Estimation, Theoretical Reasoning and Use of Growth Curves for Young Norway Spruces in Experimental Plantations in Estonia

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The height growth of up to 22-year-old Norway spruces was modelled using the power transformation $y^\beta = ct$, which allows to easily linearise the growth curve. Exponent β was estimated from the data of five experimental plantations in Estonia. The optimal value for β was found to be in between 1/4 and 1/3. The linear dependence of power-transformed height on tree age is argued also theoretically using simple biophysical assumptions that the increment of the timber volume of the tree depends on the volume of the photosynthetically active tree crown, while the latter depends on tree height. The proposed linearisation method is recommended for the preliminary transformation of growth data prior to the general linear statistical analysis of provenance data.

Key words: Norway spruce, linearisation of the height growth curve, allometric growth, statistic analysis of the height growth

Introduction

Growth of forest trees and stands has been one of the main topics of forest research for many decades. Over one hundred growth functions are proposed in the literature. An excellent overwiev and a critical analysis of a multitude of growth functions are presented in monographs completed under the supervision of A. Kiviste (Кивисте 1988, Kiviste *et al*. 2002). Typically, a growth function starts from zero and it can be expressed in the form

$$y = cf(t), \qquad (1)$$

where *y* is height, diameter, volume or some other variable of the tree or stand, *t* is the age of the tree or stand, *f(t)* is some nonlinear transformation of age, and *c* is the coefficient of proportionality. Function *f(t)* has usually an inflection point and a horizontal asymptote (Кивисте 1988). Growth of young stands can still be approximated with some type of concave functions as $y = ct^\alpha$ with $\alpha > 1$. The function

$$y = ct^\alpha \qquad (2)$$

is called allometric and can be linearised as

$$log(y) = log(c) + \alpha log(t) \qquad (3)$$

(Кивисте 1988). Some new useful recommendations for fitting this function to the scattered data of field experiments are given by A. Nilson (Nilson 2002).

In the present paper we focus on the use of growth functions as means of linearization of the interdependence between tree age and height. We suggest the use of the allometric function in the form of

$$y^\beta = ct \qquad (4)$$

and we will motivate this approach both experimentally and theoretically. Allometric transformation (4) is a simple and effective tool for data linearisation when comparing the growth of young spruce stands of different provenance. After this transformation, powerful statistical methods of a general linear analysis will become available. Transformation (4) contains only two parameters (c and β) describing the intensity of growth and its linearity. It was found in the master's thesis of R. Pihu (2002) that for the up to 22-year-old spruces of Estonian provenance, the choice β = 1/3 in (4) yields an almost linear relationship between the transformed height $h^{0.333}$ and tree age. Besides this, the variance of transformed height does not depend significantly on tree height what is essential for the correctness of statistical inference (homoscedasticity condition). In the present paper we improve the results of the above thesis.

Besides the data analytical argumentation, we demonstrate that the allometric relationship (4) follows from a few simple biophysical assumptions about tree growth, and it can therefore be considered a natural growth model for young trees. In this analysis, the height growth rate of trees is expressed mathematically proceeding from the conjecture that the increment of timber volume per year depends on the rate of photosynthesis in the live crown, while the size of the latter depends on the height of the tree. This theoretical argumentation makes linearisation (4) more transparent compared with commonly used logarithmic transformation (3).

Material and methods

Empirical material

The method of linearisation of the height growth of young spruces was worked out on the basis of the material collected from five experimental plantations during 1997–2000 (Pihu 2002): 1) two plantations in the Jäärja forest district in South-West Estonia (established in 1983 and 1985, the age of the measured trees was 22 and 18 years, respectively), 2) one plantation in the Triigi forest district in North Estonia (established in 1985, age of trees was 17 years), 3) two plantations in the Ilumetsa forest district in South-East Estonia (established in 1987 and 1988, age of trees was 15 and 14 years, respectively).

The measured trees (all of Estonian origin) were grown from the following seed lot types: 1) seeds from a plus tree (21 trees); 2) seeds from a random tree (2 trees); 3) seed mixture from several plus trees (6 trees); 4) bulk seed lots from the former Võru and Elva (both in South-East Estonia) and Viljandi (in South-West Estonia) forest enterprises. Seeds from plus trees and random trees were collected from vegetative seed orchards.

The data of the height of 3190 trees (measured at the age of 14–22 years) and the averages calculated earlier for the corresponding provenances (trees of age 2–10 years) were used in the analysis.

Methods of statistical analysis

Prior to analysis, tree height measurements were transformed using involution h^β where h is tree height and the exponent is a fixed number between 0 and 1. Regression analysis was carried out with the GLM procedure of the statistical package SAS, Release 8.1. The transformed heights for various β were approximated by the cubic polynomial of time t. Linearity of time dependence was measured by the value of the F-

statistic corresponding to the null hypothesis "h^β depends on t linearly".

Results

Empirical results

The regression line for the natural height values is presented in Figure 1. The yearly height increment of the older trees is clearly larger than that of the younger trees. Variation of the height measurements increases with age. For the trees younger than 14 years, the plotted height values represent the average values of about 30 trees and have therefore an even lower variation.
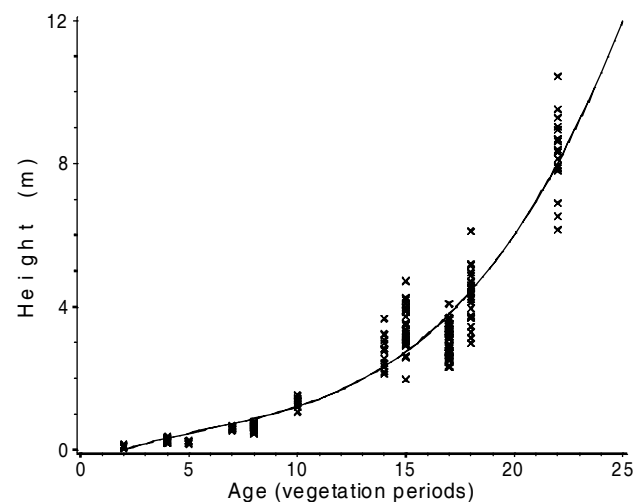

Figure 1. Height growth of studied young Norway spruce trees in Estonia

In Figure 2, the tree heights h are transformed to $h^{0.25}$ and plotted against the time t. It can be seen that after this transformation, regression is almost linear and the variation of the transformed values is much more stable. As for the young trees, height h is an average value of about 30 trees, the variance of the plotted values is still lower than it is for the older trees presented by single values.

The value 0.25 for β was obtained by experimenting with different ā values and estimating the linearity of dependence visually. To estimate the value of β more correctly, we calculated for different β values the corresponding F value. The results are presented in Figure 3. It appears that for β = 0.285, the value of F reaches a minimum and hence linearity is the best at this value.
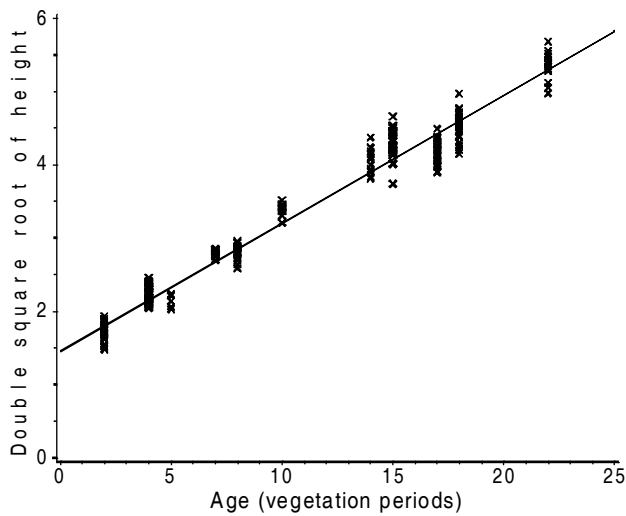
Figure 2. Growth of double square rooted height (in cm) of studied Norway spruce trees in Estonia
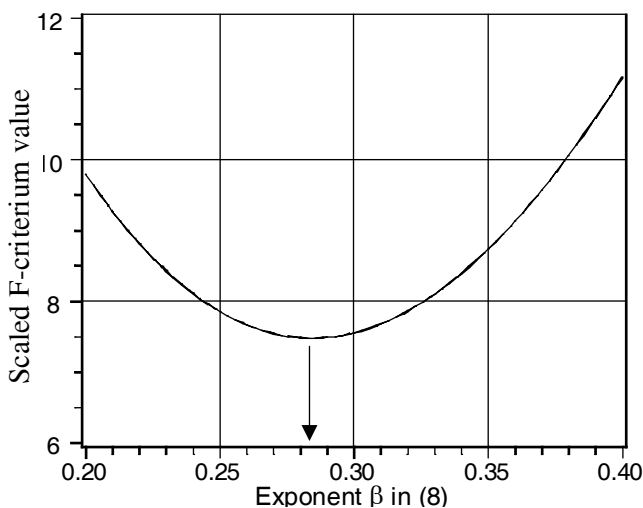

Figure 3. Estimation the optimal exponent for the power transformation

Theoretical reasoning of the height growth formula of the tree

The empirically established allometric law for the growth observed in the case of young Norway spruces can be deduced from simple biophysical considerations. Suppose that increment ΔM of tree biomass M during the vegetation period is proportional to the size of the photosynthetically active part of the tree crown. Assume further that the shape of the tree crown is a solid of revolutions (like a sphere, an ellipsoid of revolution, a circular cone, etc.). Additionally, assume that during the growth, this shape does not change except for its general size.

Next consider two hypothetical extreme situations. In the first situation, the spruce needles are assumed to be located on the crown surface only. In this case, photosynthetic mass is proportional to the crown surface area and the yearly yield of tree mass is proportional to the crown surface area. Mathematically,

$$\Delta M \sim r^2,$$

where r is the effective radius which characterises crown size, and $\sim$ means the proportionality between the two variables.

In the second situation we assume that the needles are distributed uniformly over crown volume. In this case the yearly increment of tree mass is proportional to crown volume:

$$\Delta M \sim r^3.$$

For a real tree, the situation is intermediate between the above two cases because, in general, the density of needles decreases from the crown surface to the stem. Hence, it is reasonable to suppose that

$$\Delta M \sim r^\alpha,$$

where $2 < \alpha < 3$.

The final step in this part of argumentation is to conjecture that r is proportional to tree height h. We have then the proportionality

$$\Delta M \sim h^\alpha. \tag{5}$$

Let us now express the annual increment of tree mass ΔM in a different way using a geometric argumentation. Suppose that the stem of the tree is a circular cone with bottom radius R and height h. Denote the annual ($\Delta t = 1$) increments of R and h by ΔR and Δh, respectively. In this case the annual tree mass increment is approximately proportional to the increment of stem volume V:

$$\Delta V = \pi(R + \Delta R)^2(h + \Delta h)/3 - \pi R^2 h/3.$$

Neglecting small terms Δh^2 and Δh^3 in this expression and taking into account that ΔM is proportional to ΔV, we obtain the proportionality

$$\Delta M \sim h^2 \Delta h, \tag{6}$$

where the increments ΔM and Δh are related to one vegetation period. Comparison of (5) and (6) leads to the equation:

$$\Delta h = k h^{\alpha-2} \Delta t,$$

where k is the coefficient of proportionality and $\ddot{A}h$ is the height increment during time period $\ddot{A}t$ (for one vegetation period $\Delta t = 1$). If we now consider tree growth as a continuous process, we can replace differences Δh and Δt by arbitrary small differentials dh and dt. After that we obtain the differential equation

$$dh = k h^{\alpha-2} dt. \qquad (7)$$

Equation (7) has solution $h^{3-\alpha} = ct$, where c is constant. Note that the constant of integration is equal to 0 if $t = 0$, then $h = 0$. Taking now into account that $2 < \alpha < 3$, we finally obtain the growth formula

$$h^{\beta} = ct, \qquad (8)$$

where $\beta = 3 - \alpha$ and, consequently, $0 < \beta < 1$. In other words, in the age interval where the above assumptions hold, some algebraic root of h is the linear function of age. Statistical analysis carried out in the previous paragraphs has shown that $\beta = 0.285$ (Figure 3). Taking $\beta = 0.25$, we obtain "the law of the double square root". This choice is only slightly better than the choice of $\beta = 0.333$ which was observed in (Pihu 2002) and can be called "the law of the cubic root".

Discussion and conclusions

The present study showed that for linearisation of the height growth curve of young spruces of Estonian provenance, the optimal exponent in (8) is 0.285 (Figure 3), which is intermediate between the cubic root ($\beta = 0.33$) and the double square root ($\beta = 0.25$). The transformation of height is possible by employing the cubic root or the double square root; however, for Estonian spruces the latter is superior because it is closer to the optimum. It follows from the argumentation of (8) that β depends on the distribution of needles in the tree crown. The larger value of β corresponds to the case where the concentration of needles is larger on the surface of the crown. In this way, β can be used for the characterisation of tree crown architecture.

The linear interdependence between age (t) and a certain algebraic root of the height (h^{β}), expressed by (8), has a universal meaning, whereas exponent β and proportionality factor c depend on the provenance of trees, on growth conditions, etc. In particular, β can be used for comparing the crown architecture of young spruces of different provenance. A number of simplifications were made to derive (8): height, radius at breast height and stem diameter were assumed to in-

crease proportionally relative to each other (allometry of tree shape), although in reality this assumption is not strictly satisfied. Also, several factors influencing the degree of photosynthesis, as light conditions, needle age (Schultze *et al.* 1977a, 1977b), needle location (Schultze *et al.* 1977a, Oker-Blom, Kellomäki 1982), needle density (Pulkkinen 1991), etc. were implicitly not taken into account, although they probably varied in the studied material and inflected the growth curve. Owing to these simplifications, there is no absolute coincidence between the straight line and the line obtained by the root transformation of height.

The straight line in Figure 2 does not pass the zero point (it crosses the height axis at a value of about 1.5, the corresponding height being about 5 cm). This means that the dependence (8) is not valid for very young trees (below 2 years of age).

For the above reasons, (8) is valid only approximately. Therefore, in his master's thesis, where the economic value of selected plus trees was estimated for further breeding, R. Pihu (2002) used two more methods in addition to the linearisation of the height of spruces: comparison of height at different ages and comparison of the height of trees of the same age. The method of linearisation of height serves as a complementary tool for a more thorough investigation of height as a characteristic. The advantage of this method over other methods is the fact that growth of trees will be characterized by only one index, the slope of the straight line. This method is also justified owing to the circumstance that originally heteroscedastic height data are converted to homoscedastic data after transformation (8), which is important for the validation of related statistical analysis (for variances, see Figures 1 and 2). In the above master's thesis, the results of the comparison of the height growth of spruces of four different provenances, obtained with this method, mostly coincided with the results obtained by other methods.

It is essential to take into account that investigation of the height of spruces by the method of linearisation is possible only if there exists an approximate linear interdependence between age and the algebraic root of height. As mentioned above, such dependence was revealed for spruces aged up to 22 years, for which annual height growth increased with age (Figure 1). However, it is necessary to know when the annual increments start to decrease (i.e. when the point of inflexion in the growth curve is reached), because from this point of time it is no more possible to linearise the growth curve with the allometric relationship (8). Height growth rate starts to decrease earlier for trees of higher site classes and later for trees of lower site classes (Krigul 1971, Tappo 1982). Ac-

cording to the most recent yield table compiled in Estonia, this decrease starts before 30 years of age even for site class III (Tappo 1982).

Hence, employment of the proposed linearisation of height is possible only for young spruces, while various other methods will be needed for older spruces. Nevertheless, the method of linearisation of early growth may have a potential in forestry practice for making conclusions about the genetic growth potential of trees. Usually, the age at which the breeding value of a plus tree becomes clear ranges between 1/3–1/2 of rotation age (Ромедер, Шёнбах 1962, Pihelgas 1970, Основные положения ... 1976, Коновалов, Пугач 1978, Quijada 1985, Бауманис, Пирагс 1990, Пирагс и др. 1990, Багаев 1998).

The main disadvantage of the proposed method of linearisation of height is the requirement that field data should be collected at highly different tree ages (desirably beginning from the seedling stage), which is difficult to realize.

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References

Kiviste, A., Álvarez Gonzáles J. G., Rojo Alboreca A., Ruíz Gonzáles A. D. 2002. Funciones de crecimiento de aplicación en el ịmbito forestal [Growth equations to model forest development]. Instituto Nacional de Investigación y Tehnologķa Agraria y Alimentaria. Monografķas INIA: Forestal No 4. Madrid, 190 pp. (in Spanish).

Krigul, T. 1971. Metsataksaatori teatmik [Book of reference for the forest surveyor]. Tartu, 150 pp. (in Estonian).

Nilson, A. 2002. Teisenduskaalust regressioonivõrrandite lineariseerimisel [Weight function for non-linear transformation of regression equations]. Metsanduslikud Uurimused XXXVII. Tartu, 89–112 (in Estonian).

Oker-Blom, P., Kellomäki, S. 1982. Metsikön tiheyden vaikutus puun latvuksen sisäiseen valoilmastoon ja oksien kuolemiseen [The effect of stand density on within-crown light regime and dying of branches]. Theoretical study. Folia Forestalia 509, 4–14 (in Finnish).

Pihelgas, E. 1970. Geneetika ja selektsioon metsamajanduses [Genetics and Breeding in Forestry]. Tallinn, 282 p. (in Estonian).

Pihu, R. 2002. Hariliku kuuse kasvu sõltuvus seemnepartii tüübist [Growth of Norway spruce depending on the seed lot type]. M. Sc. thesis, Faculty of Forestry, Estonian Agricultural Univ. Tartu, 65 p. (in Estonian).

Pulkkinen, P. 1991. Crown structure and partitioning of aboveground biomass before the competition phase in a mixed stand of normal-crowned Norway spruce (*Picea abies* (L.) Karst.) and pendulous Norway spruce (*Picea abies* f. *pendula* (Lawson) Sylven). Tree Physiology, 8: 361–370.

Quijada, R. M. 1985. Progeny trials. Forest Tree Improvement. Report. FAO Forestry Paper 20. Rome, 168–173.

Schultze, E.-D., Fuchs, M. I., Fuchs, M. 1977a. Spatial distribution of photosynthetic capacity and performance in a mountain spruce forest of northern Germany. I. Biomass distribution and daily CO_2 uptake in different crown layers. Oecologia 29, 43–61.

Schultze, E.-D., Fuchs, M., Fuchs, M. I. 1977b. Spatial distribution of photosynthetic capacity and performance in a mountain spruce forest of northern Germany. III. The significance of the evergreen habit. Oecologia, 30: 239–248.

Tappo, E. 1982. Eesti NSV puistute keskmised takseertunnused puistu enamuspuuliigi, boniteedi ja vanuse järgi [Medium stand parameters of Estonian stands according to the dominant tree species, site class and age]. Tallinn, 72 p. (in Estonian).

Багаев, С. С. 1998. Генетическая оценка плюсовых деревьев ели европейской по семенному потомству [Genetic estimation of plus trees of Norway spruces on the basis of generative progeny]. Вопросы использования и восстановления древесных и недревесных ресурсов леса южной тайги. Москва, с. 20–29 (in Russian).

Бауманис, И. И., Пирагс, Д. М. 1990. Селекция хвойных и перспектива образования их сортов в Латвии [Breeding of conifers and a perspective for breeding of their varieties in Latvia]. Роль селекции в улучшении Латвийских лесов. Рига, с. 37–43 (in Russian).

Кивисте А. К. 1988. Функции хода роста леса [Functions of the course of forest growth]. Эстонская Сельскохозяйственная Академия. Тарту, 108 с., Приложение 171 с. (in Russian).

Коновалов, Н. А., Пугач, Е. А. 1978. Основы лесной селекции и сортового семеноводства [Fundamentals of forest tree breeding and the forest quality seed management]. Москва, 173 с. (in Russian).

Основные положения по лесному семеноводству в СССР [Basic regulations of forest seed management in the USSR]. 1976. Москва, 32 с. (in Russian).

Пирагс, Д. М., Бауманис, И. И., Смилга, Я. Я. 1990. Динамика развития селекционного семеноводства лесных древесных [Dynamics of the development of forest tree species]. Роль селекции в улучшении Латвийских лесов. Рига, с. 3–11 (in Russian).

Ромедер, Э., Шёнбах, Г. 1962. Генетика и селекция лесных пород [Genetics and breeding of forest trees]. Москва, 268 с. (in Russian).

ОЦЕНИВАНИЕ ТЕОРЕТИЧЕСКИХ ПРЕДПОСЫЛОК И ВОЗМОЖНОСТЕЙ ПРИМЕНЕНИЯ КРИВЫХ РОСТА В МОЛОДЫХ КУЛЬТУРАХ ЕЛИ В ЭСТОНИИ

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Резюме

Рост по высоте 22-летних елей европейских был моделирован формулой $y^{\beta} = ct$, где y - высота и t - возраст дерева. Эта аллометрическая формула позволяет легко линеаризировать кривую роста, причем после преобразования рассейвание данных становится приблизительно гомоскедастным. Показатель степени β оценивали по данным пяти опытных культур в Эстонии. Оптимальное значение для β было между 1/4 и 1/3. Линейную зависимость выражали также теоретически, исходя из биофизических соображений, предполагая в частности, что годичный прирост дерева зависит от величины фотосинтетически активной части кроны, которая пропорциональна высоте дерева. Предлагаемый метод линеаризации рекомендуется для предварительного преобразования данных роста по высоте перед общим линейным статистическим анализом этих данных.

Ключевые слова: ель европейская, линеаризация кривой роста высоты, аллометрия роста, статистический анализ роста дерева