

A Unified Law of Spatial Allometry for Woody and Herbaceous Plants

H. Pretzsch

Lehrstuhl für Waldwachstumskunde, Technische Universität München, Freising, Germany

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Abstract: The objective of the present paper is to provide both proof and theoretical deduction of an overlapping, valid law of allometry for woody and herbaceous plants used in agriculture and forestry. In his attempt to find an adequate expression for stand density, independent of site quality and age, Reineke (1933^[18]) developed the following equation for even-aged and fully stocked forest stands in the northwest of the USA: $\ln(N) = a - 1.605 \cdot \ln(dg)$, based on the relationship between the average diameter dg and the number N of trees per unit area. With no knowledge of these results, Kira et al. (1953^[9]) and Yoda et al. (1957^[31] and 1963^[32]) found the boundary line $\ln(m) = b - 3/2 \cdot \ln(N)$ in their study of herbaceous plants. This self-thinning rule – also called the $-3/2$ -power rule – describes the relationship between the average weight m of a plant and the density N in even-aged herbaceous plant populations growing under natural development conditions. It is possible to make a transition from Yoda's rule to Reineke's stand density rule if mass m in the former rule is substituted by the diameter dg . From biomass analyses for the tree species spruce (*Picea abies* [L.] Karst.) and beech (*Fagus sylvatica* L.), allometric relationships between biomass m and diameter d are derived. Using the latter in the equation $\ln(m) = b - 3/2 \cdot \ln(N)$ leads to allometric coefficients for spruce (*Picea abies* [L.] Karst.) and beech (*Fagus sylvatica* L.), that come very close to the Reineke coefficient. Thus Reineke's rule (1933^[18]) proves to be a special case of Yoda's rule. Both rules are based on the simple allometric law governing the volume of a sphere v and its surface of projection s : $v = c_1 \cdot s^{3/2}$. If the surface of projection s , is substituted by the reciprocal value of the number of stems $s = 1/N$ and the isometric relationship between volume v and biomass m is considered $v = c_2 \cdot m^{1.0}$ we come to Yoda's rule $m = c_3 \cdot N^{-3/2}$ or, in logarithmic terms, $\ln(m) = \ln c_3 - 3/2 \cdot \ln(N)$.

Key words: Self-thinning, allometry, $-3/2$ -power rule, stand density rule, woody and herbaceous plants.

Introduction

The growth processes in plants lead to an increase in demands on available resources and basal area. Without treatment, stands tend to approach a maximum density quantifiable in terms of basal area of stand or plant density at given average dimensions in even-aged stands. Maximum density is related to tree species, site and the development stage of the stand. In approaching maximum density, the increase in demand on area is concomitant with a scarcity in resources and with competitive effects reflected in a characteristic decrease in the number of plants, i.e., in the so-called self-differentiating or self-thinning line.

Fig. 1 is a schematic representation of the relationship between plant dimensions and density on the log–log scale. The upper self-thinning line or limiting boundary line (dark line) marks the possible maximum density for a species at a given size or weight per plant 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 sub-optimum growth conditions. In accordance with growth and mortality, the density–dimension relationships in stands A and B approximate their corresponding stand-specific self-thinning lines and subsequently deviate from this line, at different absolute levels, with similar gradients. Under optimum growth conditions, the upper boundary and self-thinning lines may coincide (stand A). Sub-optimum site conditions, however, may also cause the self-thinning line to be positioned more or less distinctly below the upper boundary line (stand B).

Based on Galilei's principle of the similarity of forms biologists, Spencer (1864^[22]) and Thompson (1917^[26]) introduced the allometric relationships between linear extension, demand on area, basal area consumption, stand density and biomass of organisms. Bertalanffy (1951^[2]) uses the allometric principle to model changes in the forms of plants and animals. Yoda, Kira, Ogawa and Hozumi (1963^[32]) found a characteristic decrease in plant weight with increasing numbers of plants per unit area for herbaceous plants from which they derived the $-3/2$ -self-thinning rule. By establishing an allometric relationship, using the coefficient $-3/2$, between the biomass m per plant and the number N of plants per unit area in even-aged stands at maximum density, this rule combines production and population ecological aspects ($m \propto N^{-3/2}$). Numerous authors con-

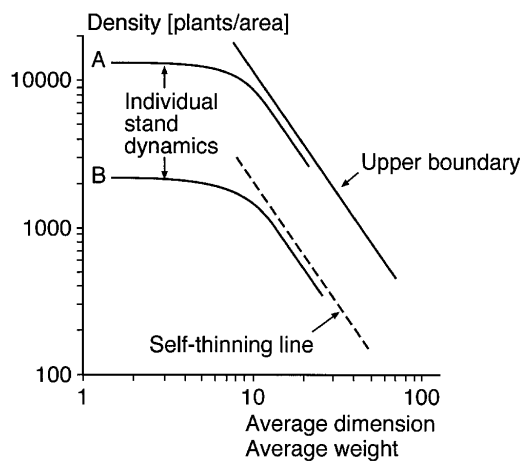


Fig. 1 Common principle of Reineke's rule (1933^[18]) and the $-3/2$ -self-thinning rule of Yoda et al. (1963^[32]).

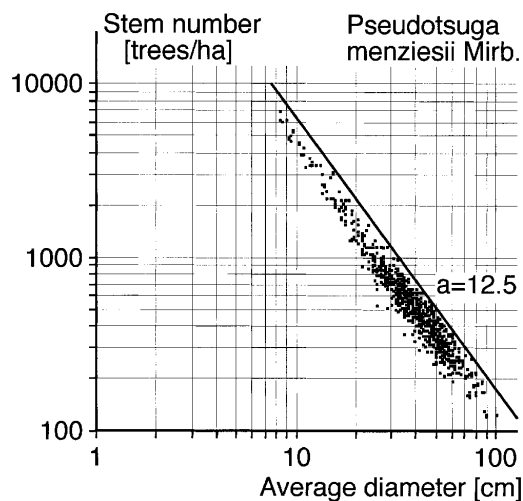


Fig. 2 Relationship between number of trees per hectare and the average diameter for even-aged Douglas fir stands (*Pseudotsuga menziesii* Mirb.) based on inventory data for Washington and Oregon. Shown is the line for the upper limit $\ln(N) = a - 1.605 \cdot \ln(dg)$ with intercept $a = 12.5$ and slope -1.605 (according to Reineke, 1933^[18]).

sider this the most important rule, or even the law with the greatest significance in population biology. Investigations on a variety of plant species provided ample proof of its validity (Harper, 1977^[8]; Weller, 1987^[27], 1990^[28]). Since the 1980s the general validity of this rule was repeatedly called into question (White, 1981^[29]; Zeide, 1987^[33]; Niklas, 1994^[13]). Recent studies, inter alia by Whittington (1984^[30]) and Sackville Hamilton et al. (1995^[20]) propose a more general version of the self-thinning rule, making it possible to retain the original basic allometric relationships, but also including further determining and explanatory parameters and allometric coefficients.

The stand density rule for forest stands had been established by Reineke (1933^[18]) a long time before Yoda et al. (1963^[32]). In forest growth research it has gained considerable importance in data inventory, analysis and modelling (Bergel, 1985^[1]; Franz, 1968^[7]; Sterba, 1975^[23], 1981^[24], 1987^[25]; Pretzsch, 2001^[17]). In analogy to Yoda's rule, the rule proposed

by Reineke describes the allometric relationship between tree dimension and the number of trees per unit area. It is based on stem diameter at height 1.30 m, easily determinable in forestry practice. In the discussions about the validity of Yoda's rule, Reineke's rule is hardly ever mentioned. The present paper therefore aims at demonstrating the common ground between Reineke's and Yoda's rule. Here, the empirically established rule by Reineke is derived theoretically from the spatial allometric laws for stereometric spheres. To demonstrate the validity of the tendencies in Reineke's rule and to diagnose specific deviations of actual stand developments from this rule, the average diameter–stem number trajectories from 327 treated test plots in spruce (*Picea abies* [L.] Karst.), beech (*Fagus sylvatica* L.), pine (*Pinus sylvestris* L.) and oak stands (*Quercus petraea* [Mattuschka] Liebl.) under long-term observation were evaluated.

The study aims at making a contribution to the Sonderforschungsbereich SFB 607 of the Deutsche Forschungsgemeinschaft (Special Research Department of the German Research Community), which focuses on the sequestration strategies of woody and herbaceous plants cultivated in agriculture and forestry (Matyssek and Elstner, 1997^[11]). The proof and the theoretical deduction of an overlapping, valid law of allometry dealt with in this paper allow a connection to be made between woody and herbaceous plants, between aspects of production ecology and population ecology, and between the allometry of individual development and stand development.

Reineke's Stand Density Rule (1933^[18])

In his search for a means of measuring stand density independent of site class and age, Reineke (1933^[18]) discovered the stand density rule for maximum stocked even-aged stands in the northwest of the USA. It describes the relationship between average diameter dg and the number of stems per unit area in fully stocked and non-managed stands which takes the form

$$N = e^a \cdot dg^{-1.605} \quad (1)$$

which may be represented as a straight line on the log–log scale:

$$\ln(N) = a - 1.605 \cdot \ln(dg) \quad (2)$$

with intercept a and slope -1.605 . This implies, for fully stocked, non-thinned stands, that with increasing average diameter dg , the number N of stems is reduced by the allometric constant -1.605 . Reineke obtained this result by representing inventory data from naturally grown observation plots on the log–log scale using paired values for average diameter and number of stems per area. On the basis of inventory data, Reineke proceeded to determine a boundary line in the form of a straight line with slope -1.605 (Fig. 2). As there were merely slight variations for different tree species, stand structures and sites, Reineke postulated the general validity of this allometric constant -1.605 , independent of tree species and site, for fully stocked even-aged forest stands.

Reineke's rule (1933^[18]) is founded on the statistical evaluation of inventory data from observation areas. The fact that the temporal development of the number of stems per hectare

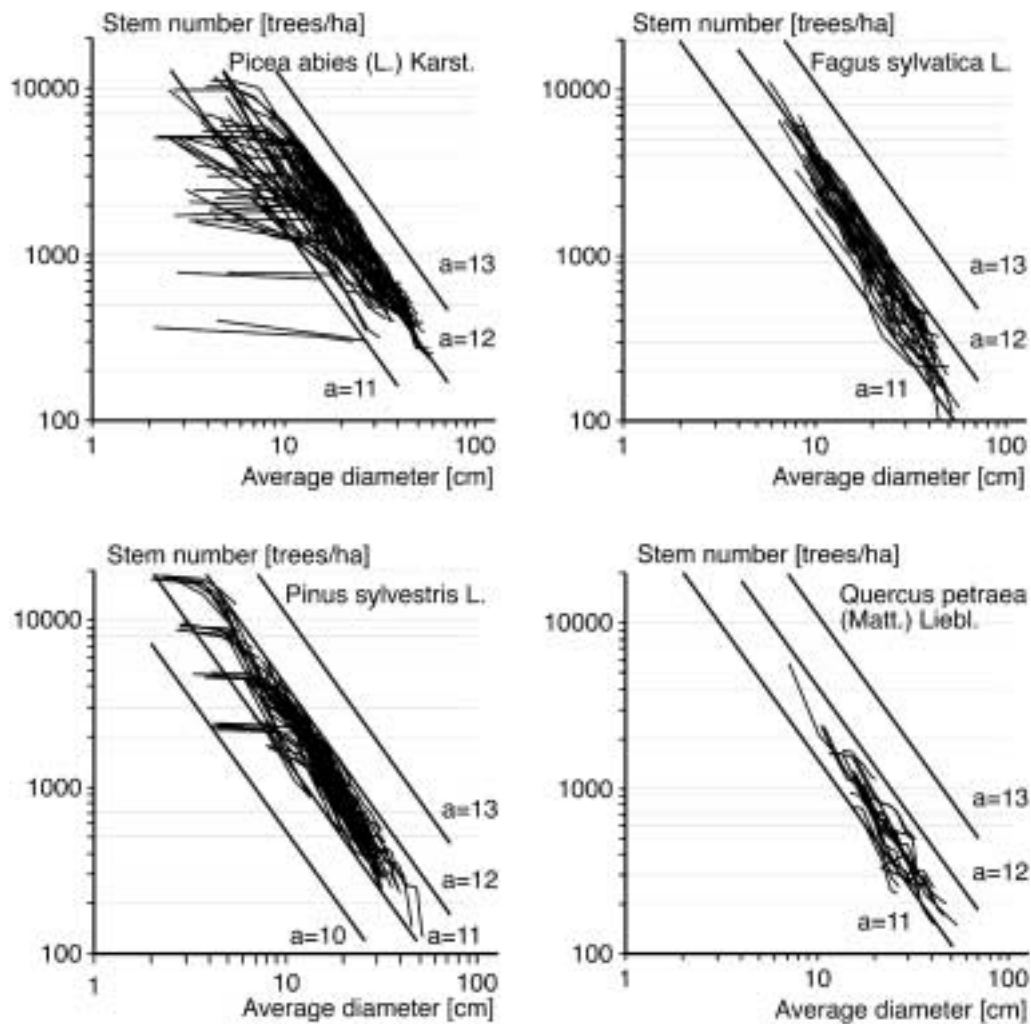


Fig. 3 Development of spruce (*Picea abies* [L.] Karst.), beech (*Fagus sylvatica* L.), pine (*Pinus sylvestris* L.) and oak (*Quercus petraea* [Mattuschka] Liebl.) stands in south Germany according to the stand density rule of Reineke (1933^[18]). Independent of the initial stand density, the diameter–stem number trajectories approximate an upper line. Plotted on the log–log scale, this may be represented by a straight line with the coefficient of slope -1.605 .

plotted against the average diameter also follows Reineke's rule is shown in Fig. 3 for long-term experimental plots in south Germany (Pretzsch, 2000^[16]). The graphs reveal that, independent of their initial density, spruce (*Picea abies* [L.] Karst.), pine (*Pinus sylvestris* L.), beech (*Fagus sylvatica* L.) and oak (*Quercus petraea* (Mattuschka) Liebl.) stands approximate the limiting boundary line between number of stems per hectare and average diameter, and subsequently, again largely in accordance with Reineke's rule, regress in the number of stems. The absolute level at which this decrease occurs and which is reflected in the position of the straight line depends on the overall growth potential of stand sites. The theoretical straight lines with slope -1.605 , drawn in each of the graphs, describes the decrease in the number of stems to be expected according to Reineke's Stand Density Rule (1933^[18]) for self-thinning in untreated stands under site conditions ranging from unfavourable to excellent ($a = 10$ to $a = 13$).

The 120 spruce (*Picea abies* [L.] Karst.) test plots, aged between 11 to 166 years, represented in Fig. 3 (upper left), are mainly located in the Bavarian Alps, the south Bavarian lowlands, Swabia and the Franconian plateau. Some of these plots have been under observation since 1882, with a scattering in mean diameters of stems of between 2.1 cm and 60.7 cm, while the

number of stems range from 232 to 12 899 trees per hectare and the basal areas from 0.1 to 92.3 m² per hectare.

Beech (*Fagus sylvatica* L.) is represented on the basis of 32 plots, mainly from Lower Franconia, under observation since 1980, with tree age ranging from 33 to 219 years (Fig. 3, upper right). Here, average diameters range from 5.7 to 71.8 cm, stem numbers from 92 to 11 242 trees per hectare, and basal areas from 13.03 to 53.35 m² per hectare. In the past few decades a positive effect on the average diameter was recorded for spruce (*Picea abies* [L.] Karst.) and beech (*Fagus sylvatica* L.), which signifies an increase in potential stand density and reflects the improvement of site conditions on these areas. This trend also becomes quite obvious when plotting basal area of the stand over average diameter (Fig. 4), with the former calculated from the average diameters and number of stems per hectare shown in the graphs of Fig. 3. On many plots the basal areas of spruce (*Picea abies* [L.] Karst.) and beech (*Fagus sylvatica* L.) stands are in the process of achieving new, hitherto unexpected peak values (Pretzsch, 1999^[15]).

The representation for pine (*Pinus sylvestris* L.) involves 152 test plots, mainly from central and northeast Bavaria, the oldest of which have been under observation since the spring of

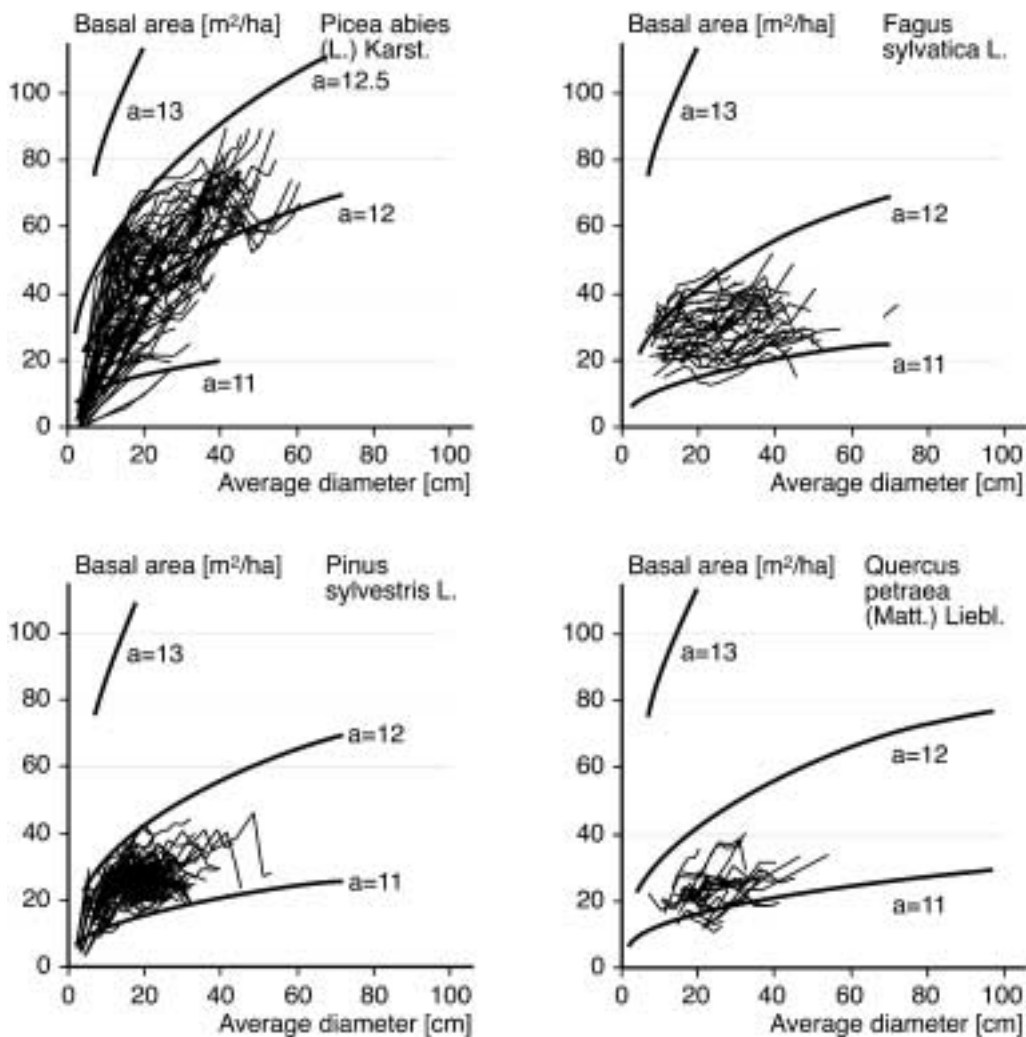


Fig. 4 Observation of basal areas of stands in relation to average diameter on long-term experimental plots stocking spruce (*Picea abies* [L.] Karst.), beech (*Fagus sylvatica* L.), pine (*Pinus sylvestris* L.) and oak (*Quercus petraea* [Mattuschka] Liebl.) in south Germany. The reference curve shows the basal area–average diameters resulting from the Reineke equation $\ln(N) = a - 1.605 \cdot \ln(dg)$, using varying values from $a = 11$ to 13.

1900. Ages range from 12 to 152 years, basal areas of stands comprise 3.12 to 53.3 m² per hectare and numbers from 127 to 18 606 trees per hectare, with a spectrum of average diameters ranging from 2.0 to 53.0 cm.

Oak (*Quercus petraea* [Mattuschka] Liebl.) representation is based on 23 plots from northern Bavaria, some of which have been observed since 1900 and are 38 to 360 years old. Stand data range from 45 to 5662 trees per hectare, average diameters from 7.1 to 84.4 cm, and basal areas from 10.68 to 40.40 m² per hectare.

On account of the great length of the observation periods and the wide range of sites, this data material may be considered unique and provides proof that growth processes on long-term test areas approximate Reineke's rule, as reported by the Bavarian Network for Long-term Experimental Plots. In the trajectory bundles representing average diameter over number of stems it is the untreated plots and those thinned according to the A-degree (slight thinning from below) that determine the limiting boundary line.

The $-3/2$ -Self-Thinning Rule of Yoda et al. (1963^[32])

With no knowledge whatsoever of the stand density rule of Reineke (1933^[18]), Kira et al. (1953^[9]) and Yoda et al. (1957^[31] and 1963^[32]) discovered a similar boundary line in their investigations of herbaceous plants. Their self-differentiating or self-thinning rule, also called the $-3/2$ -power rule or Yoda's rule, describes the relationship between the average weight m and the density N in even-aged plant populations under natural growth conditions. Kira et al. (1953^[9]) and Yoda et al. (1957^[31] and 1963^[32]), followed by Harper (1977^[8]) and Weller (1987^[27]) assumed the following relationship for herbaceous plants and shrubs:

$$m = e^b \cdot N^{-3/2} \quad (3)$$

or, in logarithmic form

$$\ln(m) = b - 3/2 \cdot \ln(N) \quad (4)$$

where the average plant weight m and plant density N (number of plants per unit area) are shown to have an allometric relationship, with the coefficient of allometry $-3/2$. The parameter b for the position of the curve, in turn, represents

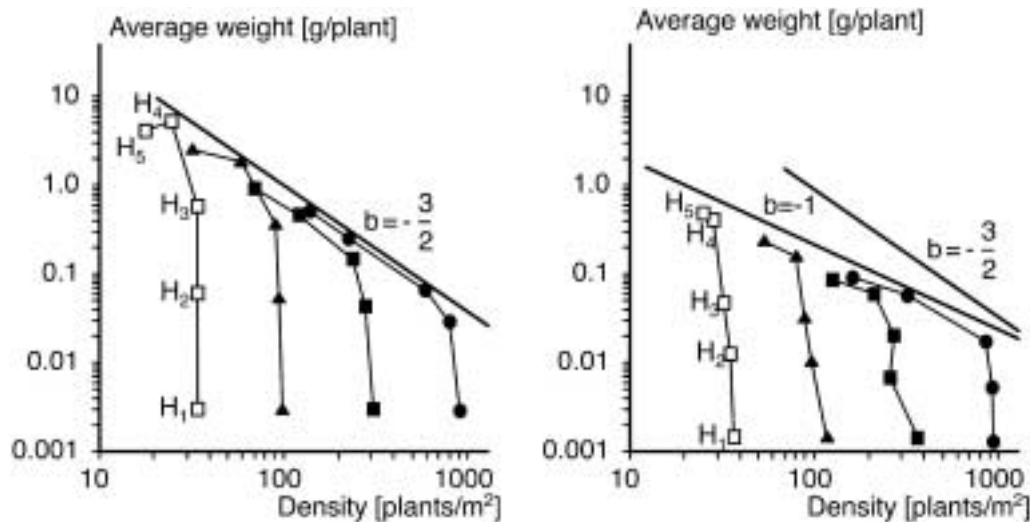


Fig. 5 Development of the relationship between density (plants/square meter) and average weight (g/plant) in stands of *Lolium perenne* L. of varying densities, with a full light regime (left) and at 30% full light (right). The points H₁, H₂ etc. represent successive stages of development (according to Harper, 1977^[8]).

an isometric constant, while e^b stands for the intercept and position of the line. Given undisturbed development, the start of self-thinning is followed by a population development along the “self-thinning line” or $-3/2$ -line, when plotting the average plant weight m and the plant density N on the log-log scale (Fig. 5, left). Contrary to Reineke, the authors derived this rule not by evaluating inventory data and artificial time series, but by monitoring the weight–density relationships of short-rotation stands of herbaceous plants plotted over time.

Harper (1977^[8]) shows numerous model examples for population developments according to the $-3/2$ -self-thinning rule. However, he also draws attention to deviations from this rule in cases where light and nutrient resources were reduced. Thus, in full daylight, the English rye grass (*Lolium perenne* L.) follows the $-3/2$ -self-thinning rule (Fig. 5, left). Based on four different original stand densities at state H₁, the trajectories (H₁-H₂-H₃-H₄-H₅) approximate the self-thinning line with the slope $-3/2$ with progressive stand development, i.e., initially the average weight per plant increases, independent of the original number of plants. With the approximation to the upper boundary line, a slowing down in the rate of weight increase is noted and mortality processes occur, so that the four stands start using different strategies to exploit available resources: many, rather light-weight, plants compete with a few heavy-weight ones in the more or less dense grassy stand. If the light supply is reduced (Fig. 5, right) the possible weight decreases with given plant density, or, conversely, less plants with a given size or given weight per unit area will be able to find adequate living conditions. A reduction in daylight by 70% will result in a limiting boundary line with a slope of -1.0 , whereas it would be $-3/2$ under full light conditions. Figs. 3 and 4 also reveal a marked displacement of the upper boundary line based on specific site conditions.

The Stand Density Rule of Reineke (1933^[18]) as a Special Case of the Self-Thinning Rule of Yoda et al. (1963^[32])

A transition from the $-3/2$ -self-thinning rule of Yoda et al. (1963^[32]) $\ln(m) = b - 3/2 \cdot \ln(N)$ to Reineke’s stand density rule $\ln(N) = a - 1.605 \cdot \ln(dg)$ becomes possible if mass m is replaced by a function of stem diameter d . The allometric func-

tion $m = k \cdot d^r$ with the isometric constant k and slope r (= allometric coefficient) proved suitable for this purpose. If we replace m in formula 4 by $k \cdot d^r$, we get $\ln(k \cdot d^r) = b - 3/2 \cdot \ln(N)$ and by rearrangement of the equation $\ln(N) = -2/3 \cdot (\ln[k] + r \cdot \ln[d] - b)$ and finally $\ln(N) = -2/3 \cdot (\ln[k] - b) - 2/3 \cdot r \cdot \ln(d)$. In the last-mentioned equation we identify $-2/3 \cdot (\ln[k] - b)$ as intercept and call it c , the product $-2/3 \cdot r$ represents the slope that can be estimated using empirical data.

On the basis of biomass analyses from Ellenberg et al. (1996^[3]) and Pellinen (1986^[14]), Meschederu (1997^[12]) parameterized the allometric relationships $m = k \cdot d^r$ between aboveground biomass m and stem diameter d at a height of 1.30 m. From regression analysis for spruce (*Picea abies* [L.] Karst.) and beech (*Fagus sylvatica* L.), respectively (see Fig. 6), this resulted in

$$m = 0.0442 \cdot d^{2.6597} \tag{5}$$

$$m = 0.1143 \cdot d^{2.5030} \tag{6}$$

Using mass m , described in formula 5, as a function of diameter d in the relationship $\ln(m) = b - 3/2 \cdot \ln(N)$, this would result in

$$\ln(N) = c - 1.773 \cdot \ln(d) \tag{7}$$

for spruce (*Picea abies* [L.] Karst.) ($-2/3 \cdot r = -2/3 \cdot 2.6597 = -1.773$) and in

$$\ln(N) = c - 1.669 \cdot \ln(d) \tag{8}$$

for beech (*Fagus sylvatica* L.) ($-2/3 \cdot r = -2/3 \cdot 2.5030 = -1.669$).

The intercept of the straight line equation has been compacted into the isometric constant c ($c = -2/3 \cdot [\ln(k) - b]$) and the slope results from $-2/3 \cdot r$. In this case, the only points of interest are the calculated coefficients of allometry -1.773 and -1.669 . These come very close to the value Reineke found empirically. The rule established by Reineke (1933^[18]) thus proves to be a special case of the self-thinning rule of Yoda et al. (1957^[31] and 1963^[32]). Proceeding from the premise that the $-3/2$ rule is valid, species-specific deviation from the Reineke

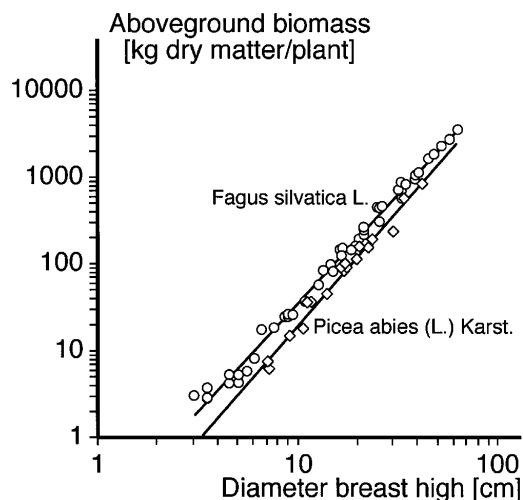


Fig. 6 Allometry between breast height diameter and aboveground biomass for spruce (*Picea abies* [L.] Karst.) and beech (*Fagus sylvatica* L.). The allometric relationships for spruce (*Picea abies* [L.] Karst.) and beech of $m = 0.0442 \cdot d^{2.6597}$ and $m = 0.1143 \cdot d^{2.5030}$, respectively, were derived by Meschederu (1997^[12]) from data of Ellenberg et al. (1996^[3]) and Pellinen (1986^[14]).

constant -1.605 may obviously be explained by the species-specific diameter–biomass relationships of tree species, e.g., caused by the species and age-dependent variation of wood density. For spruce (*Picea abies* [L.] Karst.), the slope value -1.773 derived in this manner comes close to the coefficient -1.737 calculated by Sterba (1987^[25]) or -1.75 found by Del Río et al. (2001^[19]) from their comprehensive evaluation of test areas.

Derivation of the $-3/2$ -Self-Thinning Rule from the Spatial Allometry of the Sphere

The rules established by Reineke (1933^[18]) and Yoda et al. (1957^[31] and 1963^[32]) have a common theoretical background. Both rules are based on the same simple and unambiguous allometric relationship that exists between volume, surface of projection and surface of stereometric bodies, such as e.g., the sphere.

The following allometric relationship exists between the volume $v = 4/3 \cdot \pi \cdot r^3$ and the surface of projection $s = \pi \cdot r^2$ of a sphere with radius r

$$v = c_1 \cdot s^{3/2} \text{ with } c_1 = \frac{4}{3\sqrt{\pi}} = 0.75225 \dots \quad (9)$$

The basal area s may be substituted by the reciprocal of the number of stems $s = 1/N$, as any given unit area of 1.0 will accommodate $N = 1/s$ trees. Conversely, an average basal area may be calculated by dividing the unit area by the number of trees N . After substituting s by the reciprocal of the number of stems, we derive from formula (9)

$$v = c_1 \cdot N^{-3/2}. \quad (10)$$

On account of the isometry between volume and mass $v = c_2 \cdot m^{1.0}$ the result is the self-thinning rule of Yoda $m = c_3 \cdot N^{-3/2}$ or, in logarithmic form $\ln(m) = \ln(c_3) - 3/2 \cdot \ln(N)$.

Here, c_1 to c_3 again stand for the isometric constants which act as multipliers, but have no effect on the allometric relationships under discussion.

Discussion

For even-aged, fully stocked stands in the northwest of the USA, Reineke (1933^[18]) found the relationship $\ln(N) = a - 1.605 \cdot \ln(dg)$ between the average diameter d and the number N of trees per hectare. Without any knowledge of these results, Kira et al. (1953^[9]) and Yoda et al. (1957^[31] and 1963^[32]), in their investigations of herbaceous plants, came across the boundary line $\ln(m) = b - 3/2 \cdot \ln(N)$. This self-thinning rule – also known as the $-3/2$ -power rule – describes the relationship between the average plant weight m and the density N in even-aged plant populations, given natural development. A transition is possible from Yoda's rule $\ln(m) = b - 3/2 \cdot \ln(N)$ to Reineke's stand density rule $\ln(N) = a - 1.605 \cdot \ln(dg)$, if mass m in the former rule is considered a function of the diameter dg . The coefficients of allometry calculated in this manner come very close to the coefficient found by Reineke. The rule established by Reineke (1933^[18]) thus represents a special case of Yoda's rule. Both rules are based on the same simple and unequivocal allometric law governing the volume of a sphere v and its surface of projection s , i.e., $v = c \cdot s^{3/2}$, with $c = \frac{4}{3\sqrt{\pi}} = 0.75225 \dots$; the same coefficient of allometry of $3/2$ is valid for the relationship between volume and surface area of a sphere. With increasing surface of projection or basal area s , the volume v of the sphere rises according to the progression governed by the allometric constant $3/2$. Assuming that the same allometric relationship as for a sphere exists between the volume of a tree v and the requisite basal area s , assuming, furthermore, that tree volume v is proportional to the weight of the tree m , i.e., $m = v \cdot \text{constant}$, we arrive at Yoda's rule. The coefficients of allometry in Yoda's and Reineke's rules are both therefore derived, theoretically from the spatial allometry of stereometric bodies, and empirically from the stand development on permanent observation plots.

The analogy with the stereometry of a sphere is interpreted in Fig. 7 as follows: let us proceed from the abstract concept that plants with their root system form spheres, which are densely packed and arranged on a plane, the weight and demands on basal area of which increase steadily with progressive growth from state A to D. It then follows that less and less objects will find room on an area of 10×10 m. With the increase in sphere volume from 0.13 to 1.02 (Figs. 7A,B) and 8.18 to 65.44 m³ (Figs. 7C,D), the possible density of spheres decreases from 2.56 spheres per m² (Fig. 7A) via 0.64 (Fig. 7B) and 0.16 down to 0.04 spheres per m² (Figs. 7C,D). As the relationship between volume of the sphere and density follows the equation $\ln(\text{volume}) = -0.65 - 3/2 \cdot \ln(\text{density})$, the relationship can be considered to be of an allometric nature, similar to the relationships between the change in dimensions and density in even-aged stands found by Yoda and Reineke. The decrease in the number of possible spheres per area with increasing volume of the sphere therefore follows the same gradient as the decrease in the number of possible trees with rising tree volume or biomass, in the course of stand development.

The spatial allometric relationship between area consumption and volume or weight of stereometric bodies may therefore be considered a scale-overlapping law which is based on the di-

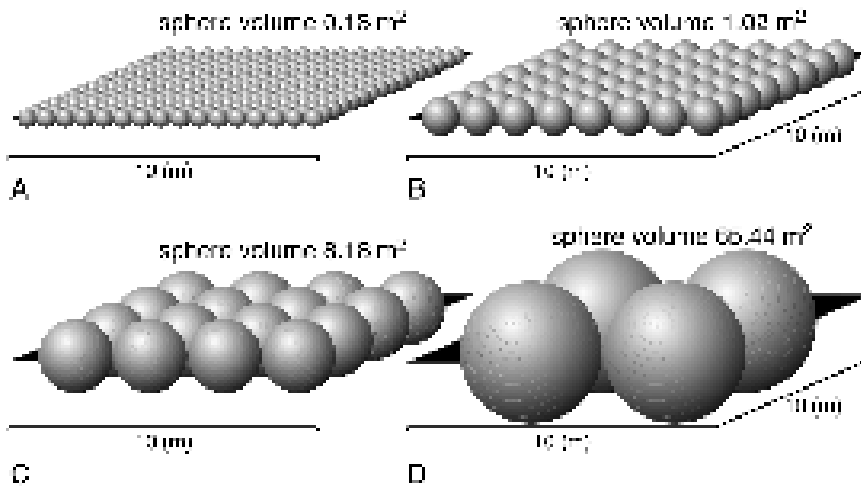


Fig. 7 The decrease in density in forest stands on account of the self-thinning process may be illustrated by drawing an analogy to the stereometric relationships of a sphere on an area of 10×10 m. The spatial allometry between the variations in volume and density in plants is similar to that in spheres, where the decrease in volume per unit area at a density to the power of -1.5 is expressed by the equation $\text{volume} = \text{constant} \cdot \text{density}^{-3/2}$.

mension–growth area relationship of individual plants and thus approximates the density–dimension relationships of stands. At the same time, this allometric relationship has an obviously systems-overlapping validity. The rules by Yoda and Reineke, separately developed for herbaceous and woody plants from agriculture and forestry, represent identical strategies for sequestration. Yoda’s rule was repeatedly verified for annual plants and trees (Silvertown, 1992^[21]). In the present paper Reineke’s rule is successfully derived from Yoda’s rule and proof is given of the fundamental validity of Reineke’s rule. Data material from the Network of Long-Term Experimental Plots in Bavaria was used, a data base that is considered unique as regards length of observation time and spatial representation (Pretzsch, 2000^[16]).

The combination of rules by Reineke and Yoda is designed to serve forestry purposes over and above satisfying a widespread interest in adding to existing knowledge in forestry sciences. Once maximum density is known, its dependence on tree species, site and development phase, it will be possible to calculate the potential performance of a stand if and when it comes under management (Franz, 1965^[5], 1967^[6] and 1968^[7]; Sterba, 1975^[23] and 1981^[24]). The position parameter a of the Reineke equation rises with increasing site quality and may be used to predict the potential yield of a stand (Bergel, 1985^[1]). The knowledge of the self-thinning line as the biological upper limit makes it possible to quantify density (Reineke, 1933^[18]; Kramer and Helms, 1985^[10]). Thus, descriptions of stand density using the percent stocking density p and the stand density index (SDI) are founded in Reineke’s rule. Furthermore, the self-thinning rule is a useful reference on which to base model descriptions of self-thinning processes and the prediction of mortality processes (Harper, 1977^[8]), as well as the diagnosis of disturbance factors and the validation of stand growth models (Pretzsch, 1999^[15] and 2001^[17]).

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H. Pretzsch

Lehrstuhl für Waldwachstumskunde
Technische Universität München
Am Hochanger 13
85354 Freising
Germany

E-mail: h.pretzsch@lrz.tum.de

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