A Re-Evaluation of Reineke's Rule and Stand Density Index

Hans Pretzsch and Peter Biber

Abstract: The self-thinning rule established by Reineke in 1933, $N \propto d^{-1.605}$ (N, d = number of stems and quadratic mean diameter, respectively) assumes the same allometric relationship between size and density for a wide spectrum of species under self-thinning conditions. We re-evaluate this rule based on 28 fully stocked pure stands of common beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* [L.] Karst.), Scots pine (*Pinus sylvestris* L.), and common oak (*Quercus petraea* [Mattuschka] Liebl.) in Germany that date back to the year 1870. OLS regression of the model $\ln(N) = a + b \cdot \ln(d)$ results in b values of -1.789 for common beech, -1.664 for Norway spruce, -1.593 for Scots pine, and -1.424 for common oak. The allometric coefficient for common beech differs significantly from the other species. There is also a significant difference between the b values of Norway spruce and common oak. Except for Scots pine, the above allometric coefficients deviate significantly (common beech) and close-to-significantly (Norway spruce, common oak) from the coefficient -1.605 postulated by Reineke in 1933. To cover the species–specific oscillation of mortality rates, we additionally calculate the self-thinning coefficient for each survey period. Ecological implications of the species-specific scaling exponents are stressed and consequences regarding tools for regulating stand density are discussed. FOR. SCI. 51(4):304–320.

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A S PLANTS GROW IN SIZE their demands on resources and growing space increase. If resources are no longer adequate for all stand components, self-thinning will be initiated and the number of plants (N) per unit area will decrease. The size–density allometry of plants under self-thinning is particularly informative under eco-physiological and production economics aspects because, under self-thinning conditions, size–density allometry reveals the species-specific, critical demand on resources and growing space of average trees at a given mean size. This article therefore focuses on the allometry between tree number per unit area N and quadratic mean diameter d ($N \propto d^r$). The allometric rules postulated by Reineke (1933) and Yoda et al. (1963) assume that the allometry between size and density is the same for a wide spectrum of species. Previous investigations tried to validate the rules from Yoda and Reineke for herbaceous and woody plants and usually relied on artificial time series or inventories (Harper 1977, Pretzsch 2002a, Weller 1987, 1990). By contrast, the present article proceeds from the hypothesis that size–density allometry is species-specific and may even be the essential reason for variations in the competitive powers of the main Central European tree species such as common beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* [L.] Karst.), Scots pine (*Pinus sylvestris* L.), and common oak (*Quercus petraea* [Mattuschka] Liebl.). We agree with Baz-zaz and Grace (1997) that, if these species-specific differences are ignored, then the way toward a morphologic-allometric understanding of the competitive mechanisms of tree species in pure and mixed stands will remain obstructed. The evaluation is based on real stem number-diameter-time series in 28 fully stocked pure stands in Germany that date back to the year 1870. This unique database was used to answer the following questions: (1) Are there species-specific differences in the allometric coefficient b of the model $\ln(N) = a + b \cdot \ln(d)$, (2) Do the calculated b values deviate significantly from the b value of -1.605 postulated by Reineke, and (3) Are any oscillations of the allometric constant $r = \Delta N/N \div \Delta d/d$ species-specific? Ecological implications of the individual species self-thinning process are stressed and consequences regarding tools for assessing, regulating, and scheduling stand density are discussed.

Background

Allometry

The principle of the similarity of forms postulated by Galileo Galilei was transferred to allometric relationships among the length, surface, content, and biomass of organisms or their organs by Spencer (1864) and Thompson (1917). Bertalanffy (1951) uses the allometric principle to

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model changes in the shapes of plants and animals. Hence, the relative growth rate of a defined organ y has a constant relationship with that of any other part of its body or to the entire body x, so that

$$\frac{dy}{y} = b \cdot \frac{dx}{x}. \tag{1}$$

The integral of this equation reads $y = a \cdot x^b$ or, in logarithmic terms $\ln(y) = \ln(a) + b \cdot \ln(x)$, where a is the integration constant and b the allometric coefficient. The integration constant a denotes the value y with $x = 1$. The allometric coefficient a describes the slope of the allometric straight line when plotted on the ln–ln scale (Figure 1). The physiological interpretation of allometric equations for which Bertalanffy (1951) saw great application potential in morphology, biochemistry, pharmacology, and comparative anatomy can be illustrated by transforming Equation 1 into

$$\frac{dy}{dx} = b \cdot \frac{y}{x}. \tag{2}$$

Here, allometry is considered the result of the distribution of resources absorbed by an organism to its organs y and x. The distribution key is based on the proportions between y and x and on the allometric coefficient b, which represents the distribution constant.

Allometry under Self-Thinning

Although the principle of allometry was derived from individual-based considerations, it can be applied meaningfully to plant communities under self-thinning conditions (Kira et al. 1953, Yoda et al. 1963). Figure 1 is a schematic representation of the relationship between average plant size and density on the ln–ln scale. The upper self-thinning or limiting boundary line (solid line) marks the possible maximum density for a species at given size or weight per plant
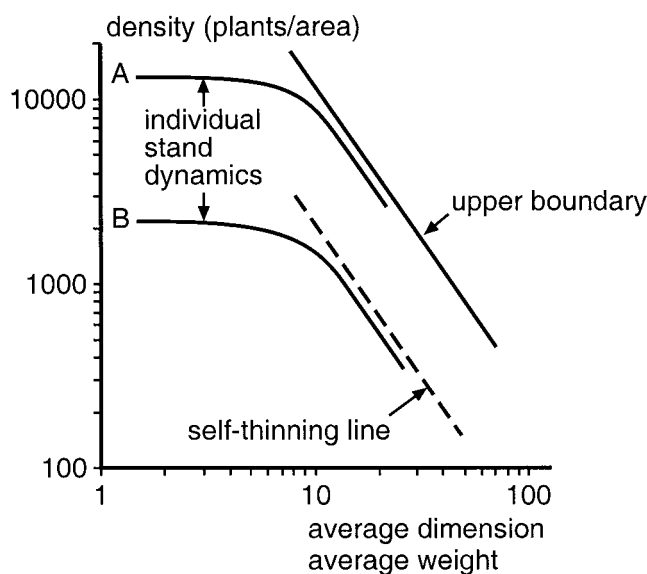

Figure 1. Common principle of Reineke's rule (1933) and the −3/2 power law by Yoda et al. (1963).

in even-aged pure stands under optimal site conditions. The lower self-thinning line (dashed line) marks the characteristic boundary relationship for any stand under suboptimal 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 optimal growth conditions, the upper boundary and self-thinning lines may coincide (stand A). Suboptimal site conditions, however, may also cause the self-thinning line to be positioned more or less distinctly below the upper boundary line (stand B).

The Stand Density Index by Reineke (1933) is based on the relationship between quadratic mean diameter d and number of stems N per unit area in fully stocked and nonmanaged stands by the equation

$$N = a \cdot d^{-1.605}, \tag{3}$$

which can be represented on the ln–ln scale as a straight line

$$\ln(N) = a' - 1.605 \cdot \ln(d), \tag{4}$$

with intercept $a' = \ln(a)$ and slope -1.605. Reineke obtained this result by using pairs of variates for quadratic mean diameter and number of stems per unit area from untreated inventory plots in the United States and representing them on the ln–ln scale. Because there were merely slight variations in various tree species, stand structures, and sites, Reineke attributed a general validity to the allometric coefficient $b = -1.605$ for fully stocked, even-aged forest stands, regardless of tree species and site. Reineke's rule has gained considerable importance for the quantification and control of stand density and modeling of stand development in pure (Bergel 1985, Ducey and Larson 1999, Long 1985, Newton 1997, Pretzsch 2001, Puettmann et al. 1993, Sterba 1975, 1981, 1987) and mixed (Puettmann et al. 1992, Sterba and Monserud 1993) stands. Reineke (1933) used the allometric coefficient $b = -1.605$ to develop his stand density index SDI $= N \cdot (25.4/d)^{-1.605}$. The SDI describes the density of stands with quadratic mean diameter d and number of trees per hectare N by calculating the number of stems per hectare in these stands related to 10 inches mean diameter ($= 25.4$ cm; 1 in. $= 2.54$ cm). In Europe, an index diameter of 25 cm is used, so that

$$\text{SDI} = N \cdot (25/d)^{-1.605}. \tag{5}$$

With no knowledge whatsoever of the stand-density rule by Reineke (1933), Kira et al. (1953) and Yoda et al. (1963) discovered a similar boundary line in their studies of herbaceous plants. Their 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) and Yoda et al. (1963), followed by Harper (1977) and Weller (1987), assumed the following relationship for herbaceous plants and shrubs: $m = a \cdot N^{-3/2}$. Although Yoda's rule incorporates the mean

aboveground biomass *m* of plants, Reineke (1933) made use of the easily determinable quadratic mean diameter, *d*, at height 1.30 m. Reineke's rule represents a special case of Yoda's law when $\Delta m/m \div \Delta d/d = 2.4075$, i.e., m $\propto d^{2.4075}$ (Pretzsch 2002a, Smith and Hann 1984).

Due to practicability, there is a flaw in Reineke's relationship that does not touch Yoda's rule. Because *d* is measured at a fixed tree height (1.30 m), it is not a fundamental scale of the trees. Thus, at different tree heights, *d* will be measured at different relative and therefore functional positions along the stem. For a very small tree (but taller than 1.30 m), *d* would be measured somewhere in the crown; for a very tall tree, *d* would be located in the root collar. For trees shorter than 1.30 m, which clearly have significant biomass and space requirements, *d* is not even defined. Nevertheless, when dealing with tree dimensions, which are normally measured on classical growth and yield research plots and which are relevant for applying Reineke's rule in practice, this problem does not become significant. At these tree dimensions, the position of *d* will stay mostly in the parts of the stem, where its taper is smallest. If not, the empirical finding that ln(*N*) and ln(*d*) are connected linearly for unthinned stands would be rather improbable.

Stand dynamics under self-thinning conditions is particularly informative under ecophysiological and production economics aspects. It reveals the species-specific critical demand on resources and growing space of average trees at given size. If mean horizontal growing space *s* ($s = 1/N$) falls below a critical limit, then this will cause the self-thinning process to start. The allometric coefficient *b* describing the relationship between density *N* and average plant size *d* ($N \propto d^{b}$) reflects the species-specific self-tolerance (Zeide 1985) and effectiveness of space sequestration. Taking the antilogarithm and deriving Reineke's equation (Equation 4) leads to $\Delta N/N \div \Delta d/d = -1.605$. This relationship transfers the allometric principle (Equation 1) to the relationship between average tree size (*d* = quadratic mean tree diameter) and stand density (*N* = number of trees per area). For instance, a *b* value of -1.605 would mean that a relative increase in quadratic mean diameter of 1% is concomitant with a decrease in the number of stems of -1.605%. For the mean growing space (*s*), we can use the reciprocal of the number of stems $s = 1/N$, because a given unit area can accommodate $N = 1/s$ trees. The relationship $N \propto d^{b}$ then becomes $1/s \propto d^{b}$ or $s \propto d^{-b}$ and $d \propto s^{-1/b}$. Differentiation of the latter term leads to $\Delta d/d \div \Delta s/s = -1/b$ and quantifies the effectiveness of space sequestration of an average tree in the stand. A *b* value of -1.605 signifies that an increase in growing space $\Delta s/s$ of 1% would result in a relative increase of quadratic mean diameter $\Delta d/d$ of merely 0.62305% ($-1/b = 0.62305$).

Data

This investigation is based on nine experimental plots in common beech (*Fagus sylvatica* L.), nine in Norway spruce (*Picea abies* [L.] Karst.), six in Scots pine (*Pinus sylvestris* L.), and four plots in common oak (*Quercus petraea* [Mattuschka] Liebl.) (Table 1). Most of these plots form part of a network of long-term experimental plots studied under yield-related aspects and are being supervised by the Chair of Forest Yield Science at Technische Universität München. The spruce test area Paderborn 697 from Westphalia and the beech area Haiger 333 from the Saarland belong to the former Prussian Network of Forest Experiments. Today, the two latter trials are being monitored by the Lower Saxony Forest Research Station in Göttingen.

All stands are reference plots of classical thinning trials in southern and central Germany (Bavaria, Saarland, North-Rhine-Westphalia). The oldest of these trial areas have been under observation since the mid-19th century when yield-related research was first introduced. They form the basis of our knowledge in yield science from which treatment regimes, yield tables, and training programs for forestry practice were developed. Because of their unique length, these time series were the subject of numerous investigations on the response to thinning of Norway spruce (Assmann 1953, 1970, Röhle 1994, Pretzsch and Utschig 2000), common beech (Kennel 1972, Franz et al. 1993, Foerster 1993), Scots pine (Foerster 1990, Küsters 2001, Pretzsch 1985), and common oak (Assmann 1970; Mayer 1958, Utschig and Pretzsch 2001). This article therefore merely reports essentials from the lightly thinned, fully stocked A-grade plots. The treatment of A-grade plots is restricted to the removal of dead or dying trees and aims at the documentation of self-thinning (Verein Deutscher Forstlicher Versuchsanstalten 1902).

About half of the experiments established in the autumn of 1870 have remained under observation to this day (cf. Table 1, period of survey). Correspondingly, the age span thus covered by measurements is fairly large (cf. Table 1, age span). The studied common beech plots represent average to very good site conditions on red marl and new red sandstone soils in central Germany (mean height at age 100 = 23.1–31.8 m). The stands are the result of natural regeneration following cutting according to the Hartig compartment shelterwood system, resulting in consistently even-aged stands despite their origin from natural regeneration. Area sizes vary between 0.25 and 0.4 hectares; they had not been treated before stand establishment and only dead or dying trees have since been removed.

With the exception of the North-Rhine-Westphalian area Paderborn 697, the Norway spruce trial areas are all located in the prealpine area of South Bavaria, the South Bavarian lowlands, and Swabia. They are concentrated on the South German pleistocene where Norway spruce grows naturally. The good to excellent site index is reflected by mean heights at age 100 of 30.1–36.6 m. The stands were artificially established, the trial areas Sachsenried 03 and Sachsenried 07 by seeding; all others by planting. Tree spacing in the individual trials was uniform, but spacings among the trial areas varied from 0.9 m × 0.9 m, 1.2 m × 1.2 m to 1.4 m × 1.4 m. The trial areas Denklingen 05, Eglharting 72, and

Table 1. Growth and yield characteristics for the first/last survey of 28 nonthinned, fully stocked experimental plots of common beech, Norway spruce, Scots pine, and common oak

Species and experiment/plot	n	First/last survey	Age span (yr)	Stem number (trees/ha)	Mean height (m)	Mean diameter (cm)
Common beech/*Fagus sylvatica* L.						
ELM 20/1	13	1871/1967	49–145	5,844– 400	13.2–35.0	7.7–36.0
FAB 15/1	12	1870/1958	48–136	6,220– 477	12.5–32.2	7.6–34.1
HG 333/3	11	1951/1999	56–104	2,368– 840	12.7–26.3	13.6–26.9
HAI 27/1	16	1870/1994	38–162	6,533– 269	12.2–36.5	6.9–43.6
KIR 11/1	10	1871/1936	49–114	5,146– 755	11.1–26.5	8.6–27.8
LOH 24/1	13	1871/1967	66–162	7,081– 292	13.5–32.3	8.2–39.6
MIS 25/1	15	1870/1981	42–153	11,242– 439	8.7–29.1	5.7–35.8
ROT 26/1	14	1871/1967	48–144	5,458– 425	13.2–34.0	8.2–37.0
WAB 14/1	15	1870/1967	48–145	6,206– 650	10.4–28.8	7.8–29.3
Norway spruce/*Picea abies* (L.) Karst.						
DEN 05/1	18	1882/1990	35–143	3,528– 508	14.4–40.6	13.5–47.3
EGL 72/1	13	1906/1990	36–120	6,256– 712	10.5–32.5	8.8–35.9
EGL 73/1	12	1906/1983	42–119	2,240– 672	14.4–33.2	15.2–36.9
OTT 08/1	14	1882/1963	32–113	4,232– 632	14.0–38.8	12.8–40.6
PB 697/2	17	1928/1999	42–113	3,623– 548	14.5–36.8	12.2–40.9
SAC 02/1	15	1882/1972	32–122	4,100– 492	14.2–38.8	12.8–44.7
SAC 03/1	14	1882/1965	33–116	7,428– 596	10.6–38.2	8.6–42.0
SAC 67/1	14	1902/1990	43–131	3,496– 443	15.9–41.4	13.7–50.7
SAC 68/1	14	1902/1990	42–130	2,952– 544	16.5–40.4	15.2–45.3
Scots pine/*Pinus sylvestris* L.						
SLU 50/1	13	1899/1991	26–118	4,900– 550	8.9–29.3	8.3–32.1
SNA 57/1	13	1901/1995	44–138	5,104– 456	9.1–23.8	7.8–28.3
BOD 229/9	8	1961/1999	36– 74	4,650– 850	8.0–19.0	6.7–19.5
WAS 234/1	9	1962/1999	86–122	1,117– 358	14.0–23.6	15.3–28.2
BUL 240/1	7	1965/1999	59– 93	1,080– 620	12.5–19.4	15.5–25.4
HED 243/6	6	1971/1996	72– 97	2,067–1,056	16.9–22.4	14.6–21.8
Common oak/*Quercus petraea* (Matt.) Liebl.						
WAL 88/2	9	1934/1989	48–103	1,676– 514	16.5–30.3	13.4–30.9
WAL 88/5	11	1934/1999	48–113	1,643– 457	16.3–31.6	13.4–33.2
ROH 90/1	8	1934/1996	70–132	1,205– 487	17.4–27.4	15.4–32.5
ROH 620/1	5	1980/2001	54– 75	1,569–1,038	18.7–24.2	15.4–21.9

n = number of surveys; survey = first and last calendar year of survey; age = stand age (yr) at the first/last survey, reference age for the yield data in columns 6 to 9; stem number = number of stems in the remaining stand (trees · ha^{-1}); mean height = height of stem of mean basal area (m); mean diameter = average diameter at height 1.3 m of stem of mean basal area (cm).

Eglharting 73 are re-afforestations after clearcutting, whereas all other areas originated from first afforestations on agricultural areas and pastures. Table 1 compiles the most important yield characteristics of the A-grade plots on these areas from the first to the most recent survey. Some of the areas were abandoned following storm calamities, while others are under observation to this day, with the last survey done perhaps several years ago.

The Scots pine trials of 0.25 to 0.3 hectares are concentrated on meager Jurassic and cretaceous sites in North Bavaria. The total of six trials covers a relatively wide site spectrum with mean heights of 20.3–28.0 m at age 100. The majority of the pine trials were established by seeding after clearcutting. About 3 to 5 kg pine seeds/ha were, in some cases, intermingled with 0.5 to 3 kg seeds from European larch (*Larix decidua* Mill.), northern white pine (*Pinus strobus* L.), or common acacia (*Robinia pseudoacacia* L.). However, these admixtures were almost completely ruled out by Scots pine when the first survey was conducted. The

area Schnaittenbach 57 is a plantation after clearcutting with 10,000 trees/ha, with a regular spacing of 1.0 m × 1.0 m.

Among the untreated trials, common oak has the weakest representation with only four trial plots ranging from 0.2 to 0.3 ha. The trials involved here are located on new red sandstone sites in the Palatinate and the Spessart region. The site conditions range from average to good as reflected by mean heights at age 100 of 22.8–26.0 m. The stands were artificially established after clearcutting; 0.5 to 0.1 tons of seeds were disseminated per hectare, the equivalent of 100,000 to 200,000 seedlings. To protect the oak trunks, an understory of beech trees was introduced 2 to 5 decades after the common oak stand had been established. The understory is irrelevant in terms of total biomass and competition with common oak and will therefore be neglected in this evaluation investigation.

Figure 2 shows the ln(*N*)–ln(*d*) relationships for common beech, Norway spruce, Scots pine, and common oak on the ln–ln scale. The plotted straight lines demonstrate what
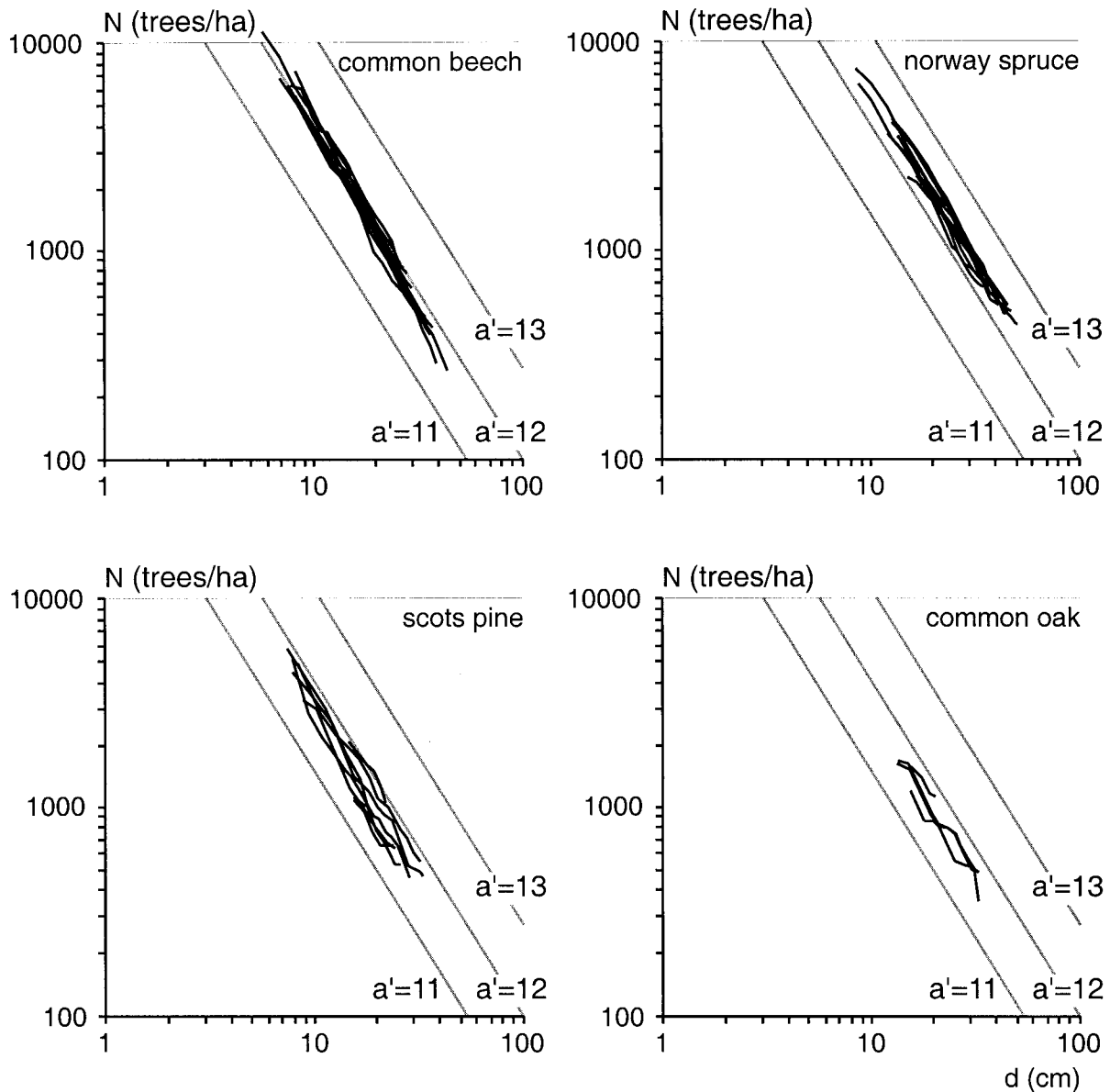
Figure 2. ln(N)–ln(d) relationship for the untreated, fully stocked nine pure common beech, nine Norway spruce, six Scots pine, and four common oak stands on which the investigation is based. Straight lines ln(N) = a' − 1.605 · ln(d) following Reineke (1933) with intercept a' = 11, 12, 13 (cf. Equation 4) are given as reference.

decrease in the number of stems is to be expected with increasing diameter if the stands followed the Stand Density Rule by Reineke ($b = -1.605$). It goes for all plots that only those inventories were included in the evaluation that represent fully stocked, untreated conditions. In a few cases the stem number–diameter pairs of variates based on inventories after the year 1992 had to be discarded, because from that time on, some of the stands suffered severe disturbance from storm calamities and snow break.

Common beech (*Fagus silvatica* L.) is represented on the basis of nine plots and 119 full surveys. The oldest plots date back to the year 1870, cover an age span from 38 to 162 years, and were surveyed 16 times. Here, stem numbers range from 11,242 to 269 trees per hectare, average diameters from 5.7 cm to 43.6 cm, and basal areas from 24.43 to 47.74 m² per hectare. The nine Norway spruce (*Picea abies* [L.] Karst.) test plots cover an age span of 32 to 143 years. For the oldest plots, 18 full surveys are available for evaluation, there is a total of 131 stem number–diameter pairs of variates for the analysis. Some of these plots have been under observation since 1882, with a variation in number of stems of between 7,428 and 443 trees per hectare, whereas the mean diameters range from 8.6 cm to 50.7 cm and the basal areas from 38.05 to 89.44 m² per hectare. The representation for Scots pine (*Pinus silvestris* L.) involves six test plots, the oldest of which have been under observation since the spring of 1899 and were surveyed 13 times. Hence, there is a total of 56 full inventories for the analysis. Ages range from 26 to 138 years and stem numbers from 5,104 to 358 trees per hectare, with a spectrum of average diameters

ranging from 6.7 cm to 32.1 cm and basal areas of stands comprising 16.39 to 44.51 m^2 per hectare. Common oak (*Quercus petraea* [Mattuschka] Liebl.) representation is based on only four plots, some of which have been observed since 1934 and were surveyed 11 times, with a total number of 33 full surveys. Stand data range from 1,676 to 457 trees per hectare, average diameters from 16.3 cm to 31.6 cm, and basal areas from 22.44 to 40.40 m^2 per hectare.

To quantify stand density, the SDI = $N \cdot (25/d)^b$ (Reineke, 1933) was calculated with the respective plot-specific b values. To get SDI$_{max}$ the SDI values were determined for all surveys of trial plot. SDI$_{max}$ hence is max(SDI$_{i=1...n}$). The SDI$_{max}$ range (mean) is in $N \cdot ha^{-1}$: for common beech, $796 - 1,013$ (885); Norway spruce, $1,246 - 1,549$ (1,395); Scots pine, $590 - 972$ (752); and common oak, $672 - 854$ (758).

Methods

For each of the 28 plots, the relationship $d \propto N^b$ was analyzed by linear regression according to the model

$$\ln(N) = a + b \cdot \ln(d), \qquad (6)$$

with d denoting the quadratic mean diameter and N the number of stems per hectare. To obtain an overall tree species-specific slope, all stem number–mean pairs of variates were integrated in an overall OLS regression for common beech, Norway spruce, Scots pine, and common oak, respectively. Before this analysis the mean values $\overline{\ln(d)}$ and $\overline{\ln(N)}$ were calculated for each stand and used for the standardization $\ln(d_i)' = \ln(d_i) - \overline{\ln(d)}$ and $\ln(N_i)' = \ln(N_i) - \overline{\ln(N)}$. The standardization has the effect of focusing all
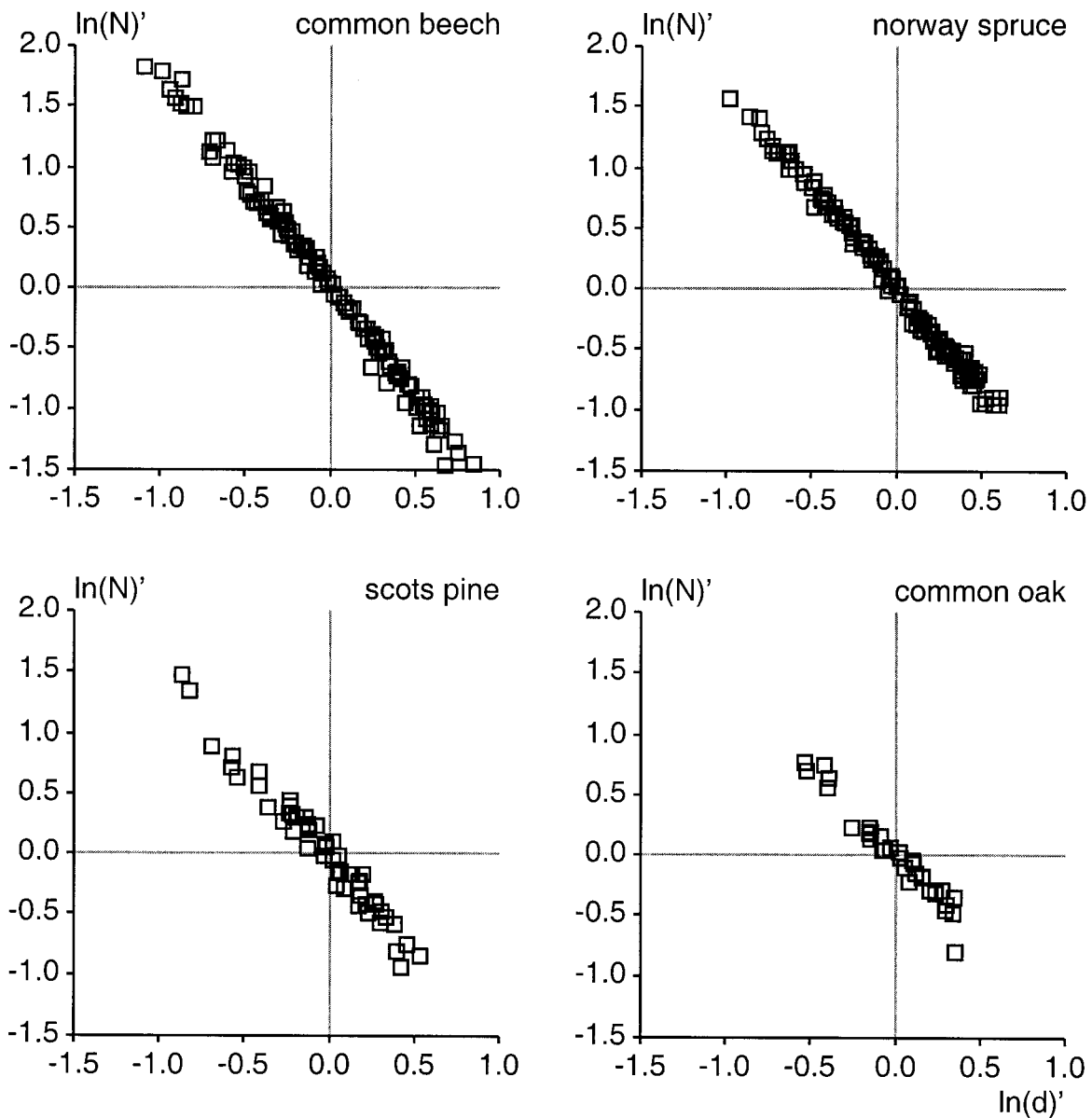

Figure 3. $\ln(N)'$ plotted over $\ln(d)'$ for all surveys on all plots, shown separately for the species common beech, Norway spruce, Scots pine, and common oak. The data are used for the OLS regression $\ln(N)' - \ln(d)'$.

straight lines on the mean value $(\overline{\ln(d)}, \overline{\ln(N)})$ and any different intercepts are eliminated (Figure 3). The OLS regression then results in an overall species-specific slope b.

When regressing data, in our case, mean tree diameter with corresponding stem number per unit area from subsequent observations of long-term research plots, we have to be aware that the inference statistics obtained by standard procedures may be biased and underestimated because of repeated measures and time series effects. The former means that we have to expect the single plots of one tree species to show plot-typical apparent deviations from the real species-specific slope b resulting from plot-specific long-term effects. The latter means that subsequent observations on one plot may be correlated. This is expressed and measured by temporal autocorrelation.

Because an unbiased estimation of the confidence intervals of these parameters is crucial for this study, we designed a two-stage bootstrap method to correctly take care of the repeated measures effects and for first-order temporal autocorrelation. We constrain to first-order autocorrelation because the more or less low number of observations in our time series (mostly, $n < 15$) is a weak basis for searching higher orders of temporal autocorrelation. In addition, it is reasonable to assume that, in case of sequential forest research plot inventories, first-order autocorrelation is the only important kind of temporal autocorrelation.

Our bootstrap algorithm takes care of the repeated measures effects by simply resampling the set of research plots for the species of interest. We address the time series effects based on a consideration by Mooney and Duval (1993), who recommend to re-sample only the residuals when the aim is to obtain bootstrapped confidence intervals for the parameters of a linear regression. This is important, because bootstrapping means re-sampling the random component of a data set, not the functional relationships. In our special case, when the residuals are not entirely random, not entirely independent from each other, this method has to be refined. We use two functional relationships: first, the relationship between independent and dependent variable; second, the relationship between subsequent residuals. Our random component for re-sampling is manifested through the residuals of the second relationship.

The part of our bootstrap algorithm that addresses temporal plot-specific autocorrelation comprises the following steps:

Step 1: Regression Based on the Original Data

Consider, we have a sample of n (x, y) pairs and apply the regression model

$$\hat{y} = a + b \cdot x. \tag{7}$$

We know that the x, y pairs are first-order autocorrelated and we want to know confidence limits for the parameters a and b. As a result of the OLS regression procedure, we

obtain the residuals $r_1, \ldots, r_n$; we call them the residual pool R:

$$R = \{r_1, r_2, \ldots, r_n\}. \tag{8}$$

The index of r describes the temporal sequence of residuals: r_1 is matching the first, r_2 the second, r_3 the third subsequent observation, etc. These residuals are assumed to be more or less autocorrelated. Please note that, to keep conventions, we use the variable name r with two different meanings in this article. Here, in the context of bootstrapping, we use it for residuals, while it symbolizes an allometric slope below (Equations 17, 18, and later).

Step 2: Regression for Determining Autocorrelation

Calculate a linear regression without intercept to capture first-order autocorrelation:

$$\hat{r}_{i+1} = c \cdot r_i. \tag{9}$$

Thus, a residual is always explained by the previous one. For this regression, we obtain residuals $rr_1, \ldots, rr_{n-1}$; we call them the rest residual pool RR:

$$RR = \{rr_1, rr_2, \ldots, rr_{n-1}\} \tag{10}$$

When there is no higher-order autocorrelation, these residuals are independent from each other. They represent the random component of our data set.

Step 3: Calculate the Expected Values for y

Calculate the expected values of y,

$$\hat{y}_i = a + b \cdot x_i \quad \forall \, i \in \{1, 2, \ldots, n\}, \tag{11}$$

according to the result of the previous regression analysis for each x value. This results in n $(x, \hat{y})$ pairs, where x comes from the original data set.

Step 4: Bootstrap the First Residual

Randomly draw a residual, with replacement, from the residual pool R. This is the first bootstrapped residual, therefore call it r'_1.

Step 5: Bootstrap the Following Residuals

Because the next residual, r'_2, is not independent from r'_1, generalized, r'_{i+1} is not independent from r'_i. Use the regression equation for autocorrelation from step 2 to estimate its deterministic component,

$$\hat{r}_{i+1} = c \cdot r'_1 \tag{12}$$

To obtain the random component, randomly draw a residual rr_{ran}, with replacement, from the rest residual pool RR. The bootstrapped residual r'_{i+1} results as

$$r'_{i+1} = \hat{r}_{i+1} + rr_{ran} \tag{13}$$

r'_{i+1} is the input variable for bootstrapping the next residual

r'_{i+2}. Step 5 is repeated until all residuals $r'_1, \ldots, r'_n$ are bootstrapped.

Step 6: Build the Bootstrapped Data Set

Add the bootstrapped residuals r' to the deterministically calculated expected values for y,

$$y'_i = \hat{y}_i + r'_i \quad \forall\, i \in \{1, 2, \ldots, n\} \qquad (14)$$

y' are the y values of the bootstrapped data set that is now readily set up by n (y', x) pairs.

Step 7: Perform Regression on the Bootstrapped Data Set

Perform a linear regression,

$$\hat{y}' = a' + b' \cdot x. \qquad (15)$$

Record the parameter values a' and b'. Repeat steps 4 to 7 a large number of times N, e.g., $N = 10{,}000$.

Step 8: Analyze Distribution of Regression Parameters

The result of the bootstrap procedure is a distribution of a' and b', respectively, which is assumed to represent the distribution of a and b, when the x, y samples would not have been bootstrapped, but drawn from the basic population. The distributions are available as cumulative frequency tables, thus all required quantiles and confidence intervals can be determined by simply counting through this table.

Application for the Full Error Structure of Our Data

The bootstrap regression procedure shown above covers an entirely first-order autocorrelated sample and shows how we address the time series nature of the data. However, it has to be enlarged to cover our full problem. Because we want to determine regression coefficients from a data set that contains time series data from different plots, we have data where there is correlation among the errors when they come from the same plot, but no correlation across the different plots. Consequently, steps 1–3 of our basic procedure have to be performed in parallel for each plot. After that, we create a bootstrapped set of plots of the same size as the original set by randomly drawing plots with replacement. This takes into account the repeated measures effects that are not covered by temporal autocorrelation.

For each of the selected plots, we proceed with steps 4–6, where we bootstrap a plot-specific data set with regard to the plot-specific autocorrelation. This will clearly lead to different bootstrapped data sets for the same plot if this plot has been selected more than one time in the step before.

Another important difference lies in step 7, regression of the bootstrapped data set. Here, the bootstrapped y', x pairs of the single selected plots are pooled together. Regression analysis is done over this whole data set, which results in the

parameters a' and b' (Equation 15) for the whole pooled data set. After the bootstrap iterations, the resulting distributions are evaluated exactly as described in step 8 above.

Test for First-Order Autocorrelation

To test residuals for first-order autocorrelation, we calculate the Durbin–Watson test statistic (DW) based on our residual pool (Equation 8),

$$DW = \frac{\sum_{i=2}^{n} (r_i - r_{i-1})^2}{\sum_{i=1}^{n} r_i^2}. \qquad (16)$$

Note that the indexes denote the temporal sequence of the observations. The theoretically possible range of values for DW is $[0; 4]$, where values smaller than 2 indicate positive and values greater than 2 indicate negative autocorrelation. Values around 2 result when there is no temporal autocorrelation. Because we have to consider that our sample sizes (number of observations per plot) are likely too small for the test statistic to be unbiased and because the distribution of DW is dependent on the data matrix, we generate its sample distribution for the case that there is no temporal autocorrelation by bootstrapping. We use a bootstrapping method referred to as BDW by Canjels (2002), which has proven to be quite effective, especially in small sample sizes. Following Canjels, we re-sample the residuals randomly with replacement ($N = 10{,}000$) and calculate DW for each series of sampled residuals.

Interspecies variations were analyzed by comparing the allometric coefficient b of pairs of species. Because the error structure of our data violates the conditions of standard test statistics, we use a simulation technique. Our bootstrap method, as shown above, delivers a simulated distribution for b per species, which in fact is a list of 10,000 values. For comparing b_1 from species 1 with b_2 from species 2, we independently draw, with replacement, random values b'_1 and b'_2 from each of the lists. We calculate the difference $d' = (b'_1 - b'_2)$ and record it. This procedure is repeated 10,000 times. Thus, we obtain a simulated distribution of the expected difference between b_1 and b_2. By counting through this distribution, we can determine whether 0, which would indicate no difference between the slopes of both species, is inside or outside certain confidence limits.

Implementation

The bootstrap algorithms have been implemented in a Pascal (Delphi) computer program BOOTREG. It has been tested with two different random number generators, the built-in random number generator of Delphi 5 and ran3 as published by Press et al. (1989). During our test runs, both generators produced the same results in terms of bootstrapped confidence intervals. In the final version of the program, we used ran3 because its algorithm and source code are published. The program allows calculation of regression confidence intervals also without caring for repeated measures and temporal autocorrelation effects. Consequently, the effect of neglecting these special properties of the error structure can be quantified.

Table 2. OLS regression results for the ln(N)–ln(d) relationship and autocorrelation, shown separately for each plot

Species and Experiment/ plot	n	Parameter a			Parameter b			r^2	c	Durbin–Watson	p(DW)
		L	estimate	U	L	estimate	U				
Beech											
ELM 20/1	13	12.220	12.239	12.257	−2.299	−1.744	−1.167	0.998	−0.021	2.04	0.36
FAB 15/1	12	12.237	12.263	12.300	−2.358	−1.728	−1.013	0.998	0.546	0.87	**0.04**
HG 333/3	11	11.827	11.866	11.909	−2.413	−1.581	−0.771	0.990	0.590	0.82	**0.03**
HAI 27/1	16	12.209	12.228	12.259	−2.228	−1.746	−1.206	0.999	0.363	1.04	**0.04**
KIR 11/1	10	12.121	12.148	12.190	−2.258	−1.652	−0.961	0.996	0.514	0.80	**0.04**
LOH 24/1	13	13.107	13.179	13.242	−2.717	−2.027	−1.342	0.995	0.545	0.88	**0.04**
MIS 25/1	15	12.534	12.627	12.739	−2.456	−1.865	−1.084	0.992	0.645	0.72	**0.01**
ROT 26/1	14	12.192	12.232	12.285	−2.372	−1.724	−1.039	0.997	0.662	0.70	**0.01**
WAB 14/1	15	12.406	12.450	12.509	−2.263	−1.748	−1.192	0.990	0.361	1.07	0.06
min	10		11.866			−2.027		0.990			
max	16		13.179			−1.581		0.999			
mean	13		12.359			−1.757		0.995			
Spruce											
DEN 05/1	18	12.342	12.392	12.468	−2.412	−1.622	−0.888	0.995	0.802	0.54	**0.00**
EGL 72/1	13	12.334	12.389	12.460	−2.362	−1.661	−0.814	0.992	0.475	1.02	0.05
EGL 73/1	12	12.097	12.143	12.242	−2.339	−1.593	−0.824	0.975	0.573	0.74	**0.02**
OTT 08/1	14	12.867	12.883	12.915	−2.147	−1.739	−1.182	0.995	0.263	1.09	0.07
PB 697/2	17	12.360	12.373	12.397	−2.124	−1.646	−1.133	0.997	0.280	1.18	0.06
SAC 02/1	15	12.876	12.893	12.925	−2.180	−1.757	−1.192	0.997	0.428	0.77	**0.01**
SAC 03/1	14	12.538	12.561	12.593	−2.197	−1.666	−1.112	0.997	0.121	1.55	0.28
SAC 67/1	14	12.359	12.398	12.431	−2.192	−1.624	−1.022	0.994	0.268	1.46	0.23
SAC 68/1	14	12.408	12.455	12.501	−2.189	−1.630	−0.892	0.990	0.399	1.17	0.10
min	12		12.143			−1.757		0.975			
max	18		12.893			−1.593		0.997			
mean	15		12.499			−1.660		0.992			
Pine											
SLU 50/1	13	11.706	11.738	11.760	−2.074	−1.561	−1.022	0.994	0.039	1.79	0.46
SNA 57/1	13	11.713	11.761	11.780	−2.067	−1.665	−1.068	0.984	−0.019	1.51	0.27
BOD 229/9	7	11.453	11.551	11.664	−2.296	−1.545	−0.587	0.957	0.311	0.95	0.17
WAS 234/1	8	11.499	11.522	11.560	−2.277	−1.627	−0.878	0.973	−0.125	2.03	0.32
BUL 240/1	6	10.488	10.560	10.626	−2.391	−1.315	−0.189	0.910	0.269	1.28	0.33
HED 243/6	6	11.870	11.918	11.963	−2.884	−1.585	−0.348	0.962	0.200	1.22	0.29
min	6		10.560			−1.665		0.910			
max	13		11.918			−1.315		0.994			
mean	9		11.508			−1.550		0.963			
Oak											
WAL 88/2	10	11.533	11.603	11.673	−2.481	−1.582	−0.570	0.950	−0.028	1.46	0.30
WAL 88/5	10	11.033	11.066	11.106	−2.045	−1.408	−0.768	0.980	−0.003	1.97	0.40
ROH 90/1	8	10.264	10.317	10.351	−1.949	−1.204	−0.415	0.950	−0.185	2.10	0.31
ROH 620/1	4	10.940	10.951	10.963	−2.713	−1.312	0.408	0.977	−0.813	3.35	**0.00**
min	4		10.317			−1.582		0.950			
max	10		11.603			−1.204		0.980			
mean	8		10.984			−1.376		0.964			

L, U, bootstrapped lower and upper 95% confidence limits for parameters a and b; c, slope of first-order autoregression (Equation 9); p(DW), bootstrapped one-tailed error probability of Durbin-Watson statistic; bold, p(DW) < 0.05.

For a detailed analysis of d–N allometry the slope,

$$r = \frac{\ln(N_2) - \ln(N_1)}{\ln(d_2) - \ln(d_1)} = \frac{\ln(N_2/N_1)}{\ln(d_2/d_1)}, \quad (17)$$

was calculated from the pairs of variates $N_{i=1,\ldots,n}$ and $d_{i=1,\ldots,n}$ from consecutive surveys. Thus, r can be quantified for each period between two surveys. For infinitely small time steps, Equation 17 corresponds to the quotient,

$$r = \frac{\Delta N/N}{\Delta d/d}, \quad (18)$$

and equals the allometric constant b in $N \propto d^b$. When the relationship of ln(N) and ln(d) is linear between two surveys, Equations 17 and 18 are equivalent for this period. Because our data were measured in discrete time steps, we use Equation 17 as an approximation for Equation 18.

The decrease in the number of stems with defined increase in diameter is quantified by r. If, within any period of time, $r = -1.5$ for tree species 1 while $r = -2.0$ for tree species 2 in the same period, this would indicate that tree species 2 has a 33% higher mortality rate, which implies a considerably lower self-tolerance than that of tree species 1 (Zeide 1985).

Table 3. Slope values and significance of their interspecific differences for OLS on the standardized data

Species		Common beech	Norway spruce	Scots pine	Common oak
	U	−1.706	−1.599	−1.445	−1.184
	E	**−1.789**	**−1.664**	**−1.593**	**−1.424**
	L	−1.877	−1.709	−1.695	−1.627
Common beech		—	**	**	**
Norway spruce		**	—	ns	*
Scots pine		**	ns	—	ns
Common oak		**	*	ns	—

Bold numbers (E), OLS estimate of slope; L, U, bootstrapped lower and upper 95% confidence limits.
**,* Significant difference with two-tailed error probability $P < 0.01$ and $P < 0.05$, respectively; ns, nonsignificant difference, $P > 0.05$.

Results

Interspecific Differences of Relationship $N \propto d^b$

Table 2 shows the results of the OLS regression between the log-transformed values for diameter and stem number (cf. Equation 6). Because the survey intervals for common beech were comparatively long, the time series for this tree species with a maximum and an average of 16 and 13 surveys, respectively, is less dense than that for Norway spruce. For common beech, variation in a and b values among experimental plots is considerably greater than for Norway spruce. The b values range from −2.027 to −1.581, with an average of −1.757. For Norway spruce, up to 18 surveys are available for model-fitting. The b values vary between −1.757 and −1.593, and their average comes to about −1.660. The r^2 values are, on average, above 0.99. In the representation of Scots pine, the number of surveys for the experimental areas under study range from 6 to 13. The b values range from −1.665 to −1.315, with an average of −1.550. The four plots for the common oak representation had a maximum of 10 and a minimum of 4 surveys. Here again, the a and b values show merely slight variations among the areas. The b values range from −1.582 and −1.204, averaging at −1.376.

Table 2 also shows the results for first-order autocorrelation (AC) in the time series. Parameter c of Equation 9 is positive in most cases, which indicates positive AC, as does the DW test statistic. Its bootstrapped one-tailed error probability indicates significant ($P < 5\%$) AC in seven of nine cases for common beech and three of nine cases for Norway spruce. For Scots pine and common oak, there is no significant AC except the oak plot ROH 620/4, which shows a highly significant negative AC, which may be an artifact resulting from the small number of only four surveys, where it is very probable that positive and negative residuals alternate.

However, because we have to consider AC to be manifest, whether it is significant in our tests or not, we used Equation 9 with the slopes c as shown in Table 2 for each plot when bootstrapping the confidence intervals for the parameters a and b. This is also justified by the values of c, which are considerably high even in most of the cases, where AC is not significant.

The resulting bootstrapped 95% confidence intervals for slope b are by far larger compared to the ones resulting when AC is not taken into account. For virtually each plot, the lower bound is smaller than −2, the upper bound is mostly near −1, often even greater. In one case, ROH 620/4, even 0 cannot be excluded. These results clearly reveal that there is no way to detect interspecific differences on single-plot level.

The OLS regression through the standardized $\ln(N)'$–$\ln(d)'$ pairs of variates (cf. Table 3) resulted in: $\ln(N) = 1.789 \ln(d)$, $r^2 = 0.992$, $n = 119$ for common beech; $\ln(N) = -1.664 \ln(d)$, $r^2 = 0.993$, $n = 131$ for Norway spruce; $\ln(N) = -1.593 \ln(d)$, $r^2 = 0.980$, $n = 53$ for Scots pine; and $\ln(N) = -1.424 \ln(d)$, $r^2 = 0.950$, $n = 32$ for common oak. All intercepts $a = 0$, due to the standardization. The bootstrapped 95% confidence intervals for slope b are narrow compared to the single-plot results reported in Table 2, although first-order temporal autocorrelation and the repeated measures effects have been fully taken into account. For common beech, the bounds of the interval are −1.877 and −1.706, for Norway spruce they are −1.709 and −1.599, and they are −1.695 and −1.445 for Scots pine and −1.627 and −1.184 for common oak. Comparing the slopes of the single species by bootstrapping the distribution of their differences shows significant (two-tailed $P < 0.01$) for the differences between common beech and all other species (Table 3). In addition, Norway spruce and common oak differ significantly (two-tailed $P < 0.05$).

Although significant differences cannot be proven for all four species, the values and confidence intervals shown in Table 3 indicate a certain species order in terms of the Reineke-line's slope: common beech < Norway spruce < Scots pine < common oak, where only Norway spruce and Scots pine on the one hand and common oak and Scots pine on the other hand cannot be clearly separated.

Comparison of Individual Species' Slopes with Reineke's −1.605

The 95% confidence interval for b (cf. Table 3) does by far not include the Reineke value $b = -1.605$ for common beech. For Norway spruce, −1.605 is close to the very upper border of the confidence interval, which indicates a close-to-significant difference (two-tailed $P = 0.071$). The same is true for common oak, the only difference being that −1.605 is near the lower 95% limit (two-tailed $P = 0.076$).

Scots pine is the only species where −1.605 is virtually in the center of the confidence interval. Because we observe a significant difference between the *b* values for Norway spruce and common oak, it is highly probable that the actual slope of at least one of these species is different from −1.605.

As shown above, our findings for parameter *b* suggest a ranking in steepness of slope. The straight line for common oak seems to be less steep than postulated by Reineke (1933), whereas the slope for Norway spruce is most probably steeper than −1.605. For common beech, the slope is significantly steeper than −1.605. For Scots pine, *b* matches quite exactly Reineke's slope. Common beech has the lowest self-tolerance by far, which is expressed by the fact that its allometric straight line starts in the initial state ($h = 1.30$ m, $d = 0.5$ cm) on the same high level as Norway spruce, but reaches the same low level at $d = 60$ cm as represented by Scots pine and common oak (Figure 4, left). The allometric lines represented in Figure 4 were calculated using the *b* values (slopes) obtained by regression with the standardized data (Table 3). For *a* values (intercepts) we used the species-specific mean intercepts from the single plot regressions (Table 2).

The average growing space *s* in square meters per tree results from $s = 10,000/N$. Representation of growing space over diameter in Figure 4 (right) shows what may be considered remarkable allometry in common beech. At the juvenile stage, its demand for growing space is, together with Norway spruce, lower than for the other species. However, with increasing age, the growing space beech occupies increases much more than it does in other species. The curious reversal in common beech under self-thinning conditions from space-saving in the juvenile stage to space-grasping in old age can be interpreted to be the strategy behind this climax tree species' success. Looked at from a different angle, common beech invests a relatively large stem diameter per unit sequestered space in the initial phase of the stand. Subsequently, it becomes increasingly efficient in its space-sequestration behavior. Compared to other tree species, beech sequesters larger portions of available growing space with a given stem diameter. As a consequence, it shows the most rapid decrease in the number of stems (Figure 4).

Species' Oscillation around the Self-Thinning Line

For all tree species, the survey periods averaged 6–7 years (common beech 6.74, Norway spruce 6.02, Scots pine 5.92, common oak 6.19). Certain deviations from Table 1 are due to the fact that some starting and ending periods were not included because calamities had caused some stands to sink below maximum density. The mean diameter increment rates in the survey intervals amount to $\Delta d/d$, calculated as $(d_2 - d_1)/d_1 = 12.8, 9.2, 12.8,$ and 10.5% for common beech, Norway spruce, Scots pine, and common oak, respectively, where d_1 and d_2 symbolize the diameter at the beginning and at the end of a survey interval. Table 4 reveals that not only do the mean *r* values show remarkable differences among the species, but the oscillations regarding the species-specific mean values also appear to vary. The *r* minimum values are relatively similar, with −2.87 for common beech, −2.73 for Norway spruce, −2.48 for Scots pine, and −2.51 for common oak. By contrast, the maximum values with −0.75 for common beech to −0.01 for common oak vary considerably. SD ranges from 0.43 in common beech stands to 0.81 in common oak. The different oscillations are particularly evident in the variation coefficient of the *r* values for the tree species. It amounts to 26% in common beech stands, 35% in Norway spruce, 46% in Scots pine, and 67% in common oak. The representation of *r* values over mean diameter (Figure 5) shows oscillation
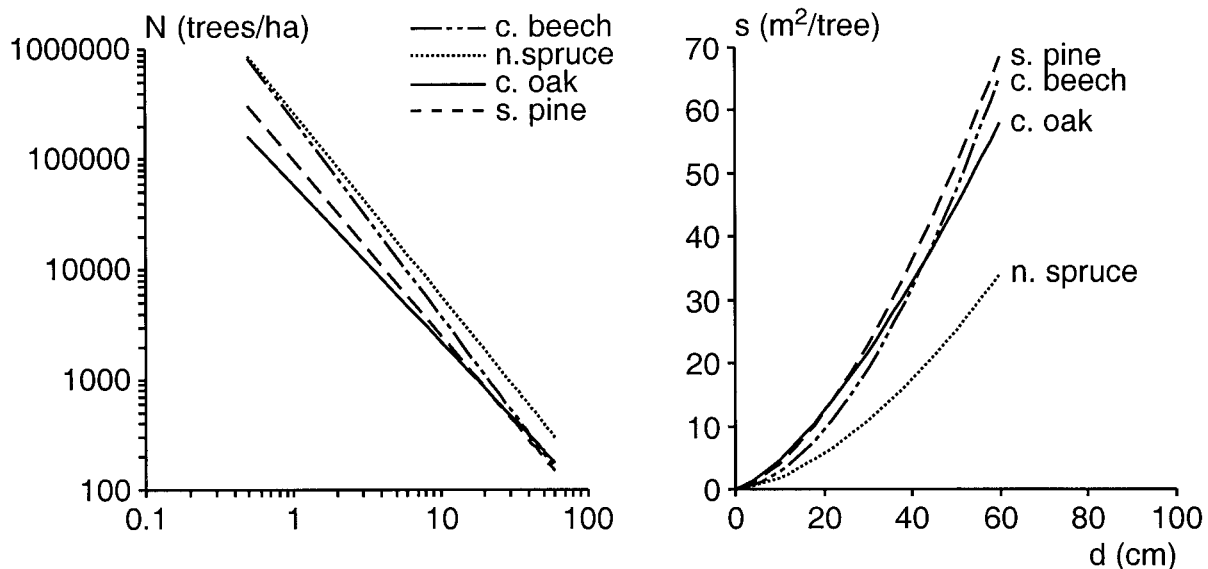

Figure 4. Mean ln(*N*)–ln(*d*) relationships (left) and *s*–*d* relationship (right) for the tree species common beech, Norway spruce, Scots pine, and common oak (*N* = stem number (trees ha^{-1}), *d* = mean diameter (cm), *s* = growing space (m^2)).

Table 4. Characteristic values for self-tolerance of the tree species common beech, Norway spruce, Scots pine, and European oak

Species	Mean period length (yr)	r (mean)	r (min)	r (max)	r (SD)	r var(%)
Common beech	6.74	−1.6878	−2.8685	−0.7512	0.4340	25.7958
Norway spruce	6.02	−1.4742	−2.7245	−0.2465	0.5300	35.4019
Scots pine	5.92	−1.3829	−2.4786	−0.1519	0.6115	45.8255
Common oak	6.19	−1.2250	−2.5067	−0.0114	0.8057	66.9594

For each tree species, the average survey cycles (yr), mean value (m), minimum (min), maximum (max), standard deviation (SD), and coefficient of variation (var) of the determined slopes $r = \ln(N_2/N_1) \div \ln(d_2/d_1)$ are shown.

around the mean value. Common beech is characterized by less pronounced oscillation of the r–d relationship, whereas common oak shows strong oscillation. Figure 5 shows selected examples of this species-specific behavior from the common beech plots KIR 11/1, ROT 26/1 (left) and the common oak plots WAL 88/2 and ROH 90/1 (right).

Discussion

If, at any time in the course of stand development, the product from the number of stems per hectare N and the basal area corresponding to the mean diameter ($d^2\pi/4$) were constant ($N \cdot d^2 = $ const), then $N \propto d^{-2.0}$ would be correct. In this case, the number of stems over the average diameter d would have to be scaled by the exponent −2. The basal area would hence remain the same during the entire stand development, which, however, is not the case in reality. Actually, the number of stems over mean diameter regresses even under self-thinning by the species-specific exponent $b > -2$, such that stand basal area rises continuously with increasing mean diameter d. The relationship hence reads $N \propto d^b$, $b > -2$. The rules established by Reineke (1933) and Yoda et al. (1963) assume the same allometric relationships between size and density for a wide spectrum of

species under self-thinning conditions. Both Harper (1977) and Weller (1987, 1990) consider them important laws in plant biology, whereas White (1981) and Zeide (1987) remain doubtful and von Gadow (1986) even reduces the rules to a myth. However, with few exceptions (Matthew et al. 1995, Sackville Hamilton et al. 1995, Whittington 1984) criticism is restricted to the falsification of these rules. This study refrains from repeating these controversial discussions. The evaluation of the present study relies on a database that is unique as far as the number of experimental areas and the lengths of the observation periods are concerned, and reveals that, in four of six possible two-species comparisons, b values differ significantly from species to species. They come to −1.789 for common beech, −1.664 for Norway spruce, −1.593 for Scots pine, and −1.424 for common oak, i.e., common beech < Norway spruce < Scots pine < common oak. Apart from the species-specific differences, this ranking is supported by significant (common beech) and close-to-significant (Norway spruce, common oak) deviations from the coefficient −1.605 postulated by Reineke (1933).

Investigations of Reineke's $\ln(N)$–$\ln(d)$ relationship and Yoda's $\ln(m)$–$\ln(N)$ law are based on different statistical
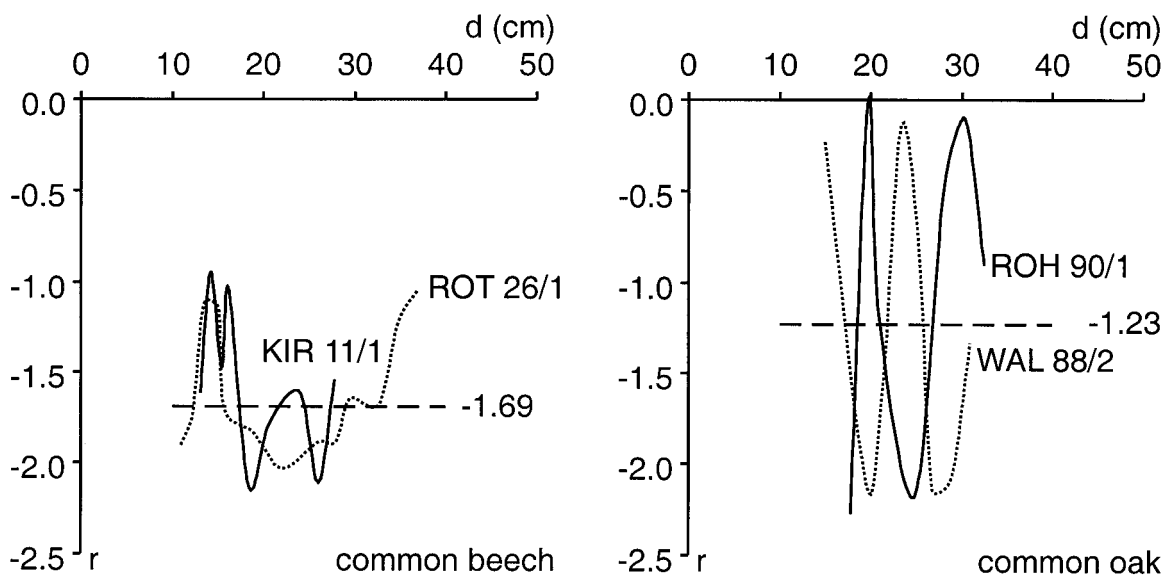

Figure 5. Survey period-specific r values over mean diameter d for the selected common beech plots KIR 11/1 and ROT 26/1 (left) and for the common oak plots WAL 88/2 and ROH 90/1 (right). d corresponds to the beginning of each survey period. The time series were smoothed by cubic spline. Broken lines represent the mean r values for common beech ($r = -1.69$) and common oak ($r = -1.23$).

methods (OLS regression, PCA, orthogonal regression, etc.). The use of these different methods leads to considerable variations in the results (Sackville Hamilton et al. 1995, Matthew et al. 1995). To eliminate these methodological differences and to concentrate on the species-specific response patterns, two different approaches were used to analyze the $\ln(N)$–$\ln(d)$ relationship: OLS regression analysis using the model $\ln(N) = a - b \cdot \ln(d)$ and through the difference quotient $r = \ln(N_2/N_1) \div \ln(d_2/d_1)$. The allometric coefficients r therefore deviate for procedural reasons, e.g., from the coefficient b determined by OLS regression, and do not lend themselves to unconditional comparison with the coefficient $r = -1.605$ determined by Reineke (1933) either. This is because the Reineke relationship is based on the OLS regression of the $\ln(N)$–$\ln(d)$ pairs of variates. The ranking of the species concerning the b and r values remains the same when using different methods for parameter estimation. Still, neither approach will necessarily produce exactly the same results unless the $\ln(N)$–$\ln(d)$ pairs of variates are exactly on a straight line.

The bootstrap method presented in this study allows us to use OLS regression, which ensures comparability of our parameter estimates to Reineke's $r = -1.605$ and to the results of most preceding studies (Sterba 1981, Bergel 1985, Zeide 1985, von Gadow 1986, Sterba and Monserud 1993). This method introduces a possibility to estimate realistic parameter confidence intervals under conditions that definitely forbid the application of standard inference statistics that are normally applied with OLS. Such conditions, where a data set for evaluation is partly burdened with autocorrelation, are inevitably quite frequent when dealing with long-term research plots.

If adherence to the rules by Reineke (1933) and Yoda et al. (1963) were to continue, species-specific differences would certainly be ignored and the path toward a morphologic-allometric explanation of the competitive mechanisms in pure and mixed stands would remain obstructed. The study goes beyond mere falsification of Reineke's rule and proceeds to prove species-specific reaction patterns in size–density allometry. Zeide (1985) introduces the quotient $r = \Delta N/N \div \Delta d/d$ as a measure of self-tolerance in tree species growing in pure stands. The larger the r value, the lower the number of dying trees $\Delta N/N$ with defined diameter increment $\Delta d/d$ will be, and the greater the self-tolerance of the species in pure stands. The ranking we revealed for the mean species-specific r values expresses the fact that, in comparison to Norway spruce and common beech, the species common oak and Scots pine are more tolerant with trees of the same species. For instance, in common beech stands, a mean diameter increase of 1% causes a decrease in the number of stems by 1.69%. Given the same diameter increment, the decrease in the number of stems is 1.47, 1.38, and 1.23 for Norway spruce, Scots pine, and common oak, respectively, which means 13%, 18%, and 27% lower than for common beech. That underlines the low self-tolerance of beech and its space-consuming investment strategy. The causes for this are seen in its wider and more dynamic lateral crown extension. The reverse side of a

species high efficiency in space sequestration is that forest management has to provide much growing space to achieve a particular stem dimension. The self-thinning process of common beech is very fast and continuous, without any great oscillations. This prevents the occurrence of large gaps in the crown canopy and guarantees common beech a more uniform presence in the area. By contrast, common oak at first maintains a higher density level even in approximating maximum density, but dies in waves. In mixed stands, this gives common beech a competitive advantage over, e.g., common oak, the reason being that the cyclic, wavelike mortality in common oak leaves gaps in the crown canopy that common beech is able to fill quickly in the mixed stand. Findings about the allometry under self-thinning in pure stands may therefore be considered an informative benchmark for the species-specific response patterns in mixed stands (Puettmann et al. 1992, Sterba and Monserud 1993). For mixed stands on comparable sites, mean r values determined for common beech, Norway spruce, Scots pine, and common oak came to $r = -0.40$, -1.02, -1.06, and -2.01, respectively, which indicates a reversal of the situation in pure stands, i.e., common beech > Norway spruce > Scots pine > common oak (Pretzsch 2005). Compared with pure stands, in mixed stands r of common beech, Norway spruce, and Scots pine increases by 76, 31, and 23%, respectively, whereas that of common oak decreases by 64%. Great expansion abilities under interspecific conditions (e.g., common beech) evidently guarantee great assertive power in the mixed stand. Low sequestration effectiveness in the pure stand (e.g., common oak) is obviously combined with low assertive power in the mixed stand (Zeide 2004). This underlines that the species-specific allometry and space sequestration are crucial for the competitiveness and success of a species in pure and mixed stands, even more important than its mere primary production (Bazzaz and Grace 1997).

Concerning our data, we have to point out that A-grade plots are not completely untreated, because dead, dying, and unsound trees are removed, mostly to prevent the spread of diseases (cf. Methods). Nevertheless, these plots were definitely established and maintained for observing self-thinning. Thus, they document at least a very close approximation to maximum stand density.

Conclusions

In view of the individual species' slopes, stand density estimation algorithms, founded on generalized allometric relations, appear unsuitable. Stand density management diagrams (SDMD), which are applied for many species as tools for regulating stand density, use the self-thinning line with generalized scaling exponents as upper boundary and are the most prominent silvicultural application of the self-thinning rule (Oliver and Larson, 1990). Bégin et al. (2001) list for a considerable number of tree species available SDMDs as guides for stand management. As long as those SDMDs ignore individual species allometry, flawed density control and contraoptimal thinning will result for the four

considered species. Equivalent shortcomings apply for prognoses by growth models, which ignore individual species' scaling exponents. Models that base thinning and mortality algorithms on generalized scaling exponents (Eid and Tuhus 2001, Xue and Hagihara 2002, Yang and Titus 2002) should be replaced by more flexible approaches (Pittman and Turnblom 2003, Zeide 2001).

Reineke's Stand Density Index (Reineke 1933), founded on the species invariant slope $r = -1.605$, is questionable. The strength of SDI as a measure of density is that it takes mean diameter *and* number of stems into account (Avery and Burkhart 1983, Ducey and Larson 1999, Zeide 2004). The mean diameter serves as an expression of the allometric development phase of the stand, thus the observed number of stems is related to the corresponding allometric phase of the stand. In Europe, SDI extrapolates an observed stem number to a fixed index diameter of 25 cm, whereas 25.4 cm is used in Anglo-American forestry. The disadvantage of the SDI is that it generally assumes the coefficient $b = -1.605$ to be valid. Wherever this allometric coefficient fails to apply there will be severe errors in stand density estimates. This study shows that, in untreated fully stocked pure stands of common beech, the b value is lower than the generalized Reineke value $b = -1.605$. Although the deviations from -1.605 are only close to significant for common oak and Norway spruce, our results concerning differences among species suggest that at least one of these species' slopes differs from Reineke's generalized value, too.

If species-specific allometry is ignored, serious errors in the estimate and control of density when using $SDI = N \cdot (25/d)^{-1.605}$ may be the consequence. Figure 6 illustrates the concept of the SDI on the ln–ln scale. Let us assume O_1 stands for a pair of values consisting of the mean diameter d and the number of stems N in an old stand for which the SDI is to be found. Proceeding from the point O_1, a straight line with slope -1.605 (solid line) may then be extrapolated up to the index diameter 25 cm and the $SDI_R(O_1)$ (R stands for Reineke) may be read off. In analogy to the above, the same can be done with the $N–d$ value pair O_2 of a young stand. Again, from point O_2, proceed to extrapolate up to the index diameter of 25 cm. Provided the $\ln(N)–\ln(d)$ development of the stands obeys the slope $b = -1.605$, then $SDI_R(O_1) = SDI_R(O_2)$. Let us assume the slope of the $\ln(N)–\ln(d)$ relationship were actually $b = -1.8$ (dotted line). Then for O_1 the actual (SDI_{act}) would be considerably higher than SDI_R calculated on the basis of the Reineke exponent. In the case of O_2 we would have $SDI_{act}(O_2) < SDI_R(O_2)$.

If the $SDI_{act} = N \cdot (25/d)^b$, which is calculated with the use of the tree species-specific allometric coefficient b, is set in relation to $SDI_R = N \cdot (25/d)^{-1.605}$ the result is

$$k = \frac{SDI_{act}}{SDI_R} = \left(\frac{25}{d}\right)^{b+1.605}. \qquad (19)$$

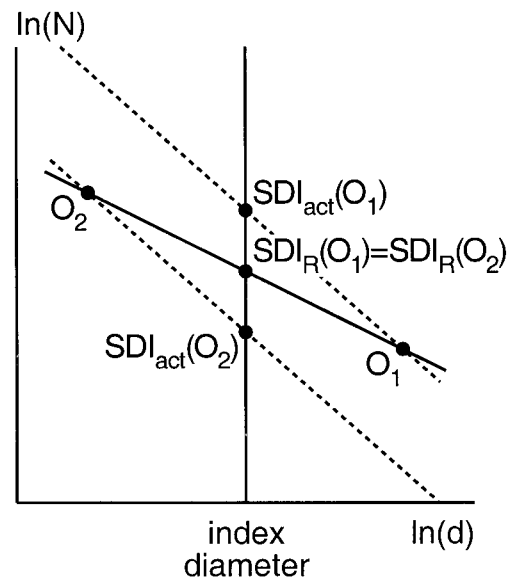The quotient k depends on the mean diameter d and on the difference between the actual species-specific and the as-

Figure 6. Bias in the determination of Reineke's SDI. If the $\ln(N)–\ln(d)$ relationship of a stand follows the slope $b = -1.605$ (solid line), the observed $\ln(N)–\ln(d)$ pairs of variates O_1 and O_2 will result in correct SDI values, i.e., $SDI_R(O_1) = SDI_R(O_2)$. If the allometric relationship is steeper ($b < -1.605$, dotted lines), this will result in an underestimate of SDI for diameters $d > 25$ cm and an overestimate for diameters $d < 25$ cm when slope $b = -1.605$ according to Reineke (1933) is used (SDI_R = SDI on the basis of Reineke's generalized $b = -1.605$, SDI_{act} = SDI on the basis of the stand specific b value; the index diameter in Europe is 25.0 cm, in the United States 10 inches = 25.4 cm).

sumed allometric coefficient $b = -1.605$. Table 5 provides the correction factor k for various mean diameters d and different actual slopes $b = -1.105$ up to -2.105 (cf. Equation 19). No extrapolation on the basis of the straight line $\ln(N)–\ln(d)$ is required if the mean diameter of any stand to be assessed comes to 25 cm. In this case and if the actual b value equals -1.605, the SDI will give correct density estimates ($k = 1$; central vertical and horizontal lines of the table). By contrast, if the actual curve drops more steeply than the slope ($b_{act} < -1.605$), then stands with diameters over 25 cm will have a tendency to be underestimated if the SDI is used, and vice versa for stands with lesser diameters (see upper part of Table 5). This bias will increase with rising Δb and will, moreover, be the greater the more the observed mean diameter deviates from the index diameter of 25 cm. For actual b values of -2.105, the SDI calculated by Reineke would have to be corrected by 0.45 ($d = 5$ cm) or 1.41 ($d = 50$ cm) to obtain the correct SDI. If the actual decrease in the number of stems is less than that from the Reineke relationship ($b_{act} > -1.605$) there will be a reversal of the relationship (see lower part of Table 5). In the latter case, the SDI values according to Reineke (1933) will have to be raised for stands with $d < 25$ cm and lowered for stands with $d > 25$ cm.

The use of Reineke's rule and SDI with $b = -1.605$ for determination of maximum density (Sterba 1975, 1981, 1987), control of stand density (Bergel 1985, Kramer and Helms 1985), or modeling of stand development (Pretzsch 2002b) is therefore called into question. For the SDI in

Table 5. Correction factor k, which adjusts biased SDI_R values to the actual species-specific SDI_{act} (cf. Equation 19)

b	Δb	$d = 5$	10	15	20	25	30	35	40	45	50
−2.105	−0.5	0.45	0.63	0.77	0.89	1	1.10	1.18	1.26	1.34	1.41
−2.005	−0.4	0.53	0.69	0.82	0.91	1	1.08	1.14	1.21	1.27	1.32
−1.905	−0.3	0.62	0.76	0.86	0.94	1	1.06	1.11	1.15	1.19	1.23
−1.805	−0.2	0.72	0.83	0.90	0.96	1	1.04	1.07	1.10	1.12	1.15
−1.705	−0.1	0.85	0.91	0.95	0.98	1	1.02	1.03	1.05	1.06	1.07
−1.605	0.0	1.00	1.00	1.00	1.00	1	1.00	1.00	1.00	1.00	1.00
−1.505	0.1	1.17	1.10	1.05	1.02	1	0.98	0.97	0.95	0.94	0.93
−1.405	0.2	1.38	1.20	1.11	1.05	1	0.96	0.93	0.91	0.89	0.87
−1.305	0.3	1.62	1.32	1.17	1.07	1	0.95	0.90	0.87	0.84	0.81
−1.205	0.4	1.90	1.44	1.23	1.09	1	0.93	0.87	0.83	0.79	0.76
−1.105	0.5	2.24	1.58	1.29	1.12	1	0.91	0.85	0.79	0.75	0.71

Compiled are k factors for slopes ranging from −2.105 to −1.105, Δb from −0.5 to 0.5, and diameters from 5 to 50 cm (SDI_R = SDI on the basis of Reineke's generalized b = −1.605, SDI_{act} = SDI on the basis of the stand-specific b value).

Norway spruce stands, Sterba (1981), using the Bavarian yield tables for Norway spruce by Assmann and Franz (1963) and assuming b = −1.605, calculated mean values of 970, 1,081, 1,203, and 1,336 for sites with 28, 32, 36, and 40 m top height at age 100 years. These values are quoted here to illustrate the extent to which values may be biased when erroneous b values are being used. Assuming we determine, according to Reineke, the SDI of a stand with mean diameter 10 cm to be 1,300, and assuming further that this stand actually follows a straight line with b = −1.805, then the determined SDI of 1,300 would have to be reduced by k = 0.83 (cf. Table 5). 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.

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