0.0248), b = −1.614 (± 0.014), b = −1.575 (± 0.048) and b = −1.592 (± 0.091) for European beech, Norway spruce, Scots pine and European oak, respectively. Multiple comparisons of group means by Scheffé's procedure revealed significant differences between b-values of European beech and Norway spruce ($p < 0.05$).

H2: Scrutinity of b' of the relation $\overline{w}'$ for each of the 20 plots yielded r^2-values from 0.910 to 0.999. The adjusted slopes b' were considerably flatter than the corresponding original b-values. Slope b' is in average (min. to max.) −1.396 (−1.432 to −1.298) for European beech, −1.365 (−1.384 to −1.353) for Norway spruce, −1.447 (−1.603 to −1.371) for Scots pine, and −1.369 (−1.543 to −1.167) for European oak. ANOVA yielded no differences between the species' adjusted slopes (F = 0.947, df = 3, p = 0.441, n = 20). The mean slopes (± standard error) were b' = −1.396 (± 0.025), b' = −1.365 (± 0.005), b' = −1.447 (± 0.043) and b' = −1.369 (± 0.078) for European beech, Norway spruce, Scots pine and European
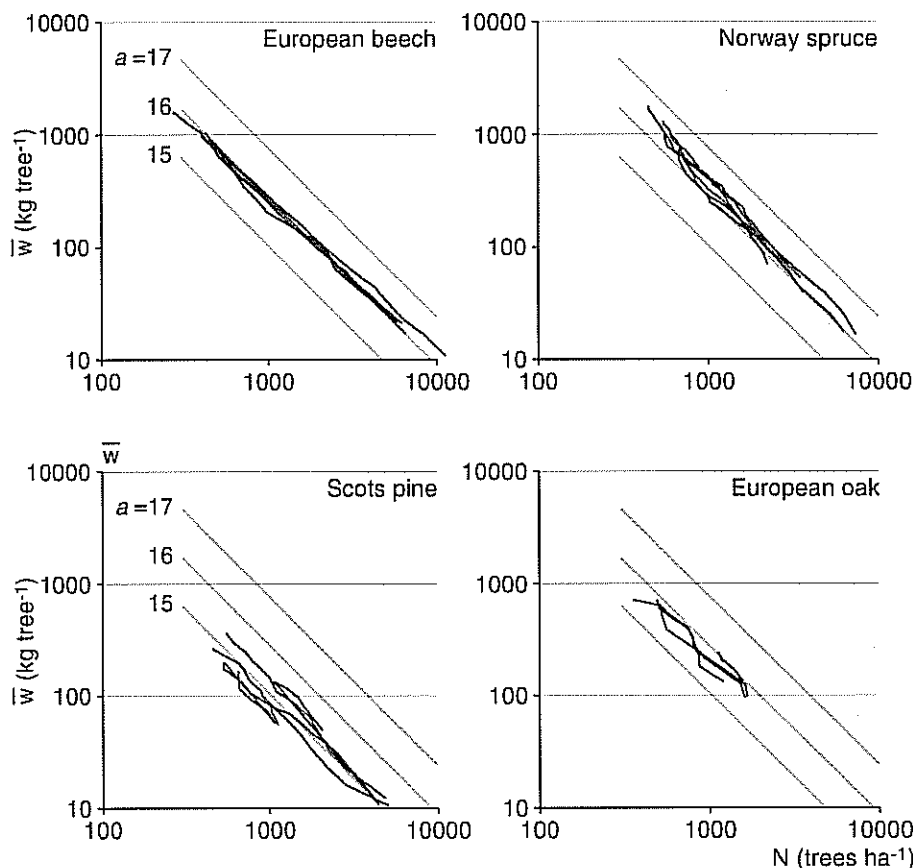
Fig. 2. Relation between logarithmic mean plant biomass ln w̄ and tree number per unit area ln N for untreated, fully stocked European beech, Norway spruce, Scots pine, and European oak pure stands. Self-thinning lines ln w̄ = a − 3/2 ln N, with Yoda's slope −3/2 and a = 15, 16, 17 are given as reference
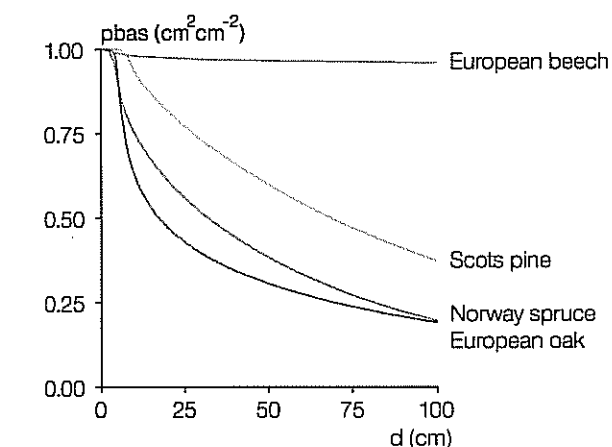

Fig. 3. Relationship between stem diameter d and portion of sapwood area at ground level pbas for the four considered species [cf. Formula (2) and Table 3]

oak, respectively. Scheffé's procedure revealed no significant differences between the species.

H3: ANOVA was used for testing, whether heartwood elimination influences slope b. The hypothesis that original slopes b and adjusted slopes b' are equal can be rejected (F = 19.708, df = 1, p = 0.0001, n = 40). Mean slope b (± standard error) after pooling the four species is $b = -1.547$ (± 0.028). Slope b' is about 10% flatter and amounts to $b' = -1.394$ (± 0.020).

H4: Comparison between observed slopes and the geometrical scaling exponent $b = -3/2$ postulated by Y o d a et al. (1963) and fractal scaling slopes $b = -4/3$ expected by W e s t et al. (1997, 1999) and E n q u i s t et

al. (1999, 2001) is based on both the individual plots' regression coefficients and the mean slopes b and b'.

For each of the 20 plots b ± 95% CI as well as b' ± 95% CI were applied to scrutinize whether the generalized coefficients $b = -3/2$ or $b = -4/3$ lie in the CI. Slopes b correspond in 50% of the cases (on 10 out of 20 plots) with geometrical scaling and in 30% (on 6 out of 20 plots) with fractal scaling rules. Elimination of dead heartwood shifts allometry remarkably towards fractal scaling; b' corresponds in 40% of the cases (on 8 out of 20 plots) with geometrical scaling and in 80% (on 16 out of 20 plots) with fractal scaling.These findings are supported by comparison of mean slopes (± 95% CI) with $b = -3/2$ or $b = -4/3$ (Table 4). Slope b amounts to −1.403 (−1.472 to −1.334) for European beech and −1.614 (−1.650 to −1.578) for Norway spruce, i.e., it corresponds neither with $b = -3/2$ nor with $b = -4/3$. By contrast, Scots pine's slope $b = -1.575$ (−1.709 to −1.440) follows geometrical scaling, and oak's slope b amounts to −1.592 (−1.882 to −1.303) and includes −1.50 as well as −1.33. Slope b' comes to −1.396 (−1.465 to −1.327) for European beech, −1.365 (−1.376 to −1.352), for Norway spruce, −1.447 (−1.566 to −1.330) for Scots pine, and −1.369 (−1.619 to −1.120) for European oak, and advocates rather for fractal scaling than for Yoda's rule.

Display of conventional and adjusted self-thinning lines

In order to depict the mean species-specific self-thinning lines before and after adjustment (Fig. 4, left and

Table 4. Parameters a and b ($\pm$ CI) for the model ln $\overline{w}= a + b$ ln N [$\overline{w}$ = mean above ground biomass per tree, N = number of trees per unit area] and a' and b' ($\pm$ CI) yielded after elimination of dead heartwood by model $\overline{w}' = a' + b'$ ln N [$\overline{w}'$ = living biomass per tree]

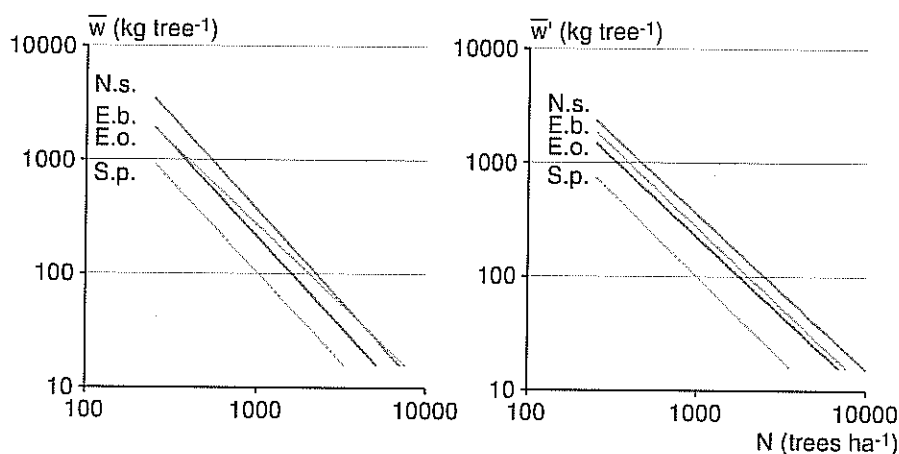| Characteristic	European beech	Norway spruce	Scots pine	European oak
n	5	6	5	4
a mean	15.30	17.06	15.52	16.36
a 95% CI	15.27 to 15.32	17.03 to 17.10	15.43 to 15.61	16.29 to 16.43
b mean	−1.403	−1.614	−1.575	−1.592
b 95% CI	−1.472 to −1.334	−1.650 to −1.578	−1.709 to −1.440	−1.882 to −1.303
a' mean	15.24	15.30	14.60	14.86
a' 95% CI	15.22 to 15.27	15.25 to 15.35	14.52 to 14.69	14.81 to 14.92
b' mean	−1.396	−1.365	−1.447	−1.369
b' 95% CI	−1.465 to −1.327	−1.377 to −1.353	−1.566 to −1.328	−1.619 to −1.119

Fig. 4. Conventional self-thinning lines ln $\overline{w}= a + b$ ln N (left) and adjusted self-thinning lines $\overline{w}' = a' + b'$ ln N (right) for European beech, Norway spruce, Scots pine, and European oak ($\overline{w}$ = mean above ground biomass per tree, $\overline{w}'$ = mean above ground living biomass per tree, N = tree number per unit area)

right, resp.) slopes b and b'^2, reported in Table 4, were used to create the models ln $\overline{w}= a + b$ ln N and ln $\overline{w}' = a' + b'$ ln N, respectively. These models, with prescribed slopes, were fitted with the respective stem number-body mass data to obtain mean species-specific self-thinning lines. The resulting parameters in Table 4 as well as the self-thinning lines (Figure 4) reflect the detected ranking of the b-slopes' steepness (Norway spruce > European oak > Scots pine > European beech) (Fig. 4, left) and the approximation of the individual species' slopes after elimination of dead heartwood (Fig. 4, right). Parameter a' of ln $\overline{w}' = a' + b'$ ln N is determined by growth form and environment. In order to analyse species-specific a'-values I calculated average slope b' over all species, subsequently called g. This step is justified, as H3 revealed no differences between the four species' slopes b'. Conditioned regression ln $\overline{w}' = a_g + g$ ln N yielded species specific intercepts a_g (Table 5).

DISCUSSION AND CONCLUSION

Unlike herbaceous plants, many tree species develop dead heartwood in the course of ontogenesis. Although physiological inactive, this dead tissue is rarely excluded when growth laws or physiological relationships are formulated. As tree diameter, basal area, and volume are easier to measure than sapwood volume or living tissue

biomass, they are often used as surrogate for physiological meaningful variables. However, relationships based on surrogate variables are always biased to some extend. This paper reveals that inert heartwood portion of trees is probably one decisive reason why allometry of trees often diverges considerably from generalized scaling rules (G a d o w, 1986; P r e t z s c h, 2005; Z e i d e, 1987), while herbaceous plants tend to follow them (H a r p e r, 1977; Y o d a et al., 1963; W e s t et al., 1997, 1999).

The size-density-allometry of plants under self-thinning, addressed in this paper, is particularly informative as it links eco-physiology of individual trees with stand dynamic and stand management. Under self-thinning conditions, size-density allometry reveals the critical demand on resources and growing space of average trees of given size. The assumption behind general size-density-allometry is that relative growth of living biomass is tightly coupled with the relative growth of growing space, and that this coupling is generalizable. No matter which particular allometric exponent b holds true, if stands follow a general scaling rule ln $\overline{w}= a + b$ ln N, it means that they differ in growth form or environment (coefficient a), but that in a given timestep dt a relative increase in biomass $d\overline{w}/\overline{w}$ is always coupled with a certain decrease of stem number per unit area dN/N ($b = d\overline{w}/\overline{w}/dN/N$).

H a r p e r (1977, p. 183) attested the −3/2 power rule a validity for annual plants and forests as well. W h i t e

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Table 5. Intercept a_g with SE and 95% CI for $\ln \overline{w}' = a_g + g \ln N$ with $g = -1.394$ for all species

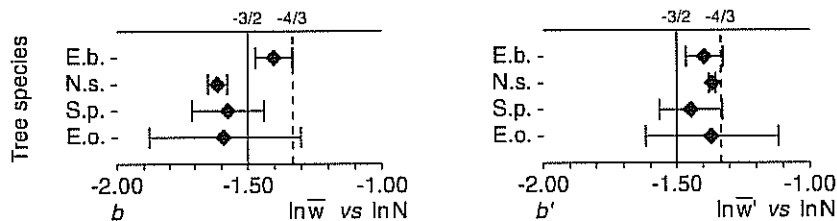| Characteristic	European beech	Norway spruce	Scots pine	European oak
n	70	84	52	32
a_g mean (± SE)	15.21 (± 0.012)	15.02 (± 0.014)	14.11 (± 0.039)	14.43 (± 0.029)
a_g 95% CI	15.19 to 15.24	14.99 to 15.05	14.03 to 14.19	14.38 to 14.50
a_g in relation to E. beech	100	83	33	46
g	−1.394	−1.394	−1.394	−1.394

Fig. 5. Observed scaling exponents (mean, 95% CI) compared to exponents, predicted by Euclidian geometrical scaling (solide, vertical line) and fractal scaling (broken, vertical line). Displayed are slope b (left) and b' after elimination of dead heartwood (right)

(1981, p. 479) even saw the "empirical generality of the rule ... beyond question". And L o n g and S m i t h (1984, p. 195) titled it "a true law instead of the mere rule". Yoda' exponent ($b = 3/2$), e.g., assumes that an increase of 3% of biomass causes a stem number reduction of 2%, regardless of species and site conditions. Of course, general scaling rules engender the risk of neglecting individual species peculiarities. The theoretical analyses of Yoda's rule brought Z e i d e (1987, p. 532) to the result, "Unlike the fixed value of −3/2, the actual slopes convey valuable information about species ... that should not be cast away". W e l l e r (1987, p. 37) outgrows the spell of the rule and turns it into a research perspective "The differences among slopes may provide a valuable measure of the ecological differences among species and plants, and a powerful stimulus for further research". Fractal scaling slope −4/3, recently postulated by W e s t et al. (1997, 1999), E n q u i s t et al. (1999, 2001) and N i k l a s (1994), is considerably flatter than Yoda's −3/2, based on Euclidian geometry.

Scrutiny of H1 confirms G a d o w (1986), P r e t z s c h (2005), W e l l e r (1987, 1990) and Z e i d e (1987) in their view, that scaling exponents b are species-specific and form a key for understanding the species' ability to cope with crowding. However, average biomass $\overline{w}$ which was used for scrutiny of H1 includes more or less dead heartwood. Therefore $\overline{w}$-N-value pairs of woody plants with dead inner xylem are strictly speaking not at all appropriate for revelation of species-specific scaling rules. The simple and provisional model for core wood enables exclusion of physiological inactive wood from $\overline{w}$. It yields living biomass $\overline{w}'$ and results in slopes b' which are remarkable similar for the four considered species (H2) and significantly different from b (H 3). The flattening of the slopes, due to elimination of inert heartwood amounts to 1% for European beech, 15% for Norway spruce, 8% for Scots pine, and 14% in the case of European oak. Of course, the applied stereometric model is a crude approximation. For instance, in the case of European beech and Norway spruce it is based merely on a small sample of stem analysis,

dead heartwood within branches was not considered, and, moreover, specific gravity was assumed to be species-specific but homogeneous within the stem. Still, as they eliminate at least parts of the crucial deadwood-dependent bias, the adjusted slopes b' are better for drawing eco-physiological meaningful comparisons between different woody plant species. Furthermore the adjustment is a prerequisite for a linkage between self-thinning rules for woody and herbaceous plants.

In view of my results geometrical scaling slope −3/2 and fractal scaling slope −4/3 appear in a new light (Fig. 5). The slopes b of $\ln \overline{w}$ vs $\ln N$ roam around $b = -3/2$ (Fig. 5, left), whereas the physiological more meaningful slope b' of $\ln \overline{w}'$ vs $\ln N$ might correspond with fractal scaling slope −4/3 expected by W e s t et al. (1997, 1999), E n q u i s t et al. (1999, 2001) and N i k l a s (1994) (Fig. 5, right). On closer examination, parameters a_g reveal, that European beech and spruce are more tightly packed together compared to Scots pine and European oak, with the ranking of packing density European beech > Norway spruce > European oak > Scots pine (100 : 83 : 46 : 33). So, species' packing density (reflected by allometric coefficient a') is different, but not size-density allometry (reflected by allometric exponent b').

My results imply that a generalization of self-thinning slopes appear unsuitable as far as the allometric relations are based on surrogate variables and ignore the effect of inert heartwood. Questionable is, e. g., Reineke's stand density index (R e i n e k e, 1933), founded on a species invariante slope and frequently used to quantify and control stand density (S t e r b a, 1981, 1987; K r a m e r, H e l m s, 1985). In the same way, stand density management diagrams (SDMD; O l i v e r, L a r s o n, 1996), which use the self-thinning line with generalized scaling exponents as upper boundary, are problematical as they hold the risk of flawed density control and contraoptimal thinning. Equivalent shortcomings apply for thinning and mortality algorithms in growth models, when they work with surrogate variables but assume general scaling rules. The presented models for estimation of biomass, sapwood area, and sapwood volume can help to adjust

other frequently applied relationships so far based on surrogate variables in order to bridge the gap between findings for woody and herbaceous plants.

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Vztah mezi pravidly přirozeného prořed'ování bylin a dřevin.

V článku je zkoumán vztah mezi průměrnou hmotností rostlinných těl $\overline{w}$ a počtem rostlin N na jednotku plochy pro buk lesní (*Fagus sylvatica*), smrk ztepilý (*Picea abies*), borovici lesní (*Pinus sylvestris*) a dub letní (*Quercus petraea*) v Německu, rostoucích za podmínek přirozeného prořed'ování (diferenciace) na pokusných plochách, sledovaných přes 130 let (tab. 1, obr. 2). Relační exponent *b* ze vztahu w∞N^b odráží pravidlo alokace zdrojů stromů, které se vyrovnávají s těsností růstového prostoru. Celá řada publikací, např. R e i n e k e (1933), Y o d a et al. (1963), W e l l e r (1987), N i k l a s (1994), W e s t et al. (1997), E n q u i s t et al. (1998) a P r e t z s c h (2002), popisuje hledání na druhu nezávislé relace mezi hmotností živého rostlinného těla $\overline{w}$ a požadavkem na růstový prostor s (s = N^{-1}).

Při vyhledávání jednotných křivek, vyjadřujících přirozené prořed'ování pro byliny a dřeviny, se často přehlíželo neživé (inertní) dřevo, tedy mrtvé jádro stromů (obr. 1). Mrtvé dřevo může dosáhnout značného podílu z celkové biomasy stromu a ovlivnit tak křivku přirozeného prořed'ování, je-li zahrnuto do $\overline{w}$. Aby se oddělila neživá tkáň od živé, vyvíjejí se proporční funkce pro biomasu listů, větví a kmenů [vzorec (1), tab. 2], funkce pro odhad oblasti živého dřeva (běle) [vzorec (2), tab. 3] a stereometrický model pro rozlišení kmenové hmotnosti živého dřeva běle a dřeva mrtvého jádra [vzorec (10)]. Křivky vyjadřující přirozené prořed'ování byly stanoveny jak pro celkovou biomasu $\overline{w}$, tak živou biomasu $\overline{w}'$.

OLS regresí byly pro křivky odpovídající jednotlivým dřevinám získány pro vztah $\overline{w}$∞N^b, exponenty *b*: –1,403 pro buk lesní, –1,614 pro smrk ztepilý, –1,575 pro borovici lesní, –1,592 pro dub letní, tedy smrk ztepilý < dub letní < borovice lesní < buk lesní (tab. 4; obr. 4 vlevo). Tyto významné rozdíly mezi druhy však mizí, pokud se stejné hodnocení provede pouze pro živou biomasu $\overline{w}'$∞N$^{b'}$. Odpovídající hodnoty jsou *b'* = –1,396, –1,365, –1,447 a –1,369 (tab. 4; obr. 4 vpravo). ANOVA odhaluje významné rozdíly mezi exponentem *b* a exponentem *b'* pro upravené křivky přirozeného prořed'ování (obr. 5). Srovnání s geometrickým relačním exponentem –3/2, jak ho navrhl Yoda, a fraktální a relačním exponentem –4/3, který předpokládají West a Enquist, ukazují, že exponenty křivek *b* se značně odlišují od zobecněných exponentů (obr. 5 vlevo). Hodnoty *b'* však ukazují, že eliminace neživého jádra stromů výrazně posunuje alometrii k fraktální relaci (obr. 5 vpravo). Podle hrubého odhadu tedy eliminace neživého jádra usnadňuje využití křivek přirozeného prořed'ování pro odhad hustoty, řízení hustoty a prognózy a umožňuje objektivní srovnání relačních pravidel mezi dřevinami a bylinami.

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