Re-Evaluation of Allometry: State-of-the-Art and Perspective Regarding Individuals and Stands of Woody Plants

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Abstract Allometry, in its broader sense, is concerned with the size of organisms and its consequences for their shape and functioning. Since the postulation of the allometric equation in the 1930s, allometry, in a narrow sense, refers to analysis

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and modelling of logarithmic transformed bivariate size data by linear regression techniques.

This chapter first points out that allometric research built up a valuable set of hypotheses and biometrical methods for analysing size of organisms and its consequences for their shape and functioning. Then, a summary of the knowledge about allometry of woody plants and populations will unmask the search for overarching general allometric exponents of shape and form development largely as a hunt for a phantom. Tree size development and self-thinning processes in forest stands give evidence that allometric exponents certainly lie in a narrow corridor, but are species specific and superimposed by site conditions, mechanical disturbances, competition, and other types of stress. The discussion states that as long as allometry searches for universal constants to a certain extent, it stills our innate desire to reduce complexity and generalise. However, time is ready to focus on and understand the differences between the species, sites etc. in order to contribute to a better system of understanding. It is concluded that allometry has to draw attention both to the internal size-driven allometric partitioning process and to the external factors, which determine optimal biomass allocation. And at best, allometric research should analyse both factors in order to understand and integrate them. A systematic analysis, ordering and causal explanation of allometric exponents, which reflects an individuals' tricks and traits of optimising fitness, may provide an important link between plant genetics, physiology, plant biology and population biology. In contrast, application of inaccurate and imprecise general scaling rules can cause considerable flaws in modelling, prognosis and ecosystem management.

1 Introduction

1.1 Concept of Allometry and Biometrical Formulation

Allometry is a field of science concerned with the size of organs, organisms and populations and its consequences for their shape and functioning. As size and size relations in and between organisms reflect the result of the phylo- and ontogenetic evolution towards a functional optimisation (Niklas 1994, p. 1), the study of allometry seeks to understand the adaptations of living organisms to their environment.

1.2 Allometry in Its Broader Sense

A plant is a means and result of photoproduction at the same time. Its current size (e.g. the proportions between root and shoot) determines its access to resources and supply of building material. The latter is allocated and used for growth in

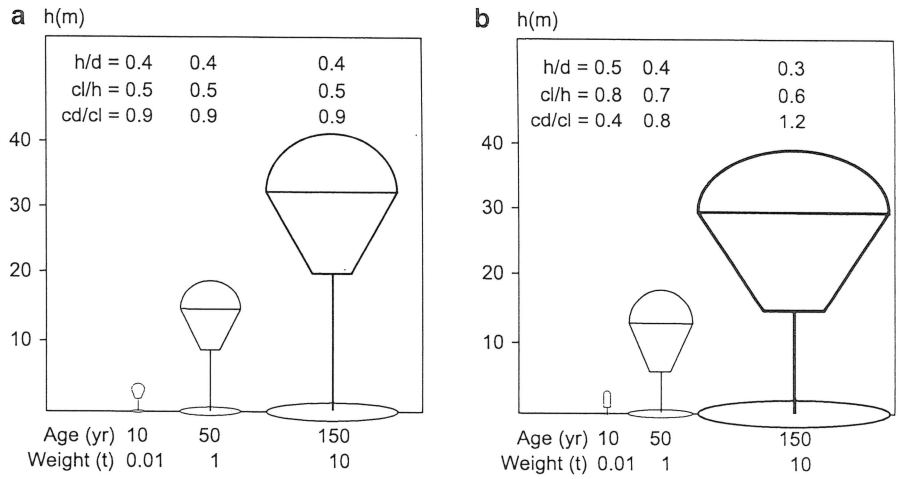

Fig. 1 European beech crown diameter-crown length development (**a**) with isometry, (**b**) with positive allometry, from age 10–150 in schematic representation (**a**) The tree represents geometrical similitude if all linear dimensions change proportionally to each other (e.g. diameter (cd) and length of the crown (cl) $cd \propto cl^{\alpha}$, $\alpha = 1$) and in general between all linear (lin), quadratic (quad) and cubic dimensions (cub) (e.g. tree height $\equiv lin$, crown projection area $\equiv quad$, tree biomass $\equiv cubic$) applies $lin \propto cub^{1/3}$, $lin \propto quad^{1/2}$, and $quad \propto cub^{2/3}$. (**b**) Mostly the relationships between tree dimensions change not proportionally but allometric with e.g. $cl \propto cd^{\alpha_{cl,cd}}$, $\alpha_{cl,cd} \neq 1$. In case of this European beech tree crown diameter (cd) and crown length (cl) are related like $cd \propto cl^{\alpha_{cl,cd}}$, $\alpha_{cd,cl} = 1.2$)

such a way that the altered plant size again fulfils the plant's functions (growth, reproduction) in an optimal way. Proportional size change (isometry) is mostly not adequate for optimal functioning. Rather, due to their specific efficiencies, organ size has to be changed unproportionally (allometry) for ensuring optimal function and supply of the plant with building material. That is the reason why with increasing size a tree's shape changes seldom proportionally, like the European beech shown on Fig. 1a. On the contrary, slender juvenile European beech trees have a rather small cd/cl-ratio between crown diameter cd and crown length cl, but with tree size width and cd/cl ratio of the crown increases as the crown diameter expands over-proportional in relation to tree height and crown length (Fig. 1b). Different phylogenetic pathways of functional optimisation lead to characteristic allometric developments of species. For example, an open grown European beech can be easily distinguished against an open grown Common oak by its shape – even from far distance. The science of allometry and the allometric biomass partitioning theory (APT) investigate the plants' internal feedback between size, shape and functioning (broken line in Fig. 2) and strive for general species-overarching rules for allometric partitioning and biomass allocation.

However, a plant's genetically determined shape (genotype) is not fixed as strictly as in animals but allows a comparably large ontogenetical plasticity (phenotype). For example, a European beech tree that grows in a forest environment

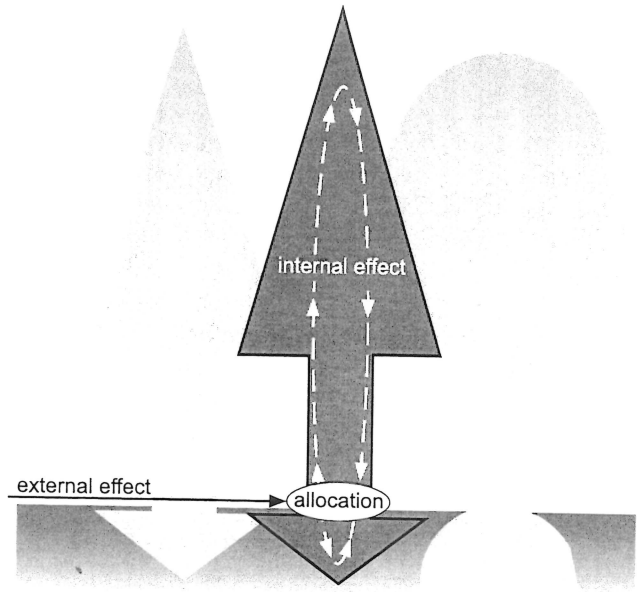

Fig. 2 Allometric research has to draw attention to both, to the internal size-driven allometric partitioning process (*broken arrow*) and to the external factors which determine optimal biomass allocation (*continuous arrow*). Competition for contested resources and externally driven disturbances like organ losses superimpose the internal size dependent allometric growth

differs substantially from the unhindered open-grown tree. Growing in a stand, a tree maximises its fitness by appropriating contested resources and adapting to the environmental conditions created by the neighbouring trees. In contrast to open-grown conditions, the tree's unhindered species-specific ontogenetic form development is superimposed by competition. According to the optimal biomass partitioning theory (OPT), light-limited trees in the understory, for example, boost their crown growth in order to improve the supply with the limiting light factor (van Hees and Clerkx 2003; Hofman and Ammer 2008). By contrast, in case of water or nutrient limitation, trees (regardless whether growing solitary or in a forest) enhance their root growth to overcome their limited access to these belowground resources (Comeau and Kimmins 1989; Kimmins 1997). In other words, external factors like a plant's competitive status within the stand, the site conditions, and the occurrence of disturbances (e.g. mechanical abrasion, crown breakage) affect the plant's supply with carbon, light, water and mineral nutrient. So, for a suppressed European beech in a dense mixed stand, species-specific allometry or generalised "spinach–redwood-allometric" relationship might apply in theory, however, competition and selective pressure modify allocation and shape to such an extent, that this tree hardly resembles an open grown or dominant beech. External factors (solid arrow in Fig. 2) continuously distract and superimpose the unhindered, primarily size driven plant allometry. So, allometry has to focus on both, the

internal size-driven allometric partitioning process and the external factors, which determine optimal biomass allocation; and at best, allometric research should analyse both factors in order to understand and integrate them.

In contrast to this wide approach to allometry as the study of relative size growth, which dates back to Thompson (1917) and is an issue again at present (e.g. McCarthy and Enquist 2007), allometry in a closer sense refers to the analysis and modelling of bivariate size relations of organisms, populations or communities by double-logarithmic relationships, which are introduced in the sequel.

1.3 *Biometrical Analysis and Modelling of Plant Allometry*

In the early 1930s, Huxley (1932) and Teissier (1934) formulated a "relative growth equation" that is today widely accepted as the allometric equation. Supposing x and y quantify the size of plant organs or a total plant, the growth x' (dx/dt) and y' (dy/dt) is related to the size x and y as

$$y'/y = \alpha x'/x. \tag{1}$$

Better known are the integrated and logarithmic representations given below.

$$y = ax^{\alpha}, \tag{1a}$$

$$\ln\ y = \ln a + \alpha \ln x. \tag{1b}$$

Allometry is the relative change of one plant dimension, dy/y (e.g. the relative height growth) in relation to the relative change of a second plant dimension dx/x (e.g. the relative diameter growth). Suppose the relationship between the two plant dimensions follows $y = a\,x^{\alpha}$, then $dy/dx = \alpha(1/x)ax^{\alpha}$ or $dy = \alpha(1/x)ax^{\alpha}dx$, so that

$$dy/y/dx/x = \frac{\alpha(1/x)ax^{\alpha}dx}{ax^{\alpha}} \Big/ dx/x = \alpha. \tag{2}$$

This shows, that the rate between the relative changes of the plant dimensions y and x is constant and equal to α, which is the allometric exponent in (1a). The allometric exponent α can be understood as a distribution coefficient for the growth resources between organs y and x: when x increases by 1%, y increases by α%. An individual tree height–diameter-allometry of $\alpha_{h,d} = 0.6$ means that height increases by 0.6% when tree diameter increase by 1%. Applied on stand level, a stem number–mean tree diameter-allometry of $\beta_{N,dq} = -1.6$ means, that the stem number per ha decreases by −1.6% when mean tree diameter d_q increases by 1%. The exponents α and β, respectively, describe the slope when we plot $\ln(h)$ versus $\ln(d)$, respectively $\ln(N)$ versus $\ln(d_q)$.

The value pairs y_i, y_{i+1} and x_i, x_{i+1} from consecutive surveys of the plots can be used to calculate the period-wise slope $\alpha'_{y,x}$. It represents the distribution key of matter allocation between y and x in a given period.

$$\alpha'_{y,x} = \frac{\ln(y_{i+1}) - \ln(y_i)}{\ln(x_{i+1}) - \ln(x_i)} = \frac{\ln(y_{i+1}/y_i)}{\ln(x_{i+1}/x_i)}. \quad (3)$$

For infinitely small time steps, (3) corresponds to the quotient $dy/y/dx/x = \alpha$ (cf. (2)). In this chapter, allometric factors (a, b, ...) are distinguished from allometric exponents (α, β, ...) by Latin respective Greek letters (cf. e.g. (1b)). By writing α or β prime (e.g. α'), it is emphasised that the allometric exponent is based on short-term consecutive surveys (3); the subscripts of the allometric exponent (e.g. $\alpha_{y,x}$) show which size variables are addressed.

Narrowly defined, allometry refers to a set of methods for analysing bivariate datasets by applying the allometric equations (1)–(3) starting with logarithmic transformation of the size variables, application of regression analysis (e.g. OLS, RMA, PCA regression) to the ln–ln-transformed data, estimation of allometric factors and exponents, and finally the application of the obtained regression line to eliminate size-effects, to reveal species-specific or site-specific allometric exponents, and finally to interpret deviations from the fitted regression line as variability or plasticity.

1.4 Geometrical and Fractal Scaling

Because of the physiological significance of allometric exponents α (1a), they have been strongly discussed ever since. Since its beginning, allometric research was mainly driven by the search for an overarching, universal, allometric exponent. Often, it was proposed that volume or mass related allometric functions scale with exponents of 1/3 due to the volume dimensionality (von Bertalanffy 1951; Yoda et al. 1963, 1965; Gorham 1979). More recently, West et al. (1997, 1999), Enquist et al. (1998, 1999) and Enquist and Niklas (2001) presented a model for a general explanation of allometric scaling with exponents of 1/4, based on fractal networks of transportation systems in organisms (West-Brown-Enquist-model, short WBE-model).

Mostly, allometric analyses assume geometrical similitude as a starting point and null hypothesis. Geometrical scaling or similitude means that between different linear dimensions lin_1, lin_2 ... lin_n (e.g. tree height, diameter, crown length, height to crown base) applies proportionality $\text{lin}_1 \propto \text{lin}_2 \cdots \propto \text{lin}_n$ (Fig. 1a). It further assumes that between quadratic tree attributes (e.g. basal area, leaf area, crown surface area, growing area) and linear dimensions applies $\text{quad} \propto \text{lin}^2$, and further between cubic variables like volume v or weight w (e.g. stem volume, crown volume, tree biomass) and linear dimensions applies $\text{cub} \propto \text{lin}^3$. That means $\text{lin} \propto \text{cub}^{1/3}$ and

$$\text{quad} \propto \text{cub}^{2/3} \quad (4)$$

This corresponds to the 1/3 exponent scaling as three is in the denominator of the allometric exponent. Application of (4) to the relationship between mean tree volume $\bar{v}$ ($\equiv$ cubic) and mean growing area $\bar{s}$ ($\equiv$ quad) yields $\bar{s} \propto \bar{v}^{2/3}$. As $N \propto \bar{s}^{-1}$, we get the $-3/2$-power rule of self-thinning $\bar{v}^{-2/3} \propto N$ or $\bar{v} \propto N^{-3/2}$, which obviously assumes geometrical scaling and isometric form development (Yoda et al. 1963, 1965; Gorham 1979). Note that the $-3/2$ power rule belongs to the 1/3 exponent scaling, as volume scales to N with the power of $-2/3$. It has only become famous in the reverse formulation, where N scales to volume with the power of $-3/2$.

Fractal scaling in contrast assumes $\text{cub} \propto \text{lin}^\alpha$ with $\alpha \neq 3$ and a deviation from 1/3 exponent scaling. For the relationship between weight (w) and tree stem diameter (d), Enquist et al. (1998, 1999) postulate $w \propto d^{8/3}$ with $ba \propto d^2$, the basal area–weight relationship results in

$$ba \propto w^{3/4}. \quad (5)$$

Obviously, fractal scaling leads to a quarter power (1/4-exponent) scaling rather than 1/3 exponent geometrical scaling. Applied on mean tree level, Enquist et al. (1998) derive $\bar{v} \propto N^{-4/3}$, which means a more shallow self-thinning line compared to $\bar{v} \propto N^{-3/2}$ from geometrical scaling. Enquist et al. (1998) stress that their model $\bar{v} \propto N^{-4/3}$does not predict self-thinning trajectories, but they do not explain why. This restraint makes their model's predictions somehow immune against falsification (Pretzsch 2006).

Note that when a statistical analysis of empirical data yields, e.g. $\bar{w}^{-2/3} \propto N <=> \bar{w} \propto N^{-3/2}$that implies not necessarily geometric scaling, e.g. a combination of fractal scaling $\bar{w} \propto \bar{d}^{8/3}$ and $\bar{s} \propto \bar{d}^{16/9}$would also yield $\bar{w} \propto \bar{s}^{3/2}$ or $\bar{w} \propto N^{-3/2}$ (as $N \propto \bar{s}^{-1}$). Specific deviations from geometrical scaling can obviously cancel each other so that an integrated view just looks like geometrical scaling, but is fractal in fact.

2 Formation of Shape and Form: Allometry on Plant Level

2.1 Above and Below Ground Allometry

The relationship between stem diameter and crown width is a good example of allometry relevant to the silvicultural management of pure and mixed stands of Norway spruce and European beech. Figure 3 displays the different space sequestration strategies of both species (crown width$\propto$stem diameter$^\alpha$) analysed for the unthinned mixed species stands, Freising 813/1-6 in South Bavaria (Pretzsch and Schütze 2008). Crown width, and hence, also the growing space requirement, increases with increasing stem diameter. Norway spruce exhibits an allometric exponent of $\alpha = 0.49$, European beech a significantly higher allometry of $\alpha = 0.60$. Consequently, for the same increase in diameter, European beech's demand

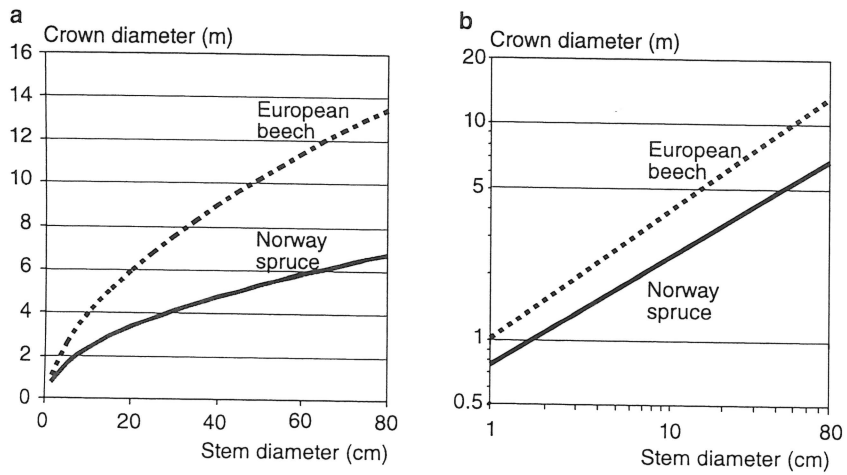

Fig. 3 Allometric relation between tree diameter (d) and crown diameter (cd) of Norway spruce (*continuous line*) and European beech (*broken line*) at long-term experimental plots Freising 813/1-6 in (**a**) Cartesian coordinate and (**b**) double-logarithmic system. The $\alpha_{cd,d}$-allometry shows the stronger crown expansion and steeper slope α of European beech ($\alpha_{cd,d} = 0.60$) compared with Norway spruce ($\alpha_{cd,d} = 0.49$)

for growing space is higher than that of Norway spruce. This species-specific allometry and growing space requirement long time is worked into the yield tables. For instance, the Norway spruce tables from Assmann and Franz (1965, cf. dominant height 40 m at age 100) and Schober's (1972) European beech tables (cf. yield class 1.0, moderate thinning) show that, at a mean tree diameter of 10 cm, there are expected some 3,500 trees ha^{-1} in a Norway spruce and 2,500 in an European beech stand (ratio 1.4:1). However, at a mean tree diameter of 50 cm, Norway spruce still has about 350 trees ha^{-1}, whereas there are less than 175 trees ha^{-1} (ratio 2:1) in the European beech stands due to its expanding crown allometry. This example has been selected to show the typically more lateral crown spread of broadleaves in comparison with the more vertical and pyramidal growth of the conifers (Niklas 1994, pp. 173–174). The species-specific differences in space requirement on individual tree level will reappear on stand level in species-specific slopes of the self-thinning lines (cf. Sect. 3).

The root–shoot development is maybe the best-analysed allometric relationship on plant level (e.g. Comeau and Kimmins 1989; Kimmins 1997; Shipley and Meziane 2002; Weiner 2004). It contributes to scrutiny of the optimal partitioning theory (OPT), which states that a plant invests always into improving the access to the limiting factor; e.g. if this is light or water, the plant invests in shoot or root growth respectively (Bloom et al. 1985). Recently, the necessity of estimating the below-ground carbon content enhanced the interest in root–shoot allometry (Levy et al. 2004), as shoot size might be used as predictor variable for root size and biomass. The root–shoot allometric exponents ($\alpha_{r,s}$ in $w_r \propto w_s^{\alpha_{r,s}}$) and root–shoot ratios $q_{r,s} = w_r/w_s$ of herbaceous and woody plants vary in a broad range between $\alpha_{r,s} = 0.2 - 1.3$ and

$q_{r,s} = 0.1 - 1.0$, respectively (Hofman and Ammer 2008; Levy et al. 2004; Müller et al. 2000; Pretzsch 2009; van Hees and Clerkx 2003). And most of the studies revealed a non-isometric root–shoot development ($\alpha_{r,s} \neq 1$), which may lead to confusion of simple size effects with plasticity (cf. Sect. 2.2). Allometric studies of herbaceous plants (Müller et al. 2000) and woody plants (Kozovits et al. 2005) attribute differences in the root–shoot ratio simply on an ontogenetic allometric size effect. According to these studies, α in $w_r \propto w_s^{\alpha_{r,s}}$ amounts to $\alpha < 1$ and values between 0.3 and 1.0; in other words, root biomass grows slower than shoot and the root–shoot ratio decreases just size dependent, i.e. allometrically (APT). Other authors (Hofman and Ammer 2008; Meier and Leuschner 2008) corroborate the OPT and find plasticity beyond allometric development. Bloom et al. (1985) and Shipley and Meziane (2002) reveal the interplay of size-dependent allometric size development and site-specific plasticity of plants; obviously, plasticity beyond allometric shape evolution decreases, when site conditions get worse and under strict water limitation, root–shoot growth is merely size dependent. As shown in Fig. 2, plants allocate biomass (and thus optimise the allometric exponent and distribution key α) not only in response to changes in size (APT), but also react on external factors like site conditions (OPT).

2.2 *Detection of Changes in Allometry and Allocation Pattern*

2.2.1 Elimination of the Size-Effect

In general, an allometric relation between two dimensions, e.g. $\alpha_{r,s}$ between root and shoot biomass, leads to a changing biomass ratio between root and shoot during development – except if it is isometric, i.e. $\alpha = 1$ between one-dimensional size variables and 1/3 exponent scaling between variables of quadratic and cubic dimensions. When the allocation pattern of two differently treated groups of plants (e.g. fertilised versus untreated reference) is to be compared, the mean size is often different, because of the accelerated growth in the fertilised group. This advance in size causes a purely ontogenetical difference in biomass ratios. So, comparisons between biomass ratios of the two groups run the risk to misconstrue simple size effects as changes in the allocation key caused by the fertiliser. In non-isometric allometric plant growth, each factor that changes size growth changes also the biomass ratios. In order to distinguish allocation effects from simple size effects, the size effect is often eliminated; there is only evidence of group differences when the group means still differ after elimination of the size effect.

Suppose organ y scales with an exponent of α_y to total plant weight x and organ z with α_z ($y \propto x^{\alpha_y}$, respectively $z \propto x^{\alpha_z}$). Then, the ratio between the biomass of organ y and z ($r_{yz} = y/z$) changes with size like

$$r_{yz} \propto x^{\gamma} \tag{6}$$

with $\gamma = \alpha_y - \alpha_z$.

Equation (6) reflects, that except for $\gamma = 1$, the biomass ratio changes nonlinear with size x, and that the size effect should be eliminated before interpretation of the differences as a changed allocation pattern caused by treatment. Suppose x_1 and x_2 are the mean sizes in groups 1 and 2, respectively, then – assuming the same allometric exponent and factor – $r_{yz,1} \propto x_1^{\gamma}$ and $r_{yz,2} \propto x_2^{\gamma}$ and

$$\hat{r}_{yz,1} = r_{yz,2}(x_2/x_1)^{-\gamma}. \quad (7)$$

That means, given the observed ratio in group 2 of treated plants, $r_{yz,2}$ and the size quotient between the two groups x_2/x_1, (7) enables us to derive the expected biomass ratio $\hat{r}_{yz,1}$ after any size effect is eliminated.

The following example shows the relevance of such an elimination of the size effect. Suppose the root biomass w_r scales with an exponent of 0.55 and the leaf biomass w_l with 0.75 to the total plant biomass w_t ($w_r \propto w_t^{0.55}$ and $w_l \propto w_t^{0.75}$), then for the ratio between root and leaf biomass ($r_{w_r w_l} = w_r/w_l$) applies $r_{wrwl} \propto w_t^{-0.20}$. If measurement would yield $r_{wrwl,1} = 1.6$ for group 1 of damaged trees and $r_{wrwl,2} = 1.5$ for reference group 2, a different allocation key between the groups seems obvious. However, if we consider that tree size in group 1 is $w_{t,1} = 400$ kg compared with $w_{t,2} = 550$ kg in group 2, we can apply (7) to eliminate the effect of the size difference and allometric change due to ontogenetic drift. The estimated ratio for group 1 would be $\hat{r}_{w_r w_{l,1}} = 1.5(550/400)^{0.2} = 1.60$. In other words, the ratio of group 1 is different from that of group 2, but behind the difference is merely the slowing down of size growth and not an altered biomass allocation key.

2.2.2 Deviation from Scaling Rules

Environmental changes can lead to deviations in the allometric development, following a constant species-specific exponent α. In plots with double-logarithmic scales, deviations from allometric behaviour are apparent by the deviations from the linear slope. For a detailed analysis of x–y-allometry, the slope α' in (3) can be calculated from the pairs of variables $y_{i=1...n}$ and $x_{i=1...n}$ from consecutive surveys, which are commonly available from long-term observations in forest growth and yield science. In Fig. 4, we illustrate the usefulness of slope α' for quantifying the effect of (a) competition, and (b) long-term ozone fumigation on the h–d-allometry of European beech and Norway spruce.

Figure 4a shows the h–d-allometry of European beech in the Norway spruce–European beech mixed stand FRE 813/1 near Freising in the period 1994–2005 (Pretzsch and Schütze 2005). The calculation of $\alpha'_{h,d} = \ln(h_{2005}/h_{1994})/\ln(d_{2005}/d_{1994})$ (cf. (3)) results in $\alpha'_{h,d} = 0.85$, on average, with a range of $\alpha'_{h,d} = 0.1$–3.5. This means, when diameter increases by 1%, height increases on average by 0.85%. However, thorough analysis reveals that, in case of small understory trees, a diameter increase of 1% corresponds with a height growth of

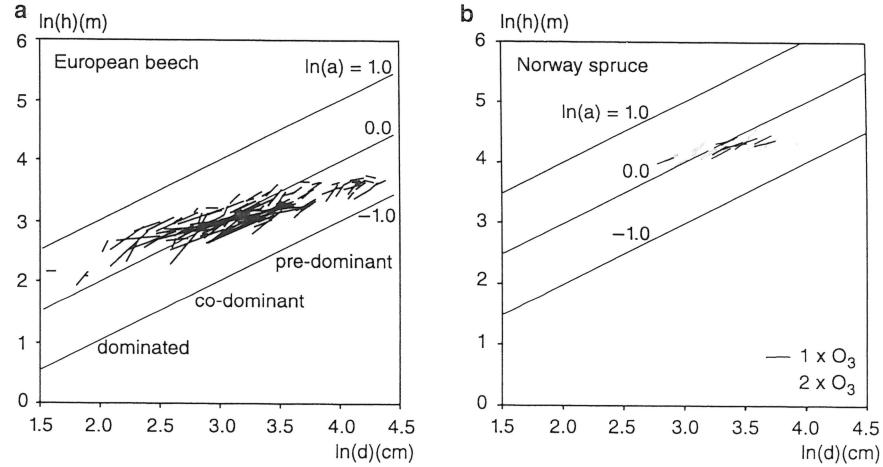

Fig. 4 Change of h–d-allometry of (**a**) European beech under competitive stress and (**b**) Norway spruce under ozone stress, shown in a double-logarithmic coordinate system (**a**) For European beeches of different social classes ($n = 107$), the h–d-allometry is shown for the period 1994–2005. (**b**) For Norway spruce ($n = 19$) trees under ambient ozone (*thin black lines*; $1 \times O_3$) show shallower slopes than trees under double ozone fumigation (*bold gray lines*; $2 \times O_3$). The *straight lines* represent the allometry expected for geometric scaling with $\alpha = 1.0$ and intercepts ln(a) = – 1.0, 0.0 und + 1.0 and serve as a reference

up to 3.5% (steep slopes on the left of Fig. 4a), whereas, in case of dominant trees, a corresponding height growth of 0.1–0.5% was found (shallow slopes in the right part of Fig. 4a).

Long-term ozone fumigation in a part of the same stand changed the h–d-allometry in the period 2000–2007 for Norway spruce. The canopy space of this part of the experimental plot is accessible by a scaffolding and a canopy crane, which enable annual high precision tree height growth measurement used for Fig. 4b. The thin black lines in the ln–ln-grid represent h–d-slopes under ambient ozone ($1 \times O_3$), bold gray lines those for $2 \times O_3$. The straight lines indicate the expected allometry under geometrical scaling ($h \propto d^{\alpha}$, $\alpha = 1$). The slopes in the period 2000–2007, equivalent with the allometric exponent, range between $\alpha'_{h,d} = 0.27 - 2.42$ (mean $\alpha'_{h,d} = 0.99$). The graphical impression that those trees growing under double ambient ozone have steeper slopes can be substantiated by analysis of their allometric exponent $\alpha'_{h,d}$. The comparison between trees growing under ambient ozone concentration with sample trees under double ozone concentration in the same stand, similar in tree size, tree age and crown parameters yields significant differences of $\alpha'^{1\times O_3}_{h,d} = 0.73(\pm 0.11, n = 8)$ and $\alpha'^{2\times O_3}_{h,d} = 1.18$ $(\pm 0.17, n = 11)$. Numbers in brackets represent standard error and sample size, respectively. Obviously, under ozone fumigation, Norway spruce enhances height growth over diameter growth; in other words, its stems alter towards top-heavy, full-formed and rather unstable shapes (Pretzsch et al. 2009).

2.3 *Effect of Allometric Scaling on Growth and Yield Curves of Plants*

Assumptions about allometric scaling have considerable consequences for the growth and yield (accumulated growth) processes. In the sequel is shown, how the surface–weight-allometry ($s \propto w^{\alpha_{s,w}}$) affects the growth and yield curves of plants. In his attempt to explain one of the most fundamental processes of organisms' growth, von Bertalanffy (1951) describes the body mass growth rate (dw/dt = ass – resp) as the result of two terms representing assimilation (ass = $a \cdot s$) and respiration (resp = $b \cdot w$)

$$dw/dt = a \cdot s - b \cdot w, \tag{8}$$

with surface area (s), plant weight (w) and a and b being species-specific factors. According to Rubner (1931), who assumed geometrical scaling, surface area s (leaf area, surface area of animal lungs or intestines) can be expressed as weight raised to the power of 2/3 ($s \propto w^{2/3}$). Assimilation is proportional to $w^{2/3}$, while respiration is proportional to weight. Consequently, (8) becomes

$$dw/dt = a\,w^{2/3} - b\,w, \tag{9}$$

with the generalised allometric exponent $\alpha_{s,w} = 2/3$ and species-specific allometric factors a and b. The S-shaped yield function, which results by integration of growth function (9)

$$w = A\left(1 - e^{-b\,t}\right)^3 \tag{10}$$

appeared too unflexible, so that von Bertalanffy (1951) and later Richards (1959) generalised (9) to

$$dw/dt = a\,w^m - b\,w, \tag{11}$$

which yields in integrated form

$$w = A\left(1 - e^{-b\,t}\right)^{\frac{1}{1-m}} \tag{12}$$

and is the most widely applied function for describing growth processes.

When this function is fitted to observed growth trajectories, e.g. by nonlinear regression, the exponent $1/1 - m$ reflects the allometric relationship behind the described growth process. Geometrical scaling, where $m = 2/3$ (cf. (11)) would yield $1/1 - m = 3$, which reflects that von Bertalanffy's original function is a special case of the Richards equation. For comparison, fractal quarter power scaling with $m = 3/4$ results in $1/1 - m = 4$. If regression analysis would yield $1/1 - m = 2$, that would indicate for the underlying surface–weight allometry $s \propto w^{\alpha_{s,w}}$, a half part fractal scaling, as then $m = \alpha_{s,w} = 1 - 1/2 = 0.5$.

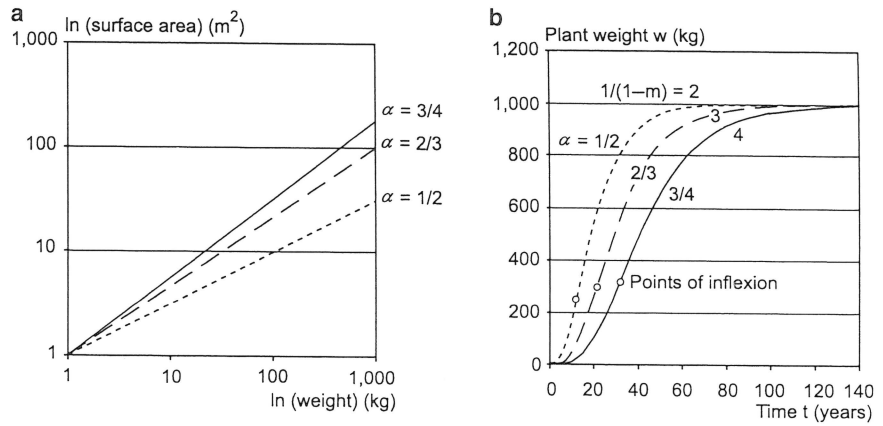

Fig. 5 Hypotheses about (**a**) the plant surface area-weight allometry $s \propto w^{\alpha_{s,w}}$ with $\alpha_{s,w}$=1/2, 2/3, and 3/4 in the double-logarithmic grid and (**b**) the resulting yield functions $y = A\left(1 - e^{-b\,t}\right)^{\frac{1}{1-m}}$ with $1/1 - m = 2$, 3 and 4, respectively

Figure 5 shows (a) for $\alpha_{s,w} = 1/2$, 2/3, and 3/4 different allometric relationships between plant weight and surface area and (b) the effect of the different scaling assumptions on the S-shape of the resulting yield curve. The biomass at the point of inflexion w_I lies at $w_I = A\,m^{(1/1-m)}$, which shows how the supposed allometry determines the form of the sigmoid yield curve. The term $w_I/A = m^{(1/1-m)}$ represents the biomass at the inflexion point relative to the maximum possible (asymptote) biomass A. It is 0.25 of the asymptote in the case of one half power scaling ($\alpha = 1/2$), and 0.296 and 0.316 in the case of geometrical and fractal scaling with $\alpha = 2/3$ or 3/4, respectively ($1/1 - m = 2$, 3, and 4 respectively). Numerous analyses of growth curves with $1/1 - m$-values between 1 and 4 underline a considerable individual, species-specific and site dependent variation (e.g. Kahn 1994; Murray and von Gadow 1993) in basic allometric relationships. Suppose the three curves represent neighbouring individuals or species in a stand, the differences of their allometry and yield curves would have considerable consequences for their competition.

3 Allometry on Stand and Community Level: Linkage of Production and Growing Space Requirements

As plants grow in size, their demands on resources and growing space increase. If resources are no longer sufficient for all individuals, self-thinning commences, and the number of plants N per unit area decreases (Fig. 6). Although the principle of allometry was derived for individual plants, its application to stands or plant communities in which self-thinning occurs, is of high value in plant ecology and forestry (Enquist and Niklas 2001; Pretzsch 2002, 2006; Weller 1987, 1990; Zeide 1987).

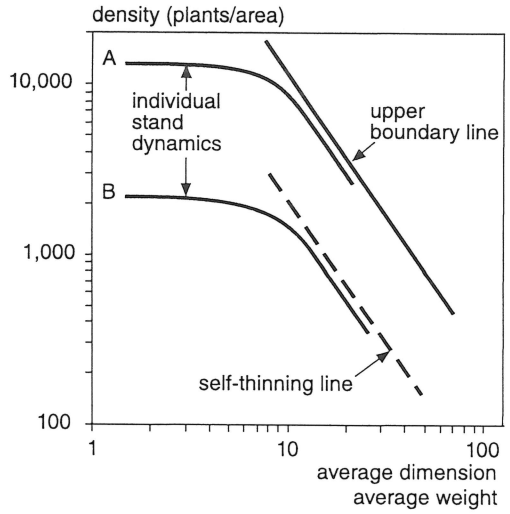

Fig. 6 The common principle of Reineke's rule (1933) and the −3/2 power law by Yoda et al. (1963) for evenaged plant populations. The relationship between average plant size or average weight and plant number forms a straight line in a double-logarithmic scale. The *upper and lower straight lines* represents the self-thinning line of the plant populations A and B and delineate the decrease of plant number under optimal respectively poor site conditions. Before crown closure the population density remains rather constant until the limited resources enhance competition and lead to self-thinning

3.1 *Linkage of Production and Growing Space Requirements*

Suppose the size of a certain organ, e.g. the crown projection area (cpa), shows an allometric relationship with the size of the total tree, e.g. the biomass weight w

$$w \propto \text{cpa}^{\alpha}. \tag{13}$$

Let us suppose furthermore, that the crown projection area cpa represents the growing space (s) and resource requirements (r) of a tree (cpa $\propto s \propto r$). Then, (13) equals $w \propto s^{\alpha}$ or $w \propto r^{\alpha}$. As an individual's growing space or resource demand is hard to assess, the relationship was mostly postulated and analysed on stand respectively mean tree level

$$\bar{w} \propto \bar{s}^{\beta}. \tag{14}$$

with mean plant weight $\bar{w}$ and mean plant growing area $\bar{s}$. The mean growing area $\bar{s}$ ($\bar{s} = A/N$, with A = unit area, e.g. hectare, N = tree number) is used as surrogate variable for the mean lateral crown extension and resource demand of a plant. Thereby, (14) represents a linkage between biomass production of the mean tree and the required growing area or resources, respectively. In other words, (14) couples production ecology with population ecology (Zeide 1987).

As the average growing area $\bar{s}$ is the inverse of number of plants N ($\bar{s} \propto 1/N$), (14) can be written as $\bar{w} \propto N^{-\beta}$. Latter forms the basis of the self-thinning rule, which is shown in Fig. 6 in schematic representation on the double logarithmic scale ($\ln(\bar{w}) \propto -\beta \ln(N)$). The upper self-thinning, or limiting boundary line

(solid line), marks the maximum possible density for a species at a given average plant size, or weight in even-aged pure stands under optimum site conditions. The lower self-thinning line (dashed line) marks the characteristic boundary relationship for any stand under suboptimum growing conditions. Given two stands A and B growing under optimum and suboptimum conditions, respectively, the size–density relationships of each stand initially approximate their stand-specific self-thinning lines, and, subsequently, follow this line. The lines may have different absolute levels, but possess similar slopes (Pretzsch 2002).

3.2 *Reineke's Self-Thinning Line*

For the relationship between tree number N and quadratic mean diameter d_q in fully stocked, even-aged forest stands, Reineke (1933) defined the "stand density rule"

$$N = b\, d_q^{-1.605}. \tag{15}$$

Reineke's rule can be represented on the ln–ln scale as a straight line

$$\ln N = b' - 1.605 \ln d_q \tag{16}$$

with the intercept $b' = \ln b$ and the slope $\beta_R = -1.605$ (note that we substitute α as the allometric exponent on individual plant level by β for the stand level; the subscript R stands for Reineke). Reineke obtained this scaling rule by plotting d_q and N for untreated forest inventory plots in the USA on a double-logarithmic grid. He found very similar allometric exponents for various tree species, stand structures, and sites, and hence, concluded that the rule had a general validity of $\beta_R \cong -1.605$ for forest stands. Reineke's rule has gained considerable importance for the quantification and control of stand density, and for modelling stand development in pure (Ducey and Larson 1999; Long 1985; Newton 1997; Pretzsch 2009; Puettmann et al. 1993; Sterba 1975, 1981, 1987), and mixed stands (Puettmann et al. 1992; Sterba and Monserud 1993).

Reineke (1933) used the allometric exponent $\beta_R = -1.605$ to develop his stand density index $\text{SDI} = N\,(25.4/d_q)^{-1.605}$. The SDI describes stand density in relation to the quadratic mean diameter d_q and the number of trees per hectare N by calculating the expected number of stems per hectare for a 10-inches mean diameter (= 25.4 cm; 1 inch = 2.54 cm). In Europe, an index diameter of 25 cm is used, so that

$$\text{SDI} = N(25/d_q)^{-1.605}. \tag{17}$$

Stand density indices at maximum stocking densities vary according to the spatial requirements of tree species and site characteristics (Pretzsch 2009, pp. 271–273). Whereas, one can expect 900–1,100 trees per hectare with a quadratic mean

diameter of $d_q = 25$ cm in a Norway spruce stand with maximum stocking density and optimal growing conditions, and similarly high values for Silver fir and Douglas fir, the stand density indices for Sessile oak and European larch are only about the half, with 500–600 trees per hectare. SDI values of 600–750 trees ha^{-1} in stands with a quadratic mean diameter of $d_q = 25$ cm are found for Scots pine and European beech.

According to Zeide (2004, p. 7), Reineke's density assessment with the SDI "... may be the most significant American contribution to forest science...". But, Zeide like von Gadow (1986), von Gadow and Franz (1989), and Pretzsch and Biber (2005) questions the general validity of exponent $\beta_R \cong -1.605$. Last-named authors re-evaluate Reineke's rule based on 28 fully stocked pure stands of European beech, Norway spruce, Scots pine, and Sessile oak in Germany, which have been inventoried since 1870. Figure 7 shows the ln(N)– ln(d_q)-relationships for European beech, Norway spruce, Scots pine and Sessile oak. OLS regression of the model $\ln(N) = b' + \beta_R \ln(d_q)$ results in values of $\beta_R = -1.789$ for European beech, -1.664 for Norway spruce, -1.593 for Scots pine and -1.424 for Sessile oak. The allometric exponent for European beech differs significantly from the other species. There is also a significant difference between the β_R-values for Norway spruce and Sessile oak. With the exception of Scots pine, the allometric exponents deviate significantly (European beech) and almost significantly (Norway spruce, Sessile oak) on a $p = 0.05$ level from the exponent $\beta_R = -1.605$, postulated by Reineke (1933). If this species-specific allometry is ignored, serious errors in the estimate and control of density may be the consequence when using the SDI (cf. Sect. 5). Physiologically, the species-specific allometric exponent β_R demonstrates how strong a species enforces self-thinning for a given increase in diameter, or, in the words of Zeide (1985), the species' self-tolerance. According to the results from above, European beech exhibits the highest self-thinning, or lowest self-tolerance, and Sessile oak, the lowest self-thinning, or highest self-tolerance as defined by Zeide (1985).

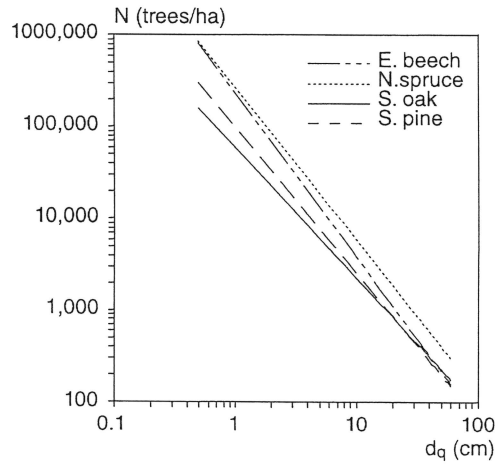

Fig. 7 Species specific ln(N)-ln(d)-relationships for untreated, fully stocked, pure European beech, Norway spruce, Sessile oak, and Scots pine stands in Bavaria/South Germany under survey since 1870 (Pretzsch and Biber 2005)

3.3 *The −3/2-Power Rule by Yoda et al.*

With no knowledge of the stand density rule by Reineke (1933), the Japanese scientists Kira et al. (1953) and Yoda et al. (1963) discovered the −3/2 power rule of self-thinning, initiating probably the most prominent controversial discussion of a scaling rule. It describes the relationship between the average shoot weight $\bar{w}$ and the plant number N per unit area in even-aged and fully stocked mono-specific plant populations as

$$\bar{w} \propto N^{-3/2} \tag{18}$$

with the species invariant scaling exponent $\beta_Y = -3/2$. Yoda et al. (1963) assume that plants are simple Euclidian objects, and all plant parts are related to each other isometrically. Effectively, Yoda's allometric coefficient −3/2 is based on the cubic relation between plant diameter $\bar{d}$ and biomass $\bar{w}$

$$\bar{w} \propto \bar{d}^3 \tag{19}$$

and the quadratic relation between $\bar{d}$ and occupied growing area $\bar{s}$

$$\bar{s} \propto \bar{d}^2. \tag{20}$$

As average growing area $\bar{s}$ is the inverse of number of plants N ($\bar{s} = 1/N$), (20) can be written as

$$N \propto \bar{d}^{-2} \tag{21}$$

or $\bar{d} \propto N^{-1/2}$. By inserting (21) in (19) and rearrangement, we get $\bar{w} \propto \left(N^{-1/2}\right)^3 \propto N^{-3/2}$ (cf. (18)). Equivalently, shoot biomass per unit area W scales over plant number N as $W \propto N^{-1/2}$, since $W = \bar{w}N$, $W \propto NN^{-3/2} \propto N^{-1/2}$. Equation (21) is similar to Reineke's (1933) formulation of the stand density rule, but predicts a Reineke exponent of $\beta_R = -2$ instead of -1.605.

Harper (1977, p. 183) attested the −3/2 power law, a validity for annual plants and forests as well. White (1981, p. 479) even saw the "empirical generality of the rule ... beyond question". And among others, Long and Smith (1984, p. 195) titled it "... a true law instead of the mere rule...". A quarter of the century after the first euphoria concerning the law, Begon et al. (1998, p. 169) revise their approving attitude towards the law and plead for detection of inter-specific characteristics in their allometry.

For $\bar{w} \propto N^{\beta_Y}$, Pretzsch (2006) revealed by OLS regression $\beta_Y = -1.403$, -1.614, -1.575 and -1.592 for European beech, Norway spruce, Scots pine and Sessile oak, using a broad dataset of real time series of un-thinned long-term experimental plots in Germany. The formulation of the Yoda rule with the exponent

β_Y on the side of the stem number results in an increase in the self-thinning (decrease in self-tolerance) in the order: European beech, Scots Pine, Sessile oak and Norway spruce (cf. also Pretzsch 2006).

Unlike herbaceous plants, many tree species develop a stem with a core of inert heartwood, which may comprise a considerable proportion of the tree's total biomass. For a better comparison between woody and herbaceous species, it may be helpful to distinguish between dead and living tissue. In Pretzsch (2005), functions for the estimation of biomass and sapwood area, and a stereometric model for distinguishing stem sapwood from dead heartwood are developed for European beech, Norway spruce, Scots pine and Sessile oak. The results showed that considerably smaller differences between the species self-thinning line occur with $\bar{w}'$, representing living and not total biomass. The allometry $\bar{w}' \propto N^{\beta'}$ provided values of $\beta' = -1.396$, -1.365, -1.447, and -1.369, respectively. With other words, the heartwood elimination yields a less biased slope β' and improves the comparability between the scaling rules for woody and herbaceous plants (Pretzsch 2005).

Comparison with the geometrical scaling exponent, $\beta = -3/2$ postulated by Yoda and fractal scaling slopes $\beta = -4/3$ expected by Enquist et al. (1998, 1999) and West et al. (1997, 1999) show that observed slopes β deviate considerably from the generalised exponents. However, values for β' show that the elimination of inert heartwood shifts allometry remarkably towards fractal scaling. This evaluation is not shown in order to argue for an overarching validity of the quarter (1/4 exponent) scaling, but to underline that heartwood's elimination may yield a less biased slope β', improves comparability between woody and herbaceous plants' scaling rules and paves the way for a more circumspect application of self-thinning slopes for density estimation, density control and growth prediction.

The difference in the exponents from Reineke and Yoda arises from the different allometry between quadratic mean diameter and mean plant weight. By rearranging the Yoda rule to $N \propto \bar{w}^{1/\beta_Y}$, and substituting it in Reineke's rule, $N \propto \overline{d_q}^{\beta_R}$, one obtains $\bar{w}^{1/\beta_Y} \propto \overline{d_q}^{\beta_R} \Leftrightarrow \bar{w} \propto \overline{d_q}^{\beta_Y \cdot \beta_R}$. The original exponents from Yoda and Reineke result in an exponent of $\bar{w} \propto \overline{d_q}^{2.4075}$ (Pretzsch 2009, p. 404) and Reineke's rule becomes just a special case of Yoda's. For the four species considered above, the relation produces exponents of 2.508, 2.686, 2.509 and 2.267 for European beech, Norway spruce, Scots pine and Sessile oak, respectively.

3.4 *Self-Thinning Versus Alien Thinning*

The slope β_{N,d_q} of Reineke's self-thinning line $\ln(N) - \ln(d_q)$ reveals the self-tolerance of a tree species growing in pure stands (Zeide 1985). The larger the β_{N,d_q}-value, the lower the number of dying trees $\Delta N/N$ for a given diameter

increment $\Delta d/d$ will be and the greater the self-tolerance of the species in pure stands (cf. (2) and (3)). The ranking we revealed for the mean species-specific, β_{N,d_q}-values European beech (-1.789) < Norway spruce (-1.664) < Scots pine (-1.593) < Sessile oak (-1.424) expresses that in comparison to Norway spruce and European beech, Sessile oak and Scots pine are more tolerant with trees of the same species. For instance, in European beech stands, a mean diameter increase of 1% causes a decrease in the number of stems by 1.79%. Given the same diameter increment, the decrease in the number of stems is 1.66%, 1.59% and 1.42% for Norway spruce, Scots pine and Sessile oak respectively, that means 7%, 11% and 21% lower than for European beech. This underlines the low self-tolerance of European beech and its space consuming investment strategy. The causes for this are its wider and more dynamic lateral crown extension, which were already discussed in Sect. 2.1 (cf. Fig. 3).

For mixed stands on comparable sites, mean β_{N,d_q}-values determined for European beech, Norway spruce, Scots pine and Sessile oak came to $\beta_{N,d_q} = -0.40$, -1.02, -1.06 and -2.01 respectively, which indicates a reversal of the ranking in pure stands, i.e. European beech > Norway spruce > Scots pine > Sessile oak (Pretzsch and Biber 2005). Compared with pure stands in which self-thinning (intra-specific) decreases tree number, in mixed stands where alien-thinning (inter-specific) occurs, β_{N,d_q} of European beech, Norway spruce and Scots pine increases, while that of Sessile oak decreases. Great crown expansion and space occupation abilities under intra-specific conditions (e.g. European beech) evidently guarantee great assertive power in the mixed stand. Low space occupation effectiveness in the pure stand (e.g. Sessile oak) is obviously combined with low assertive power in the mixed stand. This underlines, that allometry is species-specific and depends not only on size, but also on external factors (Fig. 2) and is crucial for the competitiveness and success of a species in pure and mixed stands.

4 Discussion

In the previous sections of this chapter, it was shown (1) that allometric research built up a valuable set of hypotheses and methods for analysing size of organisms and its consequences for their shape and functioning, (2) that empirical findings on organ, plant, population and community level give evidence, that allometric exponents vary in a rather narrow corridor, and (3) that it is not a single allometric exponent that carries the overarching validity but the variation within this corridor in dependence on species, environmental conditions, and resource supply. In the following discussion, the attention is drawn to methodological obstacles of allometric research, the limited benefit of hunting for general allometric rules or universal exponents, and finally to the profile of allometric research.

4.1 Methodological Considerations and Obstacles

From the broad range of methodological considerations when analysing allometric relationships and extracting allometric exponents, the following are probably the most relevant.

4.1.1 Real Versus Artificial Time Series as Source Data

The most appropriate way of analysing allometry is to record the size and form development of individuals over time by repeated measurement. By long-term measurement of the height–diameter development or by its reconstruction on the basis of stem analysis, e.g. analysis of a permanently dominant tree, we may get the dynamic h–d-allometry shown in Fig. 8a (solid line). Under stress similarity or elastic similarity, we may reveal for this tree $h \propto d^{\alpha_{h,d}}$ with $\alpha = 0.5$ or 0.66, respectively (Niklas 1994, p. 165).

However, often longitudinal data about the development of individuals or stands are not available. In such cases, the static height–diameter value pairs of a stand at a given age or in a given period (data points and broken line) are used for fitting the relationship $\ln(h) = a + \alpha \ln(d)$ and the resulting slope $\alpha_{h,d}$ is interpreted as

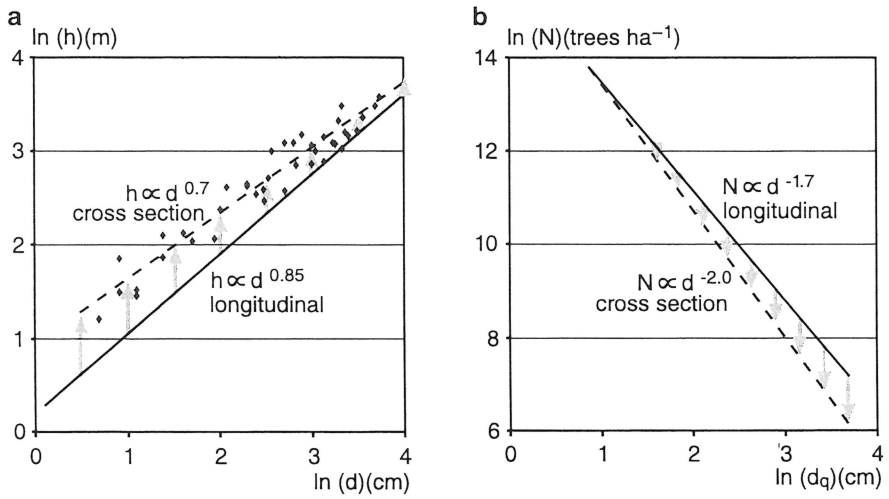

Fig. 8 Estimation of bivariate allometric relationships from longitudinal data (*continuous line* = real time series) and cross section data (*broken line* = artificial time series) in schematic representation for (**a**) the tree-height-diameter-allometry and (**b**) Reineke's self-thinning line (**a**) The slope of the cross section analysis is shallower, as suppressed trees in a stand enhance height growth (*upward arrows*) ($h \propto d^{0.85}$ *versus* $h \propto d^{0.7}$). (**b**) Slope from long-term survey and undisturbed fully stocked stands is often shallower compared with slopes from cross section inventory data, as latter includes density reduction by disturbances (*downward arrows*) ($N \propto d_q{}^{-1.7}$ *versus* $N \propto d_q{}^{-2.0}$)

allometric exponent. Such a substitution of cross section data for a real time series is often misleading as the height–diameter-relation of trees in a given period, which reflects rather the trees long-term form and shape adaptation to competitive stress than the size-dependency of their form development. In the face of competition, especially the dominated or even suppressed trees in a stand (data points on the left) increase height growth as against stem diameter growth (Pretzsch and Schütze 2005). So, the analysis on the basis of cross section data (broken line) results in a more shallow slope compared with the slope resulting from a permanently dominant tree (solid line). The two approaches are often mixed with each other, however, carefully applied they can serve to separate size dependent from competition dependent form development (Weiner 2004).

While on tree level, stem analysis or increment cores can be used to reconstruct size and shape development and reveal allometric trajectories, on stand level records of undisturbed and well-documented long-term development like those underlying Fig. 7 are very rare. So, for analysis of stand level allometry, mostly spatially adjacent stands of different ages but equal site conditions (artificial time series) substitute real time series (Enquist and Niklas 2001, Reineke 1933). However, in view of the longevity of forest stands, effects of environmental changes, disturbances like wind-throw, ice-breakage or insect calamities, which are not always documented may often be hidden in the given stand structure, so that it reflects rather the result of disturbances and adaptation than the size dependent allometric trajectory expected under undisturbed conditions.

4.1.2 Regression Techniques

When scaling exponents and scaling coefficients are computed, either Model I (ordinary least square regression, OLS) or Model II (reduced major axis regression, RMA) are applied. Zeide (1987) and Niklas (1994) argue that 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. Neither approach necessarily will produce exactly the same results, unless the $\ln(y)-\ln(x)$-pairs form a perfectly straight line. Sackville Hamilton et al. (1995) showed how slope estimates of OLS-regression, PCA and RMA-regression algorithm converge with increasing r^2 (coefficient of determination). From the examples presented in this chapter, regression yielded always $r^2 > 0.9$, and the differences between OLS and RMA slopes had no decisive effect on the final results. To take these methodological differences into account, especially when $r^2 < 0.9$, various methods should be applied to the dataset in question (Matthew et al. 1995, Sackville Hamilton et al. 1995).

4.1.3 Using Log-Transformation

The statistical analysis and extraction of allometric factors (a, b, ...) and allometric exponents ($\alpha, \beta, \cdots$) is mostly based on log- or ln-transformation of the observed

data and subsequent OLS-regression, PCA or RMA-regression. Arguments for this approach are that the effect of outliers on the result is reduced and that after transformation, the data meets the statistical assumptions of normal distribution and homoscedasticity. But logarithmic transformation involves the risk that relationships are erroneously assessed as linear as there is a linear bias of human perception, which is hard to overcome (Smith 1980). One should always keep in mind, that hardly visible differences of log-values of 4.5 and 5.0 mean a difference on the linear scale between about 32,000 and 100,000.

Analysing the self-thinning rule Zeide ((1987); Figs. 1–4) found that the $\ln(N)-\ln(d_g)$-relationship is often concave seen from below, although that is hardly visible in the double-logarithmic grid. However, application of model $\ln(N) = a_1 + a_2 \ln(d_q) + a_3 \ln^2(d_q)$ and analysis, whether a_3-values are negative or positive may reveal a concave curve, as seen from below, or a convex curve (Pretzsch 2006).

4.1.4 Transition from Plant Level Allometry to Stand or Community Level

Most studies equate without demur the allometric exponent $\alpha_{y,x}$ between the individual plant variables y and x with the respective exponent $\beta_{\bar{y},\bar{x}}$ between the same variables on mean tree or stand level. However, when individual plants follow $\alpha_{y,x}$-scaling, that does not necessarily imply, that the mean tree or stand characteristics behaves similar. If the relationship between y and x is nonlinear ($\alpha_{y,x} \neq 1.0$) and not all x-values are equal, then holds $\sum x_i^{\alpha}/n \neq (\sum x_i/n)^{\alpha}$. In other words, even if we find a constant allometric exponent $\alpha_{y,x}$ on tree level, we find a different one on mean tree level as the mean for (individual size)$^{\alpha}$ does not equal (stand mean size)$^{\alpha}$. For the relationship between leaf weight and tree diameter, Pretzsch and Mette (2008) showed that the differences between allometry on individual and mean tree level depends on the shape and development of the size frequency distribution of the stand. Blake et al. (1991) and Ford (1975) analysed the same phenomenon with respect to other plant and stand size variables.

A flawless transfer of allometry exponent α from individual level to stand level requires either $\alpha = 1$ or a steady shape of the frequency distribution of size x during the stand development. When $\alpha \neq 1$, we have to reckon with differences between plant and stand allometric exponents; the more heterogeneous and variable the frequency distribution of x, the greater is the difference between both levels of observation. Only if these differences are always of the same relative magnitude, this alters only the allometric factors (a, b, ...) and not the allometric exponents ($\alpha, \beta, \ldots$). However, normally the shape of the size distribution changes over time, due to growth, loss of individuals etc., thereby causing a difference between α and β.

Since the beginning, forest science is aware of the fact that the development of arithmetic mean diameter or height of a stand has two components, the size growth of the individual trees and the increase of the mean by prevailing loss of thin trees and coupled calculative upward shift of the mean. So, the development of the mean

is an artificial course for the description of stand growth, and does not represent individual growth. In order to give mean size development a higher stability, forest science uses, e.g. the quadratic mean diameter $d_q = \sqrt[2]{(d_1^2 + d_2^2 + \cdots + d_n^2)/n}$ instead of the arithmetic mean $\bar{d} = (d_1 + d_2 + \cdots + d_n)/n$. Especially in the case of Reineke's self-thinning law with allometric exponents close to -2, the quadratic mean stabilises the transition from tree to stand level. When y scales with a power of 2.0 to x ($y \propto x^2$), then the mean for (individual size)^2 equals (stand mean size)^2 as in this special case, when scaling exponent and weighting approach are similar, applies $\sum x_i^{\alpha}/n = (\sum x_i/n)^{\alpha}$ as $y_q = \sqrt[2]{(x_1^2 + x_2^2 + \cdots + x_n^2)/n}$ and $y_q^2 = (x_1^2 + x_2^2 + \cdots + x_n^2)/n$.

4.1.5 Refined Elimination of the Size-Effect

Often, generalised theoretical or observed empirical allometric trajectories are applied for elimination of the mere size effect from a plant or stand development in order to differentiate site-specific allocation effects from ontogenetic size effects. For this purpose, a certain size measure, mostly plant weight, has to be applied as the independent variable (cf. Sect. 2.2.1). Due to practical applicability in forest research, tree diameter or stem volume is often used instead of whole tree weight. In order to scrutinize decide whether a formerly suppressed Norway spruce tree after release follows the same allocation pattern as a neighbouring open-grown spruce tree of the same size, we can use diameter or stem volume as a reference measure. However, even if the trees possess the same diameter or stem volume, they may differ considerably in other size or shape attributes (x_1, x_2, ... x_n) like crown length, crown width, root–shoot-ratio or sapwood-core wood-ratio, which also determine the future growth of the open-grown and understory tree in a very different way. Such multivariate size differences cannot be quantified by simple univariate regressions, but require multiple approaches like $\ln(y) = a + b \ln(x_1) + c \ln(x_2) \cdots + n \ln(x_n)$. At this point, we leave the reductionistic and simplistic realm of allometry and face the complexity of the real world.

4.2 Allometry as General Allocation Principle?

In the beginning, allometry and the respective methods were perceived as an approach for taking account of differences in absolute size and thereby induced changes in organ proportions, interpreting inherited, size induced form and shape developments as adaptive reactions to specific environmental conditions (Huxley 1932), and deriving growth and yield processes in dependence on first-order processes like surface-dependent assimilation and volume-dependent respiration (von Bertalanffy 1951).

Subsequently, allometric research was driven by the striving for general rules, laws or biological constants. The search stretched over organ, individual and population level aiming to reveal overarching principles, which are so rare in biology and ecology compared with physics, mathematics or chemistry. Because of their ecophysiological significance, allometric exponents have been discussed strongly ever since (Pretzsch 2000).

The most prominent Euclidean 1/3 exponents and fractal 1/4 exponents were introduced in Sects. 1.4, 3.2, and 3.3. Evidence against a universally validity of Reineke's, Yoda's or Enquist's allometric exponents was raised in this chapter and is supported by solid literature (Yoda: Harper 1977, p. 183; Long and Smith 1984, p. 195; Weller 1987, 1990; Sackville Hamilton et al. 1995, Reineke: Pretzsch and Biber 2005; von Gadow 1986; del Río et al. 2001; WBE: Whitfield 2001; Kozlowski and Konarzewski 2004; Reich et al. 2006).

The author's perception of allometry corresponds with Zeide's (1987, p. 532) conclusion after analysing Yoda's rule: "... unlike the fixed value of −3/2, the actual slopes convey valuable information about species ... that should not be cast away", or Weller's (1987, p. 37) statement that "The differences among slopes may provide a valuable measure of the ecological differences among species and plants, and a powerful stimulus for further research". As long as allometry searches for universal constants, it may still our innate propensity to reduce complexity and generalise. However, in my opinion, the mere hunting for general rules or laws hardly contributed to a better differentiated understanding of plants and stands, but it rather maneuvred allometric research somehow into a l'art pour l'art phase and isolation from related disciplines.

4.3 *Changing Profile of Allometric Research*

With respect to spatial and temporal resolution, the allometric approach to plant and stand growth lies between a simple statistical description of relationships and a deeper mechanistic causal explanation. Due to its simplistic approach (striving for overarching exponents and leaving the rest as white noise), the results of allometric research are difficult to integrate in both, the system knowledge of neighbouring disciplines as well as practice. While neighbouring disciplines like plant physiology need differentiated and not general explanatory schemes, also for practical purposes universal laws may yield first-order estimates, but are surely not sufficiently precise for hard economic decisions (cf. Sect. 5). Model hypotheses for data interpretation or prognosis models for use in practice, for instance, do not employ such generalised exponents.

The numerous falsifications showed that the allometric exponents tend to lie in a narrow corridor, but can be species-specific or even provenance-specific and site-dependent. The individual species' scaling exponents and their relative position in the corridor are the keys for understanding the species' ability to cope with the site conditions and competitive situation and should not be cast away, although

generalisation across species is tempting. In this sense, falsification trials concerning the rules from Reineke, Yoda and West, Brown and Enquist are turned into a refined understanding of individual species allometry, and overarching scaling exponents would appear as a stimulating myth.

Recent approaches to link APT with OPT may change the profile into a more pluralistic approach aiming at an integrated understanding from both, the inherited evolutionary optimised size induced form as well as the shape development caused by the adaptive reactions on specific environmental conditions, which are revealed under selective pressure (Fig. 2).

5 Conclusions

5.1 *Avoidance of Practical Application of Inaccurate and Imprecise General Scaling Rules*

Crown diameter–stem diameter allometry on individual tree level, e.g. unmasks that European beech is more expansive and space consuming with increasing size compared with the cone-like vertically growing Norway spruce. On stand level, this is reflected by a more rapid self-thinning in pure beech stands and a more moderate decline of competing neighbours in Norway spruce stands. European beech's superior gap dynamic and shade tolerance means competitive strength facing other neighbouring species in mixed stands. However, in pure beech stands, this rigorous space occupation is directed against members of the own species.

The argument that rough general rules are required for scaling from organ to community level again is tempting. However, for example the general assumption of Enquist and Niklas (2001) shows that tree number scales as −2 power of mean tree diameter can cause considerable flaws in modelling and prognosis.

Suppose in a juvenile Sessile oak stand with a mean diameter of 1 cm and a tree number of 22,027 per hectare, self-thinning starts off with the generalised slope of $\beta_{N,d_q} = -2.0$, then $N = 22,027\ d_q^{-2.0}$ yields three oak trees per hectare in the mature stand with mean diameter $d_q = 80$ cm. Compared with this, the empirically found species-specific slope $\beta_{N,d_q} = -1.424$ predicts 43 trees per hectare, which is more than ten times of the theoretical stand density and more in accordance with silvicultural experience. Such differences matter when silvicultural prescriptions are based on scaling exponents.

5.1.1 Stand Density Management Diagrams as Silvicultural Prescriptions

In view of the individual species' slopes, stand density estimation algorithms, founded on generalised allometric relations, appear unsuitable. Stand density management diagrams (SDMD), which are applied for many species as tool for

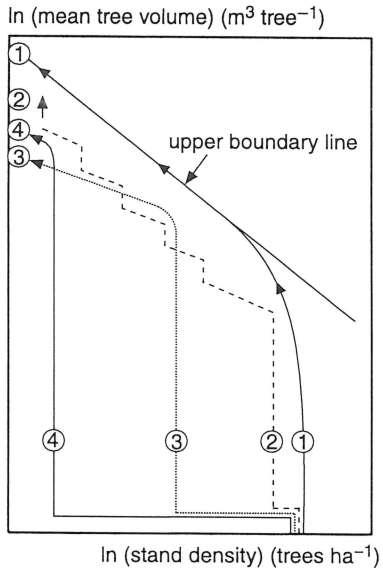

Fig. 9 Stand density management diagram (SDMD) for boreal conifer stands with four trajectories representing various thinning concepts (adopted by Weetman 2005, p. 7). The upper boundary line (*black continuous line*) represents the maximum stand density. Trajectories 1–4 all begin with dense natural regeneration, and subsequently quantify different silvicultural prescriptions. Note the logarithmic scale of the axes

regulating stand density, use the self-thinning line as upper boundary and are the most prominent silvicultural application of the self-thinning rule (Oliver and Larson 1996, pp. 352–353).

Figure 9 shows a stand density management diagram (SDMD) for boreal conifers (adapted from Weetman 2005, p. 7) with four different thinning regimes quantified by the stem number–mean volume trajectories (shown in the ln–ln-scale). The upper boundary line (solid black line) represents the maximum stand density under self-thinning with a species-specific allometric factor and exponent. The area below the line gives the scope for possible tree number–mean volume relationships. All the four trajectories 1–4 commence with dense natural regeneration, but subsequently represent different stand densities. Trajectory 1 describes un-thinned stand development yielding high total volume at low cost, but with a low mean tree volume. Trajectory 2 describes moderately dense stands established by frequent light commercial thinning to maximise volume production. In trajectory 3, a moderate pre-commercial thinning at early stand age reduces the high initial density to about half of the tree number. Trajectory 4 applies a heavy pre-commercial thinning, reducing the tree number to nearly the final level. In this context, pre-commercial is used as attribute for thinnings, which are executed in a stand development phase when stem dimensions of the removed trees are still so small that revenue does not yet cover the expense.

Bégin et al. (2001) list for a considerable number of tree species available SDMDs as guides for stand management. When those SDMDs ignore species-specific allometry but apply generalised scaling exponents, flawed density control and counter-productive thinning can result.

5.1.2 Stand Density Index by Reineke

The strength of SDI as a measure of density (cf. (17)) is that it takes mean diameter and number of tress into account (Zeide 2004). The mean diameter serves as an expression of the allometric size development of the mean tree and stand. The pure size-dependent change of tree number is eliminated by the SDI, and makes it a suitable measure for density evaluation and for comparison of stands in different stand development phases. The underlying approach for elimination of size-effects on density (cf. (17)) is analogous to the approach introduced for individual tree level in Sect. 2.2.1 (cf. (7)).

The disadvantage of the SDI is that for elimination of size-effects, it generally assumes the coefficient $\beta = -1.605$ to be valid. Wherever this allometric coefficient fails to apply, there will be severe errors in stand density estimates. This chapter shows that in untreated fully-stocked pure stands of European beech, the β-value is lower than the generalised Reineke value $\beta = -1.605$. Although the deviations from -1.605 are only close-to-significant for Sessile oak and Norway spruce, our results concerning differences among species suggest that at least one of these species' slopes differs from Reineke's generalised value, too.

If species-specific allometry is ignored, serious errors in the estimate and control of density when using the stand density index $SDI = N(25/d_q)^{-1.605}$ may be the consequence (Pretzsch and Biber 2005). The use of Reineke's rule and SDI with $\beta = -1.605$ for determination of maximum density in planning (Sterba 1975, 1981, 1987), control of stand density in the course of thinning operations or modelling of stand development (Pretzsch et al. 2002, 2008) is therefore called into question. For the SDI in Norway spruce stands, Sterba (1981), using the Bavarian yield tables for Norway spruce by Assmann and Franz (1965) and assuming $\beta = -1.605$, calculated mean values of SDI = 970, 1,081, 1,203 and 1,336 for sites with 28, 32, 36 and 40 m top height (tree height associated with the quadratic mean diameter of the 100 tallest trees in a stand) at age 100 years. These values are quoted here to illustrate the extent to which values may be biased when erroneous β-values are being used. Assuming we determine, according to Reineke, the SDI of a stand with mean diameter 10 cm to be 1,300, assuming further that this stand actually follows a straight line with $\beta = -1.805$, then the determined SDI of 1,300 would have to be reduced by $k = 0.83$. The correction of the bias would therefore signify a shift of values from the upper end (SDI = 1,300) to the lower end (SDI = 1,079) in the range of SDI values observed in Central European Norway spruce stands (Pretzsch and Biber 2005).

5.2 *Research Perspectives*

In comparison with ecophysiological and biochemical processes, which are far from being thoroughly understood, size and structure of plants are much easier to measure. Since there is a close feedback between structure and process, organisms'

size and structure can become the key for revelation and prognosis of stand dynamics. Due to the uncomplicated possibility of their spatial explicit measurement (e.g. compared with grassland and agricultural crops), organs of forest trees, whole trees, stands and communities are best suitable for revealing and tracing allometry over various levels of system organisation.

As provisional approaches for urgent upscaling climate change C-storage estimations for instance, even imprecise and inaccurate allometric relationships may be helpful. However, rest and faith in such general scaling rules would pass up the opportunity of a better understanding of ecosystem structure and functioning. Rather than continuing to search for "*the ultimate law*", further research should exploit the potential, which lies in a differentiated allometry between species, site conditions, competition, disturbances etc. in order to systemise it, integrate it in system knowledge and apply it for mechanistic understanding of plant growth.

One focus might be on a systematic revelation of plant and stand allometry with regard to different species, provenances, clones, and under varying site conditions, competitive status in pure and mixed stands and under disturbances. The concept, methods and at least a part of the data base for such an inventory are available. Methodological shortcomings of previous analysis like neglection of the dead inner core of trees, equation of individual and stand allometry, univariate description and imperfect elimination of size-effects can be considered. Maybe a plant's or stand's allometry reveals rather its tricks and traits of optimising fitness in relation to neighbours or other stands than a random deviation from a general rule. A systematic analysis, ordering and causal explanation of different allometry exponents is missing so far. A closer analysis of the species-dependency of allometric exponents and their determination by internal and external factors might provide an important link between plant genetics and physiology on the one and plant and population biology and morphology on the other hand. Allometric research should strive for a closer link to plant physiology and modelling to integrate the existing knowledge in order to find mechanistic links, causal explanations. Closer connection with stand ecology and forest dynamics would help to separate between internal and external factors and avoid to misinterpret the effect of disturbances as allometric patterns.

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