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Abstract

Relationships between diameter at breast height (dbh) versus stand density, and tree height versus dbh (height curve) were explored with the aim to find if there were functional links between correspondent parameters of the relationships, exponents and intercepts of their power functions. A geometric model of a forest stand using a conic approximation suggested that there should be interrelations between correspondent exponents and intercepts of the relationships. It is equivalent to a type of 'relationship between relationships' that might exist in a forest stand undergoing self-thinning, and means that parameters of one relationship may be predicted from parameters of another. The predictions of the model were tested with data on forest stand structure from published databases that involved a number of trees species and site quality levels. It was found that the correspondent exponents and intercepts may be directly recalculated from one another for the simplest case when the total stem surface area was independent of stand density. For cases where total stem surface area changes with the drop of density, it is possible to develop a generalization of the model in which the interrelationships between correspondent parameters (exponents and intercepts) may be still established.

Keywords (separated by '-'): Total stem surface area - Self-thinning - Conic approximation - Power function - Exponent - Intercept - Scots pine

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ORIGINAL PAPER

'Relationships between relationships' in forest stands: intercepts and exponents analyses

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Abstract Relationships between diameter at breast height (dbh) versus stand density, and tree height versus dbh (height curve) were explored with the aim to find if there were functional links between correspondent parameters of the relationships, exponents and intercepts of their power functions. A geometric model of a forest stand using a conic approximation suggested that there should be interrelations between correspondent exponents and intercepts of the relationships. It is equivalent to a type of 'relationship between relationships' that might exist in a forest stand undergoing self-thinning, and means that parameters of one relationship may be predicted from parameters of another. The predictions of the model were tested with data on forest stand structure from published databases that involved a number of trees species and site quality levels. It was found that the correspondent exponents and intercepts may be directly recalculated from one another for the simplest case when the total stem surface area was independent of stand density. For cases where total stem surface area changes with the drop of density, it is possible to develop a generalization of the model in which the interrelationships between correspondent parameters (exponents and intercepts) may be still established.

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Introduction

In forest science, a large proportion of studies represent the establishment of relationships—how one measure of a forest stand relates to another, the measures being either directly assessed or computed from basic values. Basic measures that can be obtained in the field include stem diameter (frequently as diameter at breast height), stem height and number of trees per unit area (stand density). For some time, forest mensuration practitioners have found that all three measures relate to each other, producing—as forest stand growth progresses—curvilinear interrelations (e.g., Chapman 1921).

The relationship between diameter at breast height (dbh) and stem height is known as a height curve. Typically, stem height increases in a curvilinear way with an increase in dbh and levels off closer to maximum diameter values. A number of mathematical functions have been proposed to fit height curves; they are often enumerated in forestry textbooks (Van Laar and Akça 2007) and include various polynomials, logarithmic, as well as simple power functions.

The development of stand density with time has been a frequent topic of forestry research but even greater attention has been given to relationships of various measures of tree size and number of trees because stand density has a profound effect on tree growth, and determination of stem

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Journal : Large 11676 | Dispatch : 10-8-2017 | Pages : 8
Article No. : 475 | LE | TYPESET
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growth, form and crown development. Most famous relationships are self-thinning rules by Reineke (1933) and Yoda et al. (1963) which link number of trees per unit area and mean tree size. Analyses of the intrinsic mechanics of the rules and their importance for contemporary forest science may be found in a number of studies (Sterba 1987, Pretzsch and Biber 2005; Pretzsch 2006; Vanclay and Sands 2009; Larjavaara 2010; Gavrikov 2015).

It can be noted from the literature that a relationship between stand variables is often studied separately from other relationships between variables in the same stand. Meanwhile, because of intense interactions between trees in dense forest stands, the interactions may influence all observable relationships leading to parameters of one relationship beginning to depend on parameters from another relationship. For example, a number of researchers explored covariations between exponents in relationships of biomass, tree height and dbh (Niklas and Spatz 2004; Zhang et al. 2016).

These 'relationships between relationships' present a rather profound interest because they may provide a deeper understanding of self-thinning in forest stands. Inoue (2009) developed an allometric model of maximum size–density that related stem surface area to stand density. To derive the model, Inoue (2009) considered allometric relationships between mean tree height H and mean surface area S, i.e., $H \propto S^{\alpha}$, on the one hand, and the relationship between biomass density B and mean surface area S, i.e., $B \propto S^{\beta}$, α and β being allometric exponents. When $\alpha + \beta \approx 1/2$, the total stem surface area becomes constant, independent of stand density. In other words, in the case of a constant total stem surface area, the allometric exponents can be predicted from one another and the study by Inoue (2009) gives an example of finding 'relationships between relationships'.

Gavrikov (2014) considered a geometrical model of a forest stand in which dependence of stem length l on dbh D (height curve) as well as dependence of D on stem density N (thinning curve) was analyzed. The relationships were presented as simple power functions in a generalized form such as $l(D) \propto D^{a}$ and $D(N) \propto N^{b}$, a and b being allometric exponents. When the total stem surface area remains constant and independent of stand density decrease, the exponents are tightly interrelated to each other and therefore one exponent may be predicted from the other. When the total stem surface area grows or falls with stand density decrease, the exponents predictably relate, more or less, to each other. It has been therefore shown how different relationships may be interconnected through power exponents.

Because of convenience of the mathematical form of the simple power function, the analysis of its exponents may be rather easy. History of self-thinning rule studies indicates that most of the attention was given to exponents. However an exponent is not the only parameter of power function. If one presents the simple power function as $Y = c \cdot X^{a}$ where X and Y are independent and dependent variables, respectively, then c will be the normalizing constant or coefficient. Coefficient c is also called an intercept because the function, when drawn in log–log coordinates, presents a straight line and the projection intercepts Y-axis at $X = 0$. In order to establish 'relationships between relationships' in full, both exponents and intercepts of the modeling functions have to be analyzed.

The aims of this study were: (1) to derive a modeling approach to interrelate two relationships in a forest stand, namely, height curve and dependence of mean diameter on stand density (thinning curve); and, (2) to apply the theoretical findings to available field data to find out how good the theory worked.

Materials and methods

Method

The method applied uses two approaches. The first consists in using total stem surface area $\hat{S}$ development as the basis of analysis. To get estimations of $\hat{S}$, a conic approximation of tree stem was used which is reflected in the product of dbh D, height H as suggested by Inoue (2004). For convenience, mean dbh is represented by mean stem radius r and mean stem height is substituted through cone generatrix l. The latter implies that because trees are narrow, long shapes, the genuine stem height is approximately equal to the generatrix, $l \approx H$, though a small loss of accuracy may take place. Thus total stem surface area is given through:

$$\widehat{S} = \delta \pi r l \cdot N, \tag{1}$$

where δ is a normalization constant that will be discussed under Results and Discussion. The second indicates that height curve $l(r)$, thinning curve $r(N)$ and $\hat{S}(N)$ may be analyzed through fitting by simple power functions. The supposition meets no difficulties with $l(r)$ and $r(N)$ since they are mostly monotonic curves. The total stem surface area develops, however, in such a way that the curve often appears to be non-monotonic; it may grow and it may fall. It is supposed, nevertheless, that monotonic sections of the non-monotonic curves may be fitted by power functions and parameters of the functions rightly reflect properties of the curve sections. It is use of power functions that enables a transparent analytical modeling of relationships between forest stand measures in this study. Though use of power functions does not imply that they are the best functions for fitting, it is expected that power functions do provide valuable information on the relationships studied.

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Journal : Large 11676 | Dispatch : 10-8-2017 | Pages : 8
Article No. : 475 | LE | TYPESET
MS Code : 17_00032 | CP | DISK

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The monotonic sections of $\hat{S}(N)$ are referred to here as 'tendencies'. It is supposed that stand density N can only decrease (thinning or self-thinning). A growing tendency is observed when $\hat{S}$ increases during a decrease of N. If $\hat{S}$ stays constant independent of N, this is called a flat tendency. Consequently, if $\hat{S}$ decreases with decreasing N this is called a falling tendency.

Data used

To evaluate the results of modeling, a number of datasets was extracted from a database published by Usoltsev (2010). The database contains about 10,000 descriptions of sample plots in various forest stands over the whole of Eurasia. As a rule, each description includes data on species, bonitet (Russian system of site quality estimation), mean dbh, mean height, stand density per ha and other information. The descriptions are combined in groups by name of author and geographic location where the data were gathered. From these groups, the data on individual sample plots were collected to provide datasets for the study.

One of the problems with most of the published data is that they present static descriptions of different stands while modeling implies a dynamic situation. For the purposes of this study, descriptions within a group were collected in such a way that they resembled the development of one forest stand with time. In other words, to get datasets the descriptions had to be sub-sampled. Within datasets, the data may be differentiated by bonitet (site index). It is important to note that some datasets had to be divided into sections in which a monotonic development of $\hat{S}(N)$ is observed as explained above. Such sections are denoted as having either flat, growing or a falling tendency of the total stem surface area development in the course of thinning. All the datasets were denoted by the names of the authors as cited by Usoltsev (2010). Table 1 gives an overview of the datasets used. The development of the total stem surface area with thinning in all the datasets is given graphically in Electronic Supplement (fig. S1 through fig. S19).

Estimations of regression parameters in the relationships studied were performed with STATISTICA 6 software. The software has the module of non-linear estimation that provides the tools to perform various regressions based on different loss functions. In this study, ordinary least squares were used as the loss function that was minimized by the software through the Levenberg–Marquardt algorithm. The user-specified regression model was a two-parameter power function of the form $Y = c \cdot X^a$ where Y and X are dependent and independent variables, respectively; c and a are intercept and exponent, respectively.

Results and discussion

Model and its analysis

The first part of the model is based on Eq. 1 that allows the generating of hypotheses on how total stem surface area may depend on stand density. As a reference point, consider the case where total stem surface area is equal to a constant C and therefore independent of N. To find this in a real forest stand is not improbable, and has been reported in a number of publications (Gavrikov 2014; Inoue and Nishizono 2015). In other words, there is a flat tendency in the development of $\hat{S}(N)$. Through generalization, other tendencies may be further studied. From Eq. 1 one can therefore get an expression for $l(r)$:

$$l = \frac{C}{\delta \pi r N}. \tag{2}$$

By contrast to the analysis of exponents only, a model including intercepts as well requires a thorough consideration of dimensions. In the data used here, stand density N is given in number of trees per hectare (ha^{-1}). Because C is implied to be in square meters m^2 and l and r are naturally in meters, δ has to be in ha or m^2; for consistency, ha units are converted into m^2 in all further calculations. According to Eq. 1, δ gives an idea of proportion between 'genuine' stem surface area and the area for the conic approximation of stem.

The second part of the model comes from the consideration of tree radius r dependence on stand density N. It is admitted here that the relationship $r(N)$ may be represented as in a geometric model of forest stand (Gavrikov 2014):

$$r = \varepsilon \sqrt{\frac{1}{N^{\gamma}}}, \tag{3}$$

where ε is a normalization constant. Resolving of N given in ha^{-1} from the square root gives $\sqrt{\frac{\mathrm{ha}^{\gamma}}{N^{\gamma}}} = \frac{\mathrm{ha}^{\frac{\gamma}{2}}}{N^{\frac{\gamma}{2}}} = (10000\ \mathrm{m}^2)^{\frac{\gamma}{2}} \cdot N^{-\frac{\gamma}{2}} = 100^{\gamma}\ \mathrm{m}^{\gamma} \cdot N^{-\frac{\gamma}{2}}$ and therefore Eq. 3 may be rewritten as

$$r = \varepsilon \cdot (100\ \mathrm{m})^{\gamma} \cdot N^{-\frac{\gamma}{2}}, \tag{4}$$

where N is dimensionless and ε has to be in m$^{1-\gamma}$ since r is naturally expressed in m.

To ensure that l in Eq. 2 depends only on r, N may be resolved from Eq. 4 as $N = \frac{r^{-\frac{2}{\gamma}}}{\varepsilon^{-\frac{2}{\gamma}} \cdot 100^{-2}}$ and substituted to Eq. 2 to get the final form of $l(r)$ relationship:

$$l = \frac{C}{\delta} \cdot \frac{1}{100^2 \cdot \pi \cdot \varepsilon^{\frac{2}{\gamma}}} \cdot r^{\frac{2}{\gamma}-1}. \tag{5}$$

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Journal : Large 11676 | Dispatch : 10-8-2017 | Pages : 8
Article No. : 475 | LE | TYPESET
MS Code : 17_00032 | CP | DISK

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Table 1 Overview of datasets used in the study

Dataset name[a], tendency[b], figure[c]	Geographic location	Species, origin	Bonitet[d]	Range[e] of ages/densities
Mironenko-98, p. 239, flat, fig. S1	Tambov region, Russia	*Pinus sylvestris*, cultures	I	70–150/702–309
Mironenko-98, p. 239, growing, fig. S1	Tambov region, Russia	*Pinus sylvestris*, cultures	Ia	50–90/960–515
Uspenski-87, p. 240, flat, fig. S2	Tambov region, Russia	*Pinus sylvestris*, cultures	I	30–60/1533–513
Uspenski-87, p. 240, flat, fig. S4	Tambov region, Russia	*Pinus sylvestris*, cultures	III	60–120/1138–370
Uspenski-87, p. 240, flat, fig. S4	Tambov region, Russia	*Pinus sylvestris*, cultures	II	40–100/1655–333
Uspenski-87, p. 240, growing, fig. S2	Tambov region, Russia	*Pinus sylvestris*, cultures	I	10–30/4240–1931
Uspenski-87, p. 240, growing, fig. S3	Tambov region, Russia	*Pinus sylvestris*, cultures	Ia	10–30/4182–1271
Uspenski-87, p. 240, falling, fig. S2	Tambov region, Russia	*Pinus sylvestris*, cultures	I	80–120/354–171
Uspenski-87, p. 240, falling. S3	Tambov region, Russia	*Pinus sylvestris*, cultures	Ia	40–100/656–199
Lebkov-97, p. 203, flat, fig. S5	Vladimir region, Russia	*Pinus sylvestris*, natural forests	I	25–77/4331–687
Heinsdorf-90, p. 56, flat, fig. S6	Eberswalde, Germany	*Pinus sylvestris*, natural forests	II	25–50/9399–1838
Heinsdorf-90, p. 56, falling, fig. S6	Eberswalde, Germany	*Pinus sylvestris*, natural forests	I	50–120/1385–258
Yildirim-78, p. 54, flat, fig. S7	Niedersachsen, Germany	*Picea abies*	I	30–55/3576–1387
Yildirim-78, p. 54, falling, fig. S7	Niedersachsen, Germany	*Picea abies*	I	75–100/804–416
Boiko-86, p. 36, flat, fig. S8	Belorussia	*Quercus robur*	I	40–80/1650–498
Boiko-86, p. 36, flat, fig. S8	Belorussia	*Quercus robur*	II	50–100/1392–435
Boiko-86, p. 36, flat, fig. S8	Belorussia	*Quercus robur*	III	40–90/2692–593
Boiko-86, p. 36, falling, fig. S9	Belorussia	*Quercus robur*	I	90–180/410–166
Boiko-86, p. 36, falling, fig. S9	Belorussia	*Quercus robur*	II	110–180/370–200
Moeller-46, p. 62, flat, fig. S10	Denmark	*Fagus sylvatica*	I	40–55/2176–860
Hellrigl-74, p. 69, flat, fig. S11	Italy	*Abies alba*	Ia	55–90/1060–549
Hellrigl-74, p. 69, growing, fig. S11	Italy	*Abies alba*	Ia	20–50/2548–1189
Kharitonov-71, p. 71, flat, fig. S12	Kazakhstan	*Picea schrenkiana*	II	130–230/302–244
Kharitonov-71, p. 71, flat, fig. S12	Kazakhstan	*Picea schrenkiana*	III	130–230/412–340
Kharitonov-71, p. 71, growing, fig. S12	Kazakhstan	*Picea schrenkiana*	III	50–130/992–412
Nurpeicov-76, p. 74, flat, fig. S14	Kazakhstan	*Pinus sylvestris*, natural forests	II	30–100/4848–703
Nurpeicov-76, p. 74, growing, fig. S14	Kazakhstan	*Pinus sylvestris*, natural forests	III	30–100/5902–939
Gruk-79, p. 30, growing, fig. S15	Belorussia	*Pinus sylvestris*, cultures	I	10–40/7274–2449
Kozhevnikov-84, p. 31, growing, fig. S16	Belorussia	*Pinus sylvestris*, cultures	I	15–60/7510–1360
Gabeev-90, p. 482, growing, fig. S17	Novosibirsk region, Russia	*Pinus sylvestris*, cultures	I	10–50/6763–1709
Ellenberg-86, p. 59, growing, fig. S18	Solling, Germany	*Fagus sylvatica*	III	62–67/2680–2400
Kurbanov-02, p. 211, falling, fig. S19	Yoshkar-Ola region, Russia	*Pinus sylvestris*, natural forests	I	76–128/745–259

[a] The dataset names are given according citations in Usoltsev (2010), the page number is also provided; a dataset may be sub-divided into bonitets

[b] Tendency of total stem surface area development in the course of thinning (flat or growing or falling)

[c] Reference to figure number in Electronic Supplement

[d] Russian system of bonitation, Ist bonitet being the best and Vth bonitet being the worst conditions; bonitets are given as in Usoltsev (2010)

[e] Ages in years, stand densities in trees per hectare

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In Eq. 4, there is only one unknown multiplier in the intercept (ε) and only one unknown term in the exponent (γ).

In Eq. 5, the expression *C/δ* is written as a separate ratio for the following reason. It follows from Eq. 5 that one does not have to know *C* and δ separately but only their ratio. This ratio may be determined from Eq. 2 as $C/\delta = \pi r l N$. In the right-hand term, the multipliers are either known or may be found from data and therefore the ratio C/δ may also be known. Hence, there is only one unknown term in the exponent of relation Eq. 5 (γ). After the term γ is estimated from data then only one term remains unknown in the intercept $K = \frac{C}{\delta} \cdot \frac{1}{100^2 \cdot \pi \cdot \varepsilon^{\frac{2}{\gamma}}}$ of Eq. 5; the term is ε.

As a result of the derivation of Eqs. 4 and 5, both relationships contain the same parameter ε in their

Journal : Large 11676 | Dispatch : 10-8-2017 | Pages : 8
Article No. : 475 | ☐ LE | ☐ TYPESET
MS Code : 17_00032 | ☑ CP | ☑ DISK

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intercepts and the same parameter γ in their exponents. Under the above supposition of constancy of $\hat{S}(N)$, this means that if the values of intercept and exponent in Eq. 4, for example, are known, then the corresponding values of intercept and exponent in Eq. 5 should be also computable.

To avoid confusion because γ and ε are estimated by separate fitting operations, relationships Eqs. 4 and 5 should be rewritten as follows:

$$l = \frac{C}{\delta} \cdot \frac{1}{100^2 \cdot \pi \cdot \varepsilon_1^{\frac{2}{\gamma_1}}} \cdot r^{\frac{2}{\gamma_1}-1} \quad (6)$$

and $r = \varepsilon_2 \cdot 100^{\gamma_2} \cdot N^{-\frac{\gamma_2}{2}}$. (7)

The introduction of inferior indices at γ and ε allows for the formulating of a clear hypothesis that should be verified. I If total stem surface area $\hat{S}$ is constant and independent of stand density, the values γ and ε should follow $\gamma_1 = \gamma_2$ and $\varepsilon_1 = \varepsilon_2$; if not constant, then $\gamma_1 \neq \gamma_2$ and $\varepsilon_1 \neq \varepsilon_2$.

Estimations of intercept and exponent components ε and γ

Equation 7 was used for fitting against the data. Equation 6 however, had to be fitted first as $l = K \cdot r^{\frac{2}{\gamma_1}-1}$ and then, having known values of γ_1 and K, value ε_1 was found. To compute the value ε_1 for a dataset, the value of ratio C/δ was taken as the mean product πrlN for this particular dataset.

Results of the fittings are given in Table 2. Coefficient of determination (R^2) of relations in the fitted data is usually rather high, with a single exclusion. Figures 1 and 2 depict graphically the data from Table 2. Datasets that have a flat tendency is prone to the line denoting $\gamma_1 = \gamma_2$. Datasets with growing tendencies are located *consistently* in the area above the line where $\gamma_1 < \gamma_2$. Datasets with falling tendencies are located *consistently* below the line, i.e., where $\gamma_1 > \gamma_2$. Because datasets with growing tendencies are mostly from younger, dense stands and datasets with falling tendencies are from older, sparse ones, it is quite plausible that when tendencies change from growth to decline, the values of γ_1 and γ_2 satisfy $\gamma_1 = \gamma_2$.

Moeller-46 dataset presents a noticeable deviation from the $\gamma_1 = \gamma_2$ condition (Fig. 1, rightmost closed circle). The cause of this deviation is not known but the dataset was the only that showed low confirmation of the relation $l(r)$ (height curve) (Table 2). As noted previously, each dataset resembles the development of an individual forest stand. Perhaps the Moeller-46 dataset does not quite satisfy this assumption (see also fig. S10 in the Electronic Supplement).

Figure 2 plots ε_1 against ε_2. As with the γ parameter, values of ε_1 and ε_2 for datasets with a flat tendency of $\hat{S}(N)$ development are very close to the straight line in Fig. 2. Again, datasets with a growing tendency are located *consistently* below the line denoting the condition $\varepsilon_1 > \varepsilon_2$ and datasets with a falling tendency are located *consistently* above the line that means $\varepsilon_1 < \varepsilon_2$. It may be therefore quite plausible that $\varepsilon_1 = \varepsilon_2$ when a growing tendency turns into a falling one through a flat tendency.

Among the datasets, more than half are Scots pine data. Fourteen of the total 32 datasets belong to other species. The computations showed no definite patterns relating to species, which may mean that the application of the approach depends not on species but solely on how total stem surface area develops with stand density decrease. The question of species influence requires, however, larger studies involving more data. From the data here, it might be inferred that, in terms of ε values, Scots pine tends to occupy a middle position among other species involved.

Generalization of model

It has been shown previously that qualitative information of tendencies in $\hat{S}(N)$ development allows predicting of interrelations between correspondent intercepts of $l(r)$ and $r(N)$ relationships and between correspondent exponents of these relationships. If the tendency of $\hat{S}(N)$ is flat, i.e., $\hat{S}(N)$ is a constant, then $\varepsilon_1 = \varepsilon_2$ and $\gamma_1 = \gamma_2$. But if it is known that tendencies are growing or falling, then only predictions $\varepsilon_1 > \varepsilon_2$, $\gamma_1 < \gamma_2$ or $\varepsilon_1 < \varepsilon_2$, $\gamma_1 > \gamma_2$, respectively, are possible.

Let us consider a generalization of the model when a quantitative description of tendencies is available. In compliance with the approach used here, dependence of $\hat{S}(N)$ within monotonic sections may be given as a power function. Use of a power function form provides consistency throughout the model and a possibility to derive an analytical solution.

Thus, $\hat{S}(N)$ is presented as:

$$\hat{S} = \delta \pi r l N = A \cdot N^{\lambda}, \quad (8)$$

where A is a normalization constant and λ is an exponent. It is λ that quantitatively describes monotonic segments of $\hat{S}(N)$ (tendencies). λ may be received through independent measurements. By analogy with derivations made above, $l = \frac{A}{\delta} \cdot \frac{1}{\pi r N^{1-\lambda}}$ and because (after resolving from Eq. 4 and raising to the power of $1 - \lambda$) $N^{1-\lambda} = \frac{r^{-\frac{2}{\gamma}(1-\lambda)}}{\varepsilon^{-\frac{2}{\gamma}(1-\lambda)} \cdot 100^{-2(1-\lambda)}}$ the new expression for $l(r)$ will look as follows:

$$l = \frac{A}{\delta} \cdot \frac{1}{\pi \varepsilon_1^{\frac{2}{\gamma_1}(1-\lambda)} \cdot 100^{-2(1-\lambda)}} \cdot r^{\frac{2}{\gamma_1}(1-\lambda)-1}. \quad (9)$$

Journal : Large 11676 | Dispatch : 10-8-2017 | Pages : 8
Article No. : 475 | LE | TYPESET
MS Code : 17_00032 | CP | DISK

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Table 2 Results of computations of parameters ε and γ in relationships *l*(*r*) and *r*(*N*)

Dataset[a]	*l*(*r*)[d]					*r*(*N*)[d]				
	R^2	ε_1	SE[c]	γ_1	SE	R^2	ε_2	SE	γ_2	SE
Flat tendency[b]										
Mironenko-98, I	0.9727	0.0250	0.0009	1.219	0.023	0.9996	0.0246	0.0003	1.229	0.007
Uspenski-87, I	0.9990	0.0246	0.0005	1.104	0.009	0.9998	0.0246	0.0002	1.103	0.007
Uspenski-87, III	0.9991	0.0238	0.0004	1.128	0.009	0.9998	0.0258	0.0004	1.070	0.009
Uspenski-87, II	0.9984	0.0239	0.0006	1.119	0.013	0.9992	0.0247	0.0008	1.096	0.020
Lebkov-97, I	0.9759	0.0289	0.0029	1.157	0.043	0.9898	0.0316	0.0022	1.069	0.062
Heinsdorf-90, II	0.9971	0.0288	0.0014	1.200	0.019	0.9997	0.0294	0.0003	1.157	0.015
Yildirim-78, Picea abies, I	0.9925	0.0363	0.0029	0.972	0.029	0.9982	0.0367	0.0009	0.959	0.026
Boiko-86, Quercus robur, I	0.9975	0.0242	0.0006	1.217	0.014	0.9989	0.0246	0.0008	1.205	0.025
Boiko-86, Quercus robur, II	0.9994	0.0237	0.0003	1.213	0.006	0.9999	0.0231	0.0001	1.234	0.004
Boiko-86, Quercus robur, III	0.9975	0.0227	0.0006	1.234	0.013	0.9998	0.0229	0.0002	1.224	0.008
Moeller-46, Fagus sylvatica, I	0.4161	0.0220	0.0149	1.357	0.203	0.9189	0.0269	0.0038	1.163	0.135
Hellrigl-74, Abies alba, Ia	0.9954	0.0325	0.0006	1.255	0.013	0.9998	0.0318	0.0003	1.271	0.008
Kharitonov-71, Picea schrenkiana, II	0.9966	0.0206	0.0004	1.218	0.014	0.9997	0.0204	0.0004	1.224	0.011
Kharitonov-71, Picea schrenkiana, III	0.9808	0.0214	0.0012	1.215	0.034	0.9979	0.0229	0.0010	1.174	0.027
Nurpeicov-76, II	0.9809	0.0291	0.0028	1.183	0.042	0.9998	0.0299	0.0003	1.156	0.008
Growing tendency										
Mironenko-98, Ia	0.9565	0.0277	0.0027	1.130	0.047	0.9997	0.0231	0.0003	1.267	0.010
Uspenski-87, I	0.9925	0.0242	0.0027	0.898	0.027	0.9556	0.0140	0.0021	1.809	0.227
Uspenski-87, Ia	0.9944	0.0257	0.0020	0.992	0.026	0.9894	0.0193	0.0017	1.338	0.090
Gruk-79, I	0.9801	0.0298	0.0046	0.882	0.036	0.9594	0.0228	0.0017	1.522	0.142
Kozhevnikov-84, I	0.9947	0.0292	0.0019	1.083	0.024	0.9901	0.0241	0.0018	1.434	0.091
Gabeev-90, I	0.9996	0.0321	0.0007	0.973	0.008	0.9226	0.0188	0.0055	1.846	0.380
Ellenberg-86, Fagus sylvatica, III	0.9868	0.0270	0.0026	1.096	0.033	0.9925	0.0124	0.0009	2.231	0.111
Hellrigl-74, Abies alba, Ia	0.9974	0.0368	0.0011	0.994	0.012	0.9909	0.0152	0.0013	1.972	0.090
Kharitonov-71, Picea schrenkiana, III	0.9993	0.0376	0.0006	1.009	0.008	0.9982	0.0184	0.0010	1.313	0.035
Nurpeicov-76, III	0.9767	0.0293	0.0041	1.087	0.050	0.9992	0.0272	0.0006	1.196	0.022
Falling tendency										
Uspenski-87, I	0.9998	0.0206	0.0001	1.186	0.003	0.9996	0.0272	0.0005	1.037	0.010
Uspenski-87, Ia	0.9994	0.0218	0.0002	1.166	0.006	0.9999	0.0269	0.0001	1.042	0.003
Yildirim-78, Picea abies, I	0.9760	0.0262	0.0018	1.256	0.043	0.9635	0.0607	0.0067	0.662	0.076
Heinsdorf-90, I	0.9986	0.0240	0.0003	1.277	0.008	0.9991	0.0352	0.0008	1.017	0.013
Kurbanov-02, I	0.8863	0.0266	0.0043	1.181	0.085	0.9721	0.0480	0.0050	0.775	0.065
Boiko-86, Quercus robur, I	0.9883	0.0153	0.0003	1.442	0.016	0.9999	0.0286	0.0002	1.108	0.003
Boiko-86, Quercus robur, II	0.9896	0.0145	0.0003	1.473	0.016	0.9997	0.0290	0.0004	1.094	0.008

[a] Datasets are denoted by name of authors from the book by Usoltsev (2010), all the datasets are depicted in the Electronic Supplement; if a species is not given, it means that the species = *Pinus sylvestris*; I, II etc. mean Ist bonitet, IInd bonitet etc., respectively, which denote site quality in Russian system of bonitation, Ist bonitet being the best and Vth bonitet being the worst conditions

[b] Tendency in the relationship $\hat{S}(N)$, where $\hat{S}$ is total stem surface area and N stand density; the tendencies may be 'flat' (no change of $\hat{S}$ with N decrease), 'growing' (increase of $\hat{S}$ with N decrease) or 'falling' (decrease of $\hat{S}$ with decrease of N)

[c] Standard error, the standard errors are given on the right from correspondent parameter values

[d] Relationships between studied stand measures: between mean stem length (a proxy of mean height) l and mean stem radius r, between mean stem radius r and stand density N

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The ratio A/δ may be derived from Eq. 8 as $\pi r l N^{1-\lambda}$ where all the terms are supposed to be known. By analogy with Eq. 6, there is one unknown term γ_1 in the exponent and one unknown term ε_1 in the intercept of Eq. 9. Equation 9 obviously generalizes the model because the case of $\lambda = 0$, which means a flat tendency in $\hat{S}(N)$, reduces Eq. 9

Journal : Large 11676 | Dispatch : 10-8-2017 | Pages : 8
Article No. : 475 | ☐ LE | ☐ TYPESET
MS Code : 17_00032 | ☑ CP | ☑ DISK

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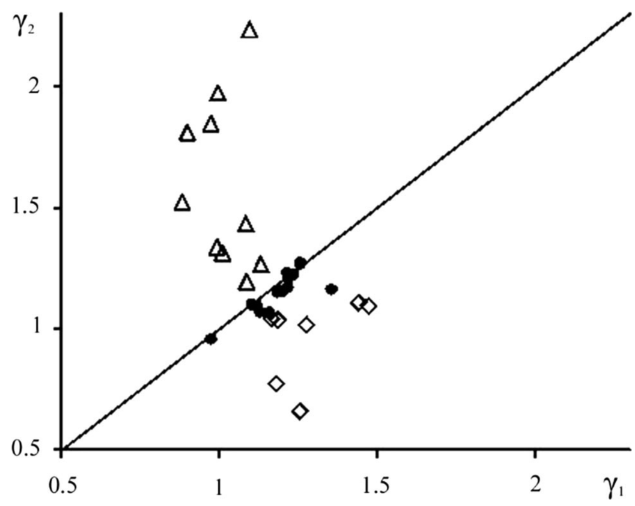

Fig. 1 Values of γ_1 plotted against γ_2 for all datasets. Key: *filled circle* datasets with a flat tendency of $\hat{S}(N)$ development, *open triangle* datasets with a growing tendency and *diamond* datasets with a falling tendency. Straight *solid line* denotes the position when $\gamma_1 = \gamma_2$

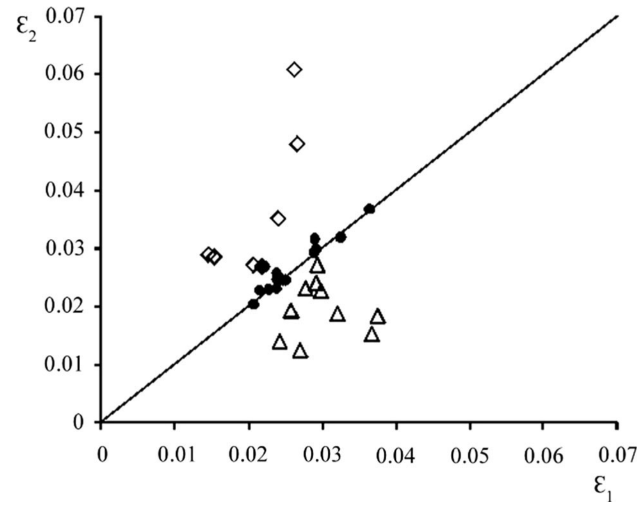

Fig. 2 Values of ε_1 plotted against ε_2 for all datasets. Legends are same as in Fig. 1. Straight *solid line* denotes the position when $\varepsilon_1 = \varepsilon_2$

to old form of Eq. 6. Note that Eq. 8 has an impact only on $l(r)$ relationship while $r(N)$ remains in the old form of Eq. 7.

Hypothetically, as it follows from Eqs. 9 and 7, provided λ is known, relations may be established between correspondent exponents in $l(r)$ and $r(N)$ as well as between intercepts in them. In other words, knowing λ and an exponent in $l(r)$, the exponent in $r(N)$ may be computed since γ_1 in Eq. 9 is hypothetically equal to γ_2 in Eq. 7. The same is hypothetically true for the intercepts, i.e., ε_1 in Eq. 9 is equal to ε_2 in Eq. 7. To verify the hypothesis, computations for dataset may be carried out, for example, the Mironenko-98 dataset, Ia bonitet, that shows a slightly growing tendency (fig. S1 in Electronic Supplement). Since Eq. 8 does not have an impact on Eq. 7, the values of $\gamma_2 = 1.267$ and $\varepsilon_2 = 0.023$ (Table 2, Mironenko-98, Ia) are ready for comparison and γ_1 and ε_1 have to be computed. Exponent λ of Eq. 8 for this dataset is $\lambda = -0.1192$ (SE = 0.0523, significant at $p < 0.1$). Next, fitting of the dataset with $l = P \cdot r^{\frac{2}{\gamma_1}(1-\lambda)-1}$ (see Eq. 9) gives $\gamma_1 = 1.265$ (SE = 0.0524, significant at $p < 0.05$), $P = 124.07$ (SE = 18.8, significant at $p < 0.05$), $R^2 = 0.9565$. Already at this point one can note that independently estimated γ_1 (1.265) and γ_2 (1.267) are close to each other. The value of ε_2 has to be extracted from P. As noted previously, the value of A/δ ratio was taken as mean value of $\pi r l N^{1-\lambda}$ for the dataset; the value was $A/\delta = 14{,}962.2$. Then, resolving ε_1 from $P = \frac{A}{\delta} \cdot \frac{1}{\pi \varepsilon_1^{\frac{2}{\gamma_1}(1-\lambda)} \cdot 100^{-2(1-\lambda)}}$ $\varepsilon_1 = \left(1496.2 \cdot \frac{1}{\pi} \cdot \frac{1}{124.07}\right)^{\frac{1.265}{2(1+0.1192)}} \cdot \frac{1}{100^{1.265}} \approx 0.0232$, SE was estimated as 0.0023.

Again, it is clear that independently estimated ε_1 (0.0232) and ε_2 (0.0231) are close to each other.

To summarize, if $\hat{S}(N) = \text{constant}$, then exponents in $l(r)$ (Eq. 6) and $r(N)$ (Eq. 7) are tightly related to each other so that information on one exponent may help to compute the other one. This is done through a common term γ in the exponents. Also, intercepts in $l(r)$ (Eq. 6) and $r(N)$ (Eq. 7) can be computed from one another through a common term ε. If $\hat{S}(N) \neq \text{constant}$ but only a tendency in $\hat{S}(N)$ is known, then relations between the exponents and intercepts may be estimated in terms of 'more/less'.

If however, $\hat{S}(N)$ may be represented as a power function of N, i.e., $\hat{S}(N) = A \cdot N^{\lambda}$ and λ may be quantitatively estimated, then exponents in $l(r)$ (Eq. 9) and $r(N)$ (Eq. 7) can be readily computed from one another with the help of λ value. The same is true for the intercepts; they can be computed from one another as well.

Conclusion

Numerous relationships have been established in forest science that served to describe structure and growth of forest stands. Some, like the '–3/2 self-thinning rule', were derived from other relations linking sizes of trees to stand density.

In this study, the 'relationships between relationships' was considered; the H versus D relationship (height curve) was sought to quantitatively relate to the D versus N relationship (thinning curve). In order to provide mathematical consistency, all analyzed relations were presented in the form of simple power functions that included an exponent and an intercept. It has been shown that putting hypotheses

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Journal : Large 11676 | Dispatch : 10-8-2017 | Pages : 8
Article No. : 475 | LE | TYPESET
MS Code : 17_00032 | CP | DISK

on how total stem surface area develops during self-thinning or thinning helps to find analytical links between exponents/intercepts of the height curve and exponents/intercepts of the thinning curve. If it is known that total stem surface area does not change in the course of thinning or an exponent is known of the area dependent on stand density, the exponents/intercepts in the relationships may be directly computed from one another. This implies an existence of profound processes that govern the development of a forest stand and this deepens our knowledge on this development. Why such ‘relationships between relationships’ may appear is a topic of special research, but it may be hypothesized that the source of the phenomenon lies in interactions of trees in the course of growth, competition and dying-off.

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