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Prediction of beech forests succession in Bieszczady Mountains using a computer model

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ABSTRACT: **This work presents the results of investigation into beech forests succession in Bieszczady Mountains using the FORKOME (FORest KOzak MEnshutkin) model. The model was verified in field trials in 1998–2001 in the forests with dominating beech *(Fagus sylvatica* L.*)* in Stuposiany Forest District in Poland. For the natural beech forest the model assumes cyclic changes in the number and biomass of beech and fir in a single simulation run and Monte Carlo realizations. The cutting out of trees does not change the general tendency of the dynamics of beech and fir stands. Under the logging management only the time of this dynamics varies.**

Keywords: beech; forest; computer model; Bieszczady Mountains

Since the 1970s progressive mathematisation in the field of ecology has developed. As a result different models of forest dynamics were constructed (Waggoner, Stephens 1970; Sullivan, Clutter 1972; Suzuki, Unemura 1974; Mitchell, 1975; Horn, 1975; Solomon 1977; Shugart, West 1977).

The forest gap model approach has proved to be useful in many respects (Shugart 1984). The first models (Botkin et al. 1972) were rather simple. Subsequent research led to more complicated models. These models included detailed information such as soil processes (Pastor, Post 1985), phytosociological concepts (Kienast 1987), explicit modelling of tree crown structure (Leemans, Prentice 1989), detailed treatment of ecophysiological (Friend et al., 1993) and biophysical processes (Bonan, van Cleve 1992; Martin 1992) and intraspecific competition (Pawłowski 1996).

The increasing complexity of forest gap models may have helped to make detailed and presumably more accurate projections of forest succession. Development of an ecological model of forest stand applicable under environmental conditions prevailing in Polish forest stands is presented (Brzeziecki 1991; 1999).

The main aim of the present study is to investigate the succession dynamics of beech forest in the Bieszczady in different cutting conditions using the FORKOME model.

MATERIALS AND METHOD

Permanent research plots are situated on the northern slope of Kosowiec mountain at the altitude of 800–900 m a.s l. (Stuposiany Forest District) and with inclination 14–18°. Brown soils over the Carpathian flysch are characteristic of the plots. The average age of beech stands is 92 years.

In our FORKOME model we investigate forest changes on 30 small plots of 30 × 30 m in size (Kozak, Menszutkin 1999). Shugart (1984) used 1/12 ha plots. The model was based on the main assumption that the dynamics of the whole forest stand is a sum of processes taking place in small units of the size comparable to canopy gaps. The forest dynamics was simulated in such gaps.

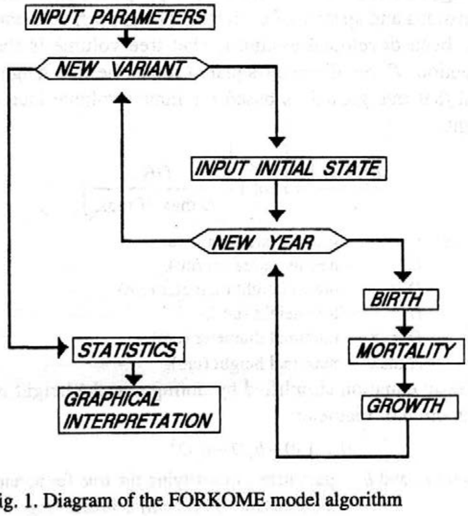

Fig. 1. Diagram of the FORKOME model algorithm

Table 1. Basic parameters of growth for main tree species in Bieszczady Mountains used in the FORKOME model

Tree species	Hmax (cm)	Dmax (cm)	Age (years)	B2	B3	G	DGD_{min}	DGD_{max}
Fagus sylvatica L.	4,500	150	300	58.26	0.194	290	4,650	12,700
Abies alba Miller	6,000	150	400	78.26	0.261	200	3,855	12,684
Picea abies (L.) Karsten	5,500	150	400	71.60	0.239	370	882	3,960
Betula pendula Roth	3,200	100	100	61.40	0.307	500	0	3,840
Pinus sylvestris L.	4,500	150	400	58.30	0.194	330	270	2,500

Our FORKOME model was constructed on the basis of FORET model (SHUGART, WEST 1977) with the authors' modifications considering, for example, temperature or other elements.

In our FORKOME model different modules (blocks) are distinguished (Fig. 1). The block "INPUT PARAMETERS" represents the estimation of tree and stand parameters. One of them is maximal tree diameter at standard height of 130 cm above the ground (Dmax). Maximal height (Hmax), maximum age (AGEmax) and minimal and maximal sums of degree-days (DGDmin, DGDmax) are also considered.

Basic growth parameters by the species in the FORKOME model are listed in Table 1. The FORKOME model simulates the dynamics of 5 species that dominate on the 15 investigated plots.

Since this model is stochastic, the study of its dynamics requires running through many variants (block "NEW VARIANT"). These processes are controlled by the block entitled "NEW YEAR". The model includes such variables as mortality, birth, and growth for each year of the run. The mortality of trees is a stochastic process depending on tree age and growth conditions in the previous year. The simulation of tree regeneration (block "BIRTH") is represented in the model as a stochastic process depending on the species of tree seedling, soil surface conditions and average temperature at the litter level. The growth rate (block "GROWTH") depends on the dimensions and species of each tree. The growth equation has been developed assuming that tree volume is the function of tree diameter squared times the tree height and that tree growth is based on annual volume increment:

$$\frac{d[D\ H]}{dt} = rLa\left(1 - \frac{DH}{D\max H\max}\right)$$

where: r – growth rate parameter,
La – tree leaf area (m^2/m^2),
D – breast height diameter (cm),
H – tree height (cm),
$D\max$ – maximal diameter (cm),
$H\max$ – maximal height (cm).

Basic equation simplified by noting that the height is a function of diameter:

$$H = 130 + b_2 D - b_3 D^2$$

where: b_2 and b_3 – parameters quantifying the tree form, and the constant 130 (in cm) is breast height.

If a tree has maximum height when it has maximum diameter ($dH/dD = 0$ and $H = H_{max}$ when $D = D_{max}$), then it is possible to calculate b_2 and b_3 parameters:

$$b_2 = 2\left(\frac{H_{max} - 130}{D_{max}}\right)$$

and

$$b_3 = \left(\frac{H_{max} - 130}{D^2_{max}}\right)$$

The growth rate depends on the most important ecological agents such as light, temperature, and supply of nutrients as well as other elements.

The light that reaches a given tree is calculated by attenuating the incident radiation by the sum of leaf areas taller than the tree:

$$Q(h) = Q_{max} E^{-0.25LA(h)}$$

where: $LA(h)$ – distribution of leaf area as a function of height,
Q_{max} – incident radiation,
$Q(h)$ – radiation at height (h),
– 0.25 – constant.

We used two equations; the first for light demanding trees:

$$r = 1 - e^{-1.136[Q(h) - 0.08]}$$

and the second for shade-tolerant trees:

$$r = 1 - e^{-4.64[Q(h) - 0.05]}$$

The growth rate depends on temperature conditions. We applied the following equation (BOTKIN et al. 1972):

$$T = \frac{4(DGD - DGD_{min})(DGD_{max} - DGD)}{(DGD_{max} - DGD_{min})^2}$$

where: T – growth reduction due to temperature effects,
DGD – base heat sum for a site,
DGD_{min} – minimum degree-day value where the species is known to occur,
DGD_{max} – maximum degree-day value where the species is known to occur.

For the block of nutrients we used this polynomial function (WEINSTEIN et al. 1982):

$$GMF = a + b[RNA] + c[RNA]^2$$

where: a, b, c – constants estimated by regression from field data,
RNA – relative nutrient availability,
GMF – growth-modifying factor to modify the growth rate of trees under limited supply of nutrients.

In this case

$$RNA = 1 - \frac{B}{B_{max}}$$

and

$$B = 0.1193 \sum_{i=1} D_i^{2.393}$$

where: B – actual trees biomass,
B_{max} – maximum tree biomass.

The probabilities of tree mortality are calculated. If $D^{t+1} - D^{t} < 0.1$ cm, then $P_n = 0.368$
or:

$$P_n = 1 - \left(1 - \frac{4.605}{AGE_{max}}\right)^n$$

The equations are open to modifications that take into account the influence of other agents on tree growth.

After the realization of all variants of the model, the programme carries out a statistical analysis of the obtained results (block "STATISTICS"). In the simplest case the analysis consists of the calculation of the mean and standard deviation values, whereas in more complex cases serial- and cross-correlation functions are calculated.

The interface of FORKOME model (Fig. 2) has different pictures for SINGLE SIMULATION RUN: "PARAMETERS", "INITIAL STATE", "SHOW GRAPHICS", "PRINT GRAPHICS". After having pressed the left button of the mice in the position of each tree in the picture, information about age, height and diameter of the tree can be obtained. The right button of the mice allows cutting of the tree.

The statistical processing "MONTE-CARLO REALIZATION" can simulate as much as 200 runs under the same starting and management conditions. It was accepted that 30–40 simulations were sufficient to estimate statistical parameters of the model in each variant.

The position of each tree in the forest is projected along the diagonal of research plots. The year 1999 was taken as the first year of the model time. In this study time is used as the model time.

RESULTS AND DISCUSSION

For a natural beech forest the model predicts cyclic changes between beech and fir biomass in one realization (Fig. 3a). The cutting of beech trees after the first year (Fig. 3b) and after 20 years (Fig. 3c) of model time does not change this cyclic dynamics. Cutting out beech trees after the first year resulted in a long-term dominance of fir.

Cutting all the trees after the first year and after 20 years does not change the dynamics of beech and fir biomass, either. Depending on the cutting conditions only the time of transformation of beech stand into fir stand differed.

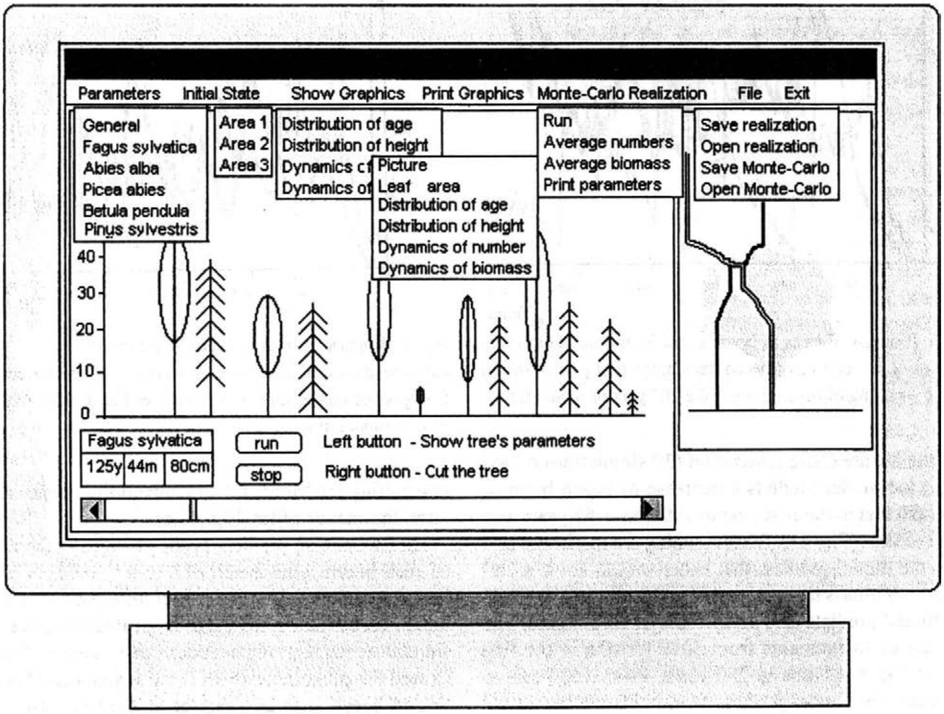

Fig. 2. Interface of FORKOME model

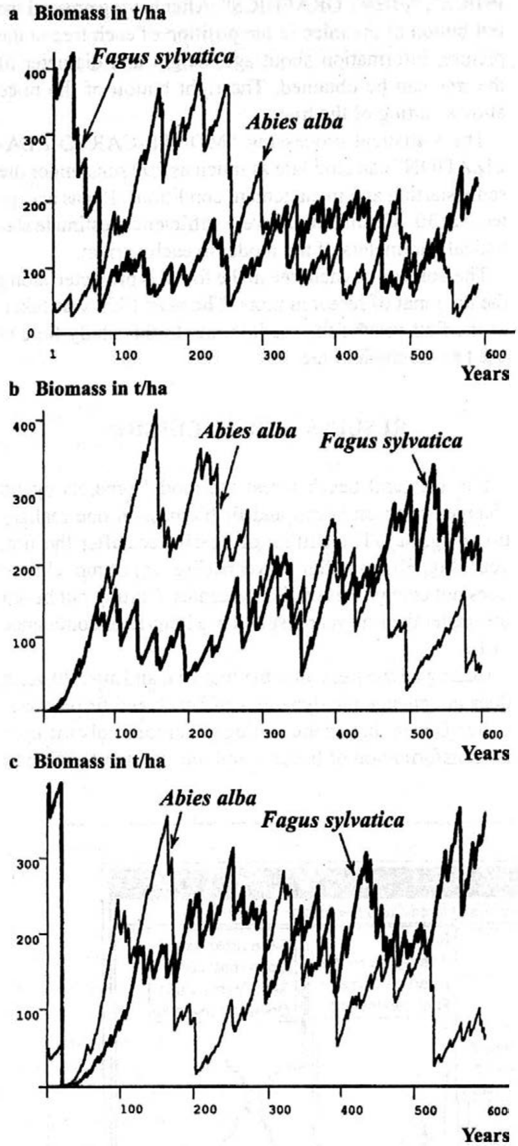

Fig. 3. Biomass of trees in beech stand in one simulation run; a – control, b – cutting of beech trees in the first year of model time, c – cutting of beech trees in the 20th year of model time

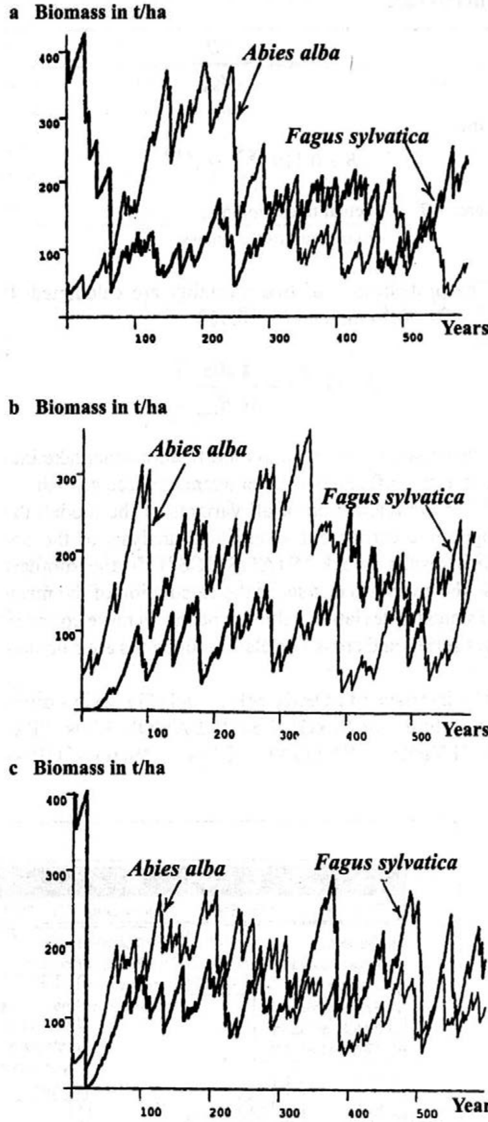

Fig. 4. Biomass of trees in beech stand in Monte Carlo statistical simulation run; a – control, b – cutting of beech trees in the first year of model time, c – cutting of beech trees in the 20th year of model time

In the Monte Carlo realization (30 simulations on average) the model predicts a decrease of beech biomass from 400 t/ha in the first year to 140 t/ha in 65 years also in the control (Fig. 4a). After reaching the minimum biomass the model predicts that beech would show a tendency to biomass increase to 196 ± 7.3 t/ha in 130 years. The model predicts also an increase of fir biomass. The biomass of fir increases from 50 ± 1.1 t/ha in the first year to 195 ± 4.1 t/ha in 280 years. From 150 years to 280 years the model predicts fir dominance and in the following time beech dominance. In different variants of tree cutting the Monte Carlo realization assumes a long-term dominance of fir (Fig. 4b,c).

The model also predicts cyclic changes in the number of trees: beech dominated for 180 years, and then fir dominated for 250 years of the model time. This transformation of beech stand into fir stand repeated twice in a single simulation run. Cutting out beech trees after the first year caused the dominance of fir for 120 years and later cutting of beech after 20 years of model time also caused the dominance of fir for 150 years.

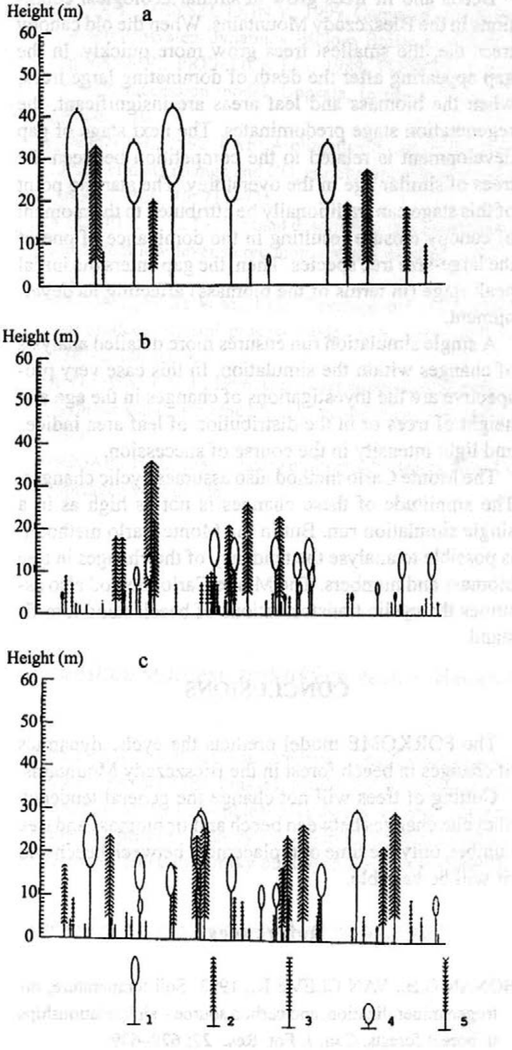

Fig. 5. The position of each tree in the forest patch projected along a diagonal of the plot; a – in the model time 1 year; b – in the model time 66 years; c – in the model time 66 years after cutting in year 1

The Monte Carlo realization predicts the dominance of the number of beech trees up to 190 years. After 190 to 240 years fir began to dominate and after that time beech dominated for 560 years followed by fir dominance. The model predicts more dominance stages of the fir when cutting the beech trees.

A single simulation run ensures more detailed analysis of changes within the simulation. Noteworthy is the investigations concerning the changes in species compositions. For example, in 1 and 66 years of simulation runs the species compositions are different (Fig. 5a,b,c). In the first year there were two groups (Fig. 6a) of age on the research plots (to 20 years and from 50 to 200 years).

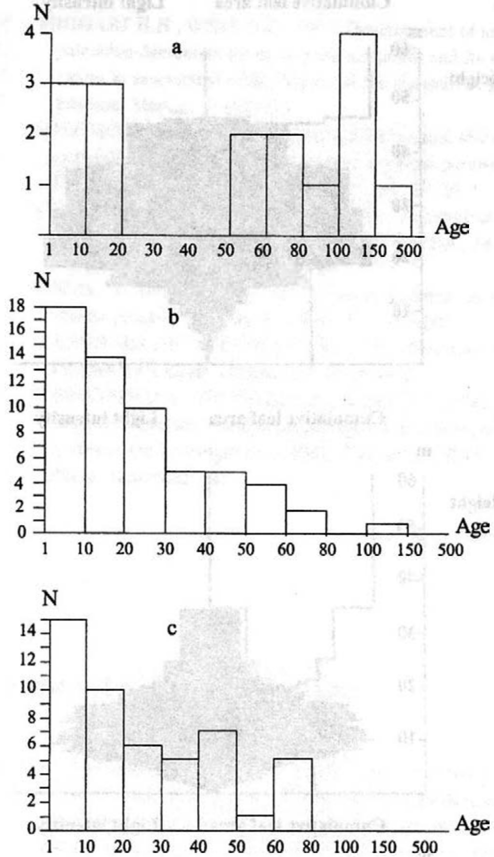

Fig. 6. The age tree distribution on the plot; a – in the model time 1 year; b – in the model time 66 years; c – after cutting in year 1 in the model time 66 years

In 66 years of model time young trees dominated. The number of trees decreased with age (Fig. 6b). In 66 years of model time after cutting the distribution of trees up to 80 years is different (Fig. 6c). The character of the distribution of cumulative leaf area and light intensity (Fig. 7a,b,c) is different in the course of succession.

The FORKOME model presented in this study is based on the gap-phase theory of a natural forest. The structure of our model is open and modular, enabling its easy development and modification. The important feature of the FORKOME model is its possibility to assess the impact of changing environmental conditions on forest growth and functioning, the question that is also emphasised in the literature (BERNADZKI 1993; BRZEZIECKI 1999). Generally, the model may be used for quantitative estimates of the effects of various factors (cutting, climatic changes, introductions of new tree species) on the dynamics of forest stand.

The model confirms the cyclic nature of stand development trends. Such cycles were already described in the literature (SHUGART 1984). The FORKOME model as-

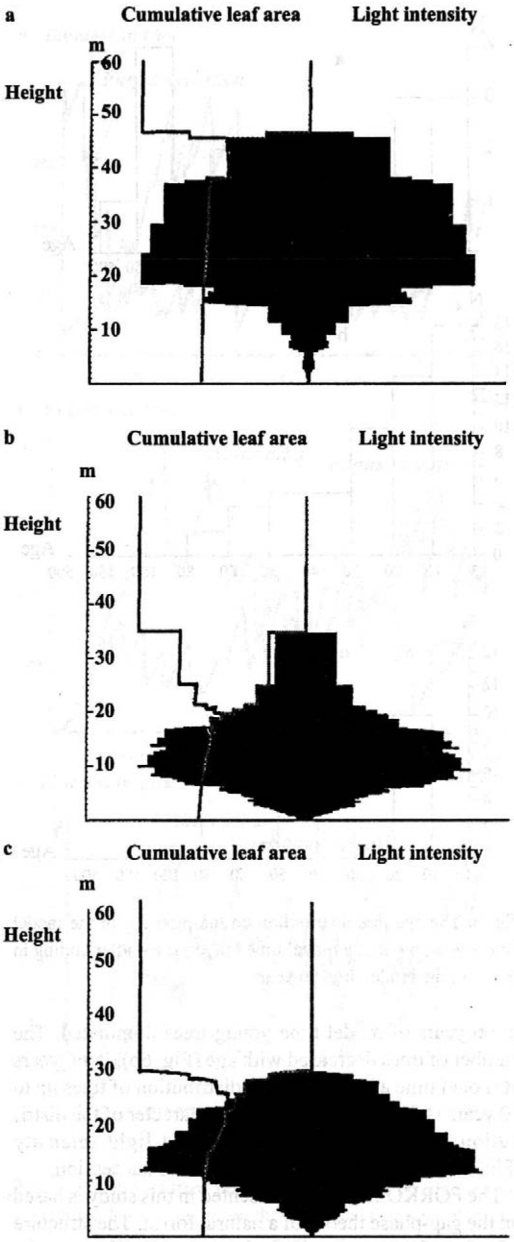

Fig. 7. The distribution of leaf area indices and light intensity in the succession; a – in the model time 1 year; b – in the model time 66 years; c – in the model time 66 years after cutting in year 1

sumes the cyclic dynamics of tree numbers and biomass. In variants with cutting the beech trees only and cutting all trees in the first and in the 20th year of simulation, this tendency of cyclic changes is confirmed too. The cycles were more frequent for the number of trees than the biomass. Under the cutting conditions only the time of this dynamics varies.

Beech and fir trees grow in similar ecological conditions in the Bieszczady Mountains. When the old canopy trees die, the smallest trees grow more quickly. In the gap appearing after the death of dominating large trees, when the biomass and leaf areas are insignificant, the regeneration stage predominates. The next stage of gap development is related to the competition between the trees of similar age in the overstorey. The starting point of this stage can traditionally be attributed to the moment of canopy closure resulting in the dominance of one of the large-size tree species. Then, the gap enters the initial peak stage (in terms of the biomass) affecting its development.

A single simulation run ensures more detailed analysis of changes within the simulation. In this case very prospective are the investigations of changes in the age and height of trees or in the distribution of leaf area indices and light intensity in the course of succession.

The Monte Carlo method also assumes cyclic changes. The amplitude of these changes is not as high as in a single simulation run. But in the Monte Carlo method it is possible to analyse the tendency of the changes in tree biomass and numbers. The Monte Carlo method also assumes the cyclic transformations of beech stand into fir stand.

CONCLUSIONS

The FORKOME model predicts the cyclic dynamics of changes in beech forest in the Bieszczady Mountains.

Cutting of trees will not change the general tendency of cyclic changes between beech and fir biomass and tree number, only the time of replacement between beech and fir will be variable.

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Predikce sukcese bukových lesů v Beskydech pomocí počítačového modelu

ABSTRAKT: V práci jsou uvedeny výsledky šetření sukcese bukových porostů v Beskydech pomocí modelu FORKOME (FORest KOzak MEnshutkin). Model byl ověřován v terénních pokusech v letech 1998–2001 v porostech s převahou buku (*Fagus sylvatica* L.) v polesí Stuposiany v Polsku. Během jedné simulační operace a realizací Monte Carlo model předpokládá pro přírodní bukový les cyklické změny počtu stromů a biomasy buku a jedle. Vykácení stromů nevede ke změně obecné tendence dynamiky bukových a jedlových porostů. Při použití těžeb se mění pouze časový průběh této dynamiky.

Klíčová slova: buk; les; počítačový model; Beskydy

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Determining potential natural composition of forests by means of a mathematical model using the example of the Ještěd Ridge

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ABSTRACT: A simple mathematical model has been developed for calculating the natural species composition of forests according to their site. The model is based on the response of individual tree species to climatic and soil characteristics of the environment. Values of so-called partial vitality have been defined for each tree species and each of the sets of variables. These are then connected on the principle of multiplication. After corrections, we can derive potential representation of each tree species at the given site comparing general (relative) vitalities for individual tree species. The model was applied to the ecologically varied area of the Ještěd Ridge in Northern Bohemia. Its usability has been tested on a wide range of localities in the Czech Republic and in the neighboring countries. The model has also been tested for predicting future natural vegetation in the case of climatic changes or vegetation reconstruction in earlier Post-Glacial periods. In many cases, however, the results did not agree with expected values. This is caused by the model not being perfect, specifically with regard to the description of competitive relationships between tree species. At the same time the model points out the complexity of natural processes, which even the best model by definition cannot cover. The factor of "randomization" is the ecological (and genetic) variability of tree species within themselves, dynamic scope of succession and continuing development of forest ecosystems and specific nature of some environmental characteristics. Inconsistent results from vegetation reconstruction in middle Holocene raise a number of interesting questions.

Keywords: natural forest composition; mathematical model; Ještěd Ridge; Northern Bohemia; potential natural vegetation; site potential; paleobotany; climatic changes

Foresters and natural scientists have traditionally taken primary interest in the natural species composition of forest stand. Its knowledge has considerable practical significance as simulating natural processes and natural relationships in forest silvicultural activities are a basic prerequisite for increasing the ecological stability of stands. There are however different opinions concerning the concept of the natural tree species composition of forest in a specific area. They differ according to what method of determination has been used and often according to the person carrying out the assessment.

We can compare the results of the following procedures in Central Europe: (i) forestry typology; (ii) phytosociology; (iii) paleobotany; (iv) historical research. These disciplines are unique by their very subject matter. Forestry typology emphasizes the study of the environment (site) in which forest communities develop. Well-conserved forest stands of natural appearance are extrapolated on related habitats, where natural forest is missing. Geobiocenology deals with the analogy of typological approach. Professor Zlatník is the founder of this discipline in this country (ZLATNÍK 1975, 1976). Phytosociology focuses on the plant element of a forest ecosystem, specifically concerning the representation of certain plant species, characteristic species combinations and their diagnostic values as regards vegetation system units – syntaxa. Paleobotany works with the remains of forests from the recent and distant past – fossils. It puts together a picture of the past vegetation from the qualitative and quantitative composition of preserved plant remains, especially pollen grains, i.e. microfossils. Historical research draws on the study of written records related to forests. These, unlike fossils, tell us about the composition of forests in the relatively recent past few centuries when forests were more or less influenced by humans.

The above-mentioned methods diverge in their time-space resolution. Forestry typology and phytosociology deal in detail predominantly with small areas. However, they can utilize only some rough sketches without a precise time setting. Conversely, paleobotany and historic research are more accurate as far as the time is concerned. They are not as detailed in space orientation (especially paleopalynology).

The benefits and drawbacks of individual methods lead to a logical requirement for parallel study of natural forest vegetation by means of several methods and a synthesis of partial results. This requirement, however, cannot always be met due to the laboriousness involved and poor accessibility to some data, especially those of palynology.

A possible alternative or rather a complement to these methods could be a mathematical model. Finding a suitable algorithm would make the formalized assessment of natural vegetation possible. This method would not be so laborious and would offer a considerable degree of space (or time) resolution. The basic presupposition of such a model concerns the quality of the input and output data.

The input data must be easily accessible even for some large areas, they should be topologically connected, space resolution being at the scale of at least 1:50,000. The input data should already be available in a certain form, so that not much time is taken by collecting them in the field. What has been said suggests that the results from typological research shown on maps with scales of 1:10,000 will be an important source of data. The model should provide the basic idea about the tree species composition of forest in view of dominant, subdominant and associated or incidental species. Simply determining the potential vegetation belt (in VINŠ et al. 1996) cannot be considered sufficient.

There has been developed a number of mathematical models focusing on the structure and species composition of plant communities including forests. LEPŠ (1988) offers their basic summary and classification. The models are based on biological and ecological properties of the plants in question and the characteristics of the environment in which they grow.

More complex models include the space structure of plant communities and deal with the plant individual, i.e. mostly individual trees (e.g. Forest Gap Model – BOTKIN et al. 1972). Simpler mo-dels are static, that means they do not study the dynamics of vegetation changes but merely approximate the result of succession whose duration has not been defined. These models are usually based on comparing the "supply" of the environment (a set of ecological variables) and the "demand" of available plant species, especially tree species or whole plant communities.

The analyzed area is divided into segments of homogeneous properties (pixels in grid systems or polygons with the average value ascertained in the case of vector systems). Calculation for each of these segments is made automatically. Its outcome is either the most probable vegetation formation or plant community (see e.g. BOX 1981; FISCHER 1994; LINDACHER 1996; TICHÝ 1997; VINŠ et al. 1996) or combination of probably represented plant species with their approximate quantitative representation (KESSEL 1979). After the data has been converted to the map, we get a map of potential natural vegetation or a forest typological map; however, it is called a simulated map of natural (forest) vegetation (FISCHER 1994) considering that a different method has been used.

MATERIAL AND METHODS

MATHEMATICAL MODEL

I have developed a static model of quantitative representation of woody species in the tree layer, dealing with the problem of the natural species composition of forests in the area of the Ještěd Ridge. The model operates on ecological principles, i.e. its results denote the site potential as to its vegetation. This characteristic is connected with a significant limitation of the model discussed below. The model contains 26 woody species in all (23 trees and 3 shrubs). All of them grow naturally in the Czech forests. *Cerasus avium*, *Populus nigra* and *Salix alba* are important species that are not represented here; *Betula pubescens*, *Populus tremula*, *Sorbus aria*, *S. torminalis*, *Taxus baccata* are less important excluded tree species here.

CHOOSING CONTROL VARIABLES

Such variables were chosen that meet the following criteria: a) they are significantly correlated to the habitats of individual tree species, b) their sufficiently accurate values are easily available for extended areas. The selected site variables comprise two groups:

a) Climatic characteristics – average temperature in January; average temperature in July; the difference in the average temperature in July and January; the length of the period with average temperature above 10°C ("season"); aridity (annual sum of precipitation divided by the temperature in °C increased by 10); climatic anomalies contingent on specific relief forms.
b) Edaphic (soil) characteristics – trophic and hydric sequences according to ZLATNÍK (1976), complemented by some other, ad hoc defined inter-sequences and subsequences. These variables are of complex nature and therefore they are expressed in categories.

DETERMINING CONTROL VARIABLES FOR SPECIFIC LOCALITY

All the control variables are acquired indirectly, i.e. by conversion of other variables. Climatic variables come from a net of points of reference. These are climatic stations where long-term meteorological measurements are carried out. The values for a specific locality were professionally estimated (extrapolated) in view of the altitude, exposure, slope, and specific relief form (a special variable "anomaly"). The variable "season" was calculated as a chord of sinusoid. This simplification motivated by an attempt to minimize the input data is subject only to a small error in Central European conditions. Soil characteristics are derived from typological and soil units in available maps (forestry typological maps 1:10,000 and maps of complex research on agricultural soils of the same scale).

Within the framework of the control variables, curves of so-called potential vitality were designed for each tree species. These curves were constructed by evaluating (by means of regressive analysis) anticipated vitalities of tree species in a set of 413 localities representing climatic sites (174 in the Czech Republic, 27 in Slovakia, the rest in other European countries). The required environmental variables (only climatic ones) were derived from climatic diagrams (WALTER, LIETH 1964; MAYER 1984) and from tables pertaining to the Czech Republic and Slovakia (VESECKÝ et al. 1961).

The potential vitality of individual tree species was estimated for the environment of each climatic site by the following scale: 1 – tree species on the verge of ecological amplitude with limited vitality, in stands usually as an incidental species only, 2 – diminished vitality, in stands usually as an associated species only, 3 – good vitality, often a subdominant species of stands, 4 – clear ecological optimum, striking dominant of stands. The needed data was obtained from available vegetation maps, area maps of individual tree species, from other literature and from the author's own knowledge. The synthesis of this data helped determine optima and in a number of cases negatives of individual variables and tree species. Degrees of vitality were transformed into the values: 0.2, 0.5, 0.75, and 1.0. The environmental variables (ecological gradients) were divided into short intervals and from these semiquantitative values an arithmetic mean was calculated for each interval and each tree species. Gaussian unimodal curves or their parts then interpolated these values. Some curves were asymmetrical or they were not rising or falling. The so-called partial vitalities w_{ijk} for the tree species *i*, the site variable *j* and the average value of this variable *k* were then derived from the curves. Partial vitality takes the value between 0 and 1, 1 corresponding to ecological optimum. The complex of site variables is expressed in the form of a product (multiplicative model). This ensures the validity of the LIEBIG law of minimum (the factor in minimum is what limits) and at the same time the law of substitution of factors. If one of partial vitalities equals 0, relative vitality w_i will also be of zero value. To reinforce the limiting effect of the variables being in the negative, transformation ln(20x+1) is used. This logarithmic transformation also moderates the steepness of curves with the values near the optimum.

Since the competitive qualities of individual tree species determine the representation of tree species in a stand to a great extent, the calculation includes so-called competition exponent C_i. This favors competitively strong tree species, esp. the beech, and on the other hand it suppresses the presence of competitively weak tree species (birch, mountain-ash, alder and willow). It was necessary to set the competitive exponent for each tree species empirically. Dilatation exponent D emphasizes the difference between tree species with lower and higher vitalities. However, the exponent is not specific in terms of species. The results of the model are the site potential expressed as approximate percentage representation of tree species.

Mathematically, the principle of the model is described by the following equation:

$$F_i = \frac{w_i}{\sum_{i=1}^{n} w_i} 100$$

$$\sum_{i=1}^{n} F_i = 100\,\%$$

where: F_i – the final representation of *i*-th tree species expressed as percentage,
w_i – the total relative vitality of *i*-th tree species.

The value w_i is derived from the formula:

$$w_i = \left[\left(\prod_{j=1}^{m} \ln(20 v_{ijk} + 1) \right)^{C_i} \right]^{D}$$

where: v_{ijk} – a tabulated value of partial vitality of the tree species *i* for the site variable *j* and the interval *k*;
C_i – a competitive exponent of the *i*-th tree species,
D – a dilatation exponent.

The model implies that it can be applied not only to the current conditions of the environment but to any hypothetical situation, including reconstructed situations in the past or an expected state of the environment in the future.

I applied the model to so-called site categories in the target area. These categories resulted from overlapping of a simple relief map (of medium altitude, exposure and slope) and maps of soil units. About 250 site categories in all were defined in this way. For each of these categories represented in the map, I calculated the species composition for various situations by at least one polygon. The following situations were assessed: (i) current PNV (i.e. potential natural vegetation corresponding to the current climate), (ii) PNV with suppressed beech, (iii) PNV with excluded fir and spruce, (iv) PNV for the anticipated climatic change in 2030, (v) PNV for the main periods of Holocene. The results of calculations were shown in hand-drawn maps. For each of the mentioned cases, it is possible to make both a map of vegetation formations (i.e. by means of combination of prevailing tree species) and maps of percentage representation of individual tree species.

THE TARGET AREA

The target area itself is about 200 km² and is made up by three sites and biotically contrasted units: (i) The Ještěd Ridge is the axis of the target area (about 24 km long) and its main part at the same time. Geomorphologically, it is efficiently divided into three districts (DEMEK et al. 1987): the Kryštof Ridges, the Hlubocký and the Kopaninský Ridges. The latter extends to the target area northwest of the Mohelka valley. (ii) The Zittau Basin begins at the northeast slopes of the Ještěd Ridge. It is then broken up to the Liberec Basin and Hrádek Basin. It extends to the target area only by its smaller southwestern part. (iii) The Sub-Ještěd Hills comprise geomorphologically the marginal parts of the Ralsko Hills and Kotel

Highlands, the Českodubsko Hills and Hodkovice Basin. Only their marginal parts adjacent to the Ještěd Ridge represent these units.

The ecological conditions of the area are unusually varied, which is caused by the contrasts both between the above-mentioned units and within them. The Ještěd Ridge itself is marked by considerable altitude variances – the altitude difference between the level of the Lužická Nisa River near the village of Bílý Kostel and the top of Ještěd is about 750 m. The Ridge runs toward the Sudetic Mountains (i.e. in the NW-SE axis). Most of the slopes are oriented more or less toward southwest and northeast, which enlarges temperature differences contingent on the elevation.

As to the geologic structure, there is a complex mosaic of igneous, metamorphic and sedimentary rocks in the complete stratigraphic sequence Proterozoic–Perm with profuse occurrence of the Upper Cretaceous and Quaternary sediments. The Paleozoic crystalline rocks (phyllites, quartzites, mica schist and slates), Turonian even Coniacian sandstone and Pleistocene eolian and diluvian sediments. Ecologically notable is the occurrence of crystalline limestone, even dolomites, paleo- and neovulcanic rocks as well.

There are largely light soils, medium or more acidic soils or soils with less favorable form of humus. The predominant soils on geests of crystalline and granitoid sediments are dystric cambisol or typical cambisol, acid variety and at higher elevations spodo-dystric cambisol and marginally ferro-humic podzol. There are cambic arenosol and ferro-orthic podzol widely represented on the sandstone bedrock of the Sub-Ještěd Hills. Albic and albo-gleyic luvisol, in some places accompanied by orthic luvisol cover Pleistocene sediments of the Zittau Basin and the Sub-Ještěd Hills. Other soil types prevalent in rather smaller areas are lithosol, ranker, rendzina, fluvisol and gleysol. For basic characteristics of the soil cover see NOVÁK (1993) and the nomenclature of soils by HRAŠKO et al. (1991) with FAO-nomenclature equivalents.

The climate of the target area is influenced by the windward system of the borderland hills and highlands, which make for higher humidity, rather low average temperatures and sub-oceanic character of climate. Average annual temperatures on the Ještěd Ridge usually range from 4 to 6°C (on top of Ještěd only 3.3°C); only at elevations below 400 m it is about 7°C. Average temperatures in January range from –2 to –5°C, in July from 12.5 to 17°C. The amount of annual precipitation does not get below 700 mm anywhere in the area; it is noticeably higher in the southeast where it reaches 1,000 mm (HOSTÝNEK 1984). July is the rainiest month, but precipitation is quite consistent throughout the year.

In terms of phytogeographical division (SKALICKÝ et al. 1988), the area along with prevalent parts of the districts of the Ještěd Ridge, Lužice Basin and the Sub-Ještěd Hills is included in the phytogeographical districts of Czech and Moravian Mesophyticum (Ještěd itself is considered to be an island of Oreophyticum). A number of maps (15 in all) show the natural vegetation of the area. Some of these show the whole area of the Czech Republic at various scales, while the others show only parts of the country in greater detail. A closer description and assessment of maps is beyond the scope of this work.

The main part of the area falls into the Jizera Mountains and Ještěd Natural Forest Region (NFR) 21. The North-Bohemian Sandstone Basin NFR 18, the Lužice Highlands (part of which is the Zittau Basin) NFR 20 and the Krkonoše foothills region NFR 23 marginally cover the target area.

RESULTS

This is a comment on the maps constructed on the basis of a mathematical model. The appendix to this article contains examples of three of them.

A) Current potential natural vegetation. Four units prevail in the simulated map and stand types: (i) beech wood, i.e. predominantly a beech stand with admixture of fir up to 15%, it covers most of the Ještěd Ridge, (ii) silver fir-beech wood, with the presence of fir up to 30%, it mostly covers higher eastern slopes of the Ještěd Ridge, (iii) mixed silver fir wood, it covers accumulative areas at the foot of the ridge on both sides, especially in the Liberec Basin, (iv) mixed stand of pine and beech, it is located in the Sub-Ještěd Hills along with the previous unit. It follows from the maps of percentage representation of individual tree species that only beech is consistently predominant. Silver fir is represented to a lesser extent while more numerous occurrences of the other tree species are confined to limited extreme localities. The mathematical apparatus indicates a tendency to a larger mixture – the domination of the main tree species is suppressed by smaller percentage gains of tree species that would not probably find their place in real stands. Therefore, a tree species having an approximately 50% share in the output of the model without any other species being represented to a larger extent can be considered as the major tree species.

B) Potential natural vegetation with suppressed beech. This map basically simulates the influence of forest pasture in the past centuries, which has put mainly beech at a disadvantage in favor of fir and spruce (MÁLEK 1983). The calculated species composition shows the prevalence of both these coniferous tree species in almost all the Ještěd Ridge. They are complemented by pine on poorer soils in the Sub-Ještěd Hills and on the ridge itself. Beech has kept its dominant position only on the nutrient richest substrata, especially carbonate bedrocks at medium elevations, where it appears in mixture with oak and fir. Aside from fir, oak and pine partly replace the suppressed beech in lower locations.

C) Potential natural vegetation with excluded fir and spruce. It is basically a modified natural composition

Table 1. Calculated species composition for typical site conditions – contemporary climate

Soil type	Height (m)	Expos.	Slope (°)	% conifer	% br.-leav.	Species with 5% and more presence (in descending order)
FMG	250	0	0	2	98	Fr 33, Sa 30, Al 27, Pa (E2) 64, others 10
LMg	250	0	0	32	68	Qu 43, Ab 25, Fa 10, Co (E2) 15, others 22
KMm(a)	250	0	0	16	84	Fa 65, Qu 12, Pi 7, Ab 6, others 10
HMm, HMl	250	0	0	13	87	Fa 40, Qu 20, Ca 7, Ti 7, Ab 7, Ac 9, Co (E2) 18, others 10
FMm	350	0	0	26	74	Ab 19, Qu 16, Ac 17, Fa 15, Pc 7, Fr 7, Ti 6, Pa (E2) 11, Co (E2) 35, others 13
FMG	350	0	0	5	95	Fr 32, Sa 26, Al 29, Pa (E2) 52, Co (E2) 5, others 13
HMm, HMl	350	0	0	25	75	Fa 45, Ab 14, Qu 12, Pc 7, Ac 7, Co (E2) 13, others 15
LMg	350	0	0	54	46	Ab 40, Qu 26, Pc 12, Fa 10, Co (E2) 10, others 12
KMm(a)	350	0	0	24	76	Fa 63, Ab 12, Qu 6, Pc 6, Pi 6, others 7
KMm(a)	350	SW	30	15	85	Fa 64, Qu 15, Pi 9, others 12
KMa	350	0	0	51	49	Fa 38, Pi 35, Ab 13, Be 6, others 8
PGm	350	0	0	58	42	Ab 42, Qu 21, Fa 14, Pc 12, others 11
GLm	350	0	0	8	92	Al 49, Fr 34, Sa 8, Pa (E2) 91, others 9
PZa	350	0	0	84	16	Pi 68, Ab 13, Fa 11, others 8
HMm, HMl	500	0	0	30	70	Fa 49, Ab 17, Pc 11, Qu 8, Ac 5, Co (E2) 8, others 10
KMm(a)	500	0	0	26	74	Fa 64, Ab 13, Pc 9, others 14
KMa	500	0	0	48	52	Fa 43, Pi 28, Ab 15, Be 6, Pc 5, others 3
PGm	500	0	0	66	34	Ab 46, Pc 17, Fa 15, Qu 13, others 9
GLm	500	0	0	14	86	Al 47, Fr 31, Pc 7, Ab 6, Sa 5, Pa (E2) 53, others 4
RAm, RAk, KMv	500	N	30	5	95	Fa 81, Qu 6, Co (E2) 15, others 13
KMe	500	N	30	18	82	Fa 61, Ab 11, Ac 9, Pc 6, Co (E2) 10, others 13
KMd	500	0	0	31	69	Fa 60, Ab 15, Pc 10, Pi 6, others 9
KMd	500	SW	30	25	75	Fa 61, Ab 10, Pi 10, Qu 7, others 12
KMd	500	NE	30	37	63	Fa 55, Ab 18, Pc 14, others 13
PZa	500	0	0	81	19	Pi 59, Ab 16, Fa 13, Pc 6, Be 5, others 1
LIm(q)	500	0	0	66	34	Ab 30, Pi 27, Fa 25, Pc 8, Be 7, others 3
GLm-GLo	500	0	0	76	24	Pc 34, Ab 22, Pi 20, Al 15, others 9
KMg	500	0	0	62	38	Ab 44, Qu 20, Pc 16, Fa 8, Co (E2) 12, others 12
KMm(a), PZk	700	SW	30	25	75	Fa 64, Ab 12, Pc 8, Pi 5, others 11
KMe	700	SW	30	13	87	Fa 72, Ab 7, Ac 6, Co (E2) 8, others 15
KMd	700	SW	30	30	70	Fa 60, Ab 13, Pc 9, Pi 7, others 11
PZG, PZo	700	SW	30	61	39	Pc 31, Al 24, Ab 19, Pi 11, Fr 6, Pa (E2) 33, others 9
GLm-GLo	700	0	0	86	14	Pc 47, Ab 26, Pi 13, Al 6, others 8
KMm(a), PZk	700	NE	30	31	69	Fa 64, Ab 16, Pc 13, others 7
KMd- shallow	700	NE	30	37	63	Fa 56, Ab 25, Pc 8, others 11
KMg	700	0	0	79	21	Ab 54, Pc 23, Fa 11, others 12
PZm	850	NE	30	46	54	Fa 50, Pc 27, Ab 19, others 4
RNp-PZm (PZk)	850	NE	30	38	62	Fa 57, Ab 23, Pc 13, others 7
RNp-PZm (PZk)	850	SW	30	32	68	Fa 59, Ab 20, Pc 8, others 13
PZk	850	SW	12	33	67	Fa 62, Pc 16, Ab 16, others 6
RNp, RNm(a)	850	SW	30	64	36	Ab 39, Pc 15, Sr 15, Fa 12, Pi 10, Be 9, others 0
RNp, RNm(a)	950	SW	30	64	36	Ab 37, Pc 22, Sr 18, Fa 11, Be 7, Pi 5, others 0
RNp-PZm	950	SW	30	34	66	Fa 58, Ab 19, Pc 12, Sr 5, others 6
RNp-PZm	950	NE	30	34	66	Fa 61, Ab 17, Pc 17, others 5
PZm	950	0	0	44	56	Fa 53, Pc 28, Ab 16, others 3
RNp, RNm(a)	950	NE	30	71	29	Ab 35, Pc 34, Sr 14, Fa 12, others 5

Explanations of abbreviations used in tables

Soil type – soil units according to Morphogenetic Soil Classification System (HRAŠKO et al. 1991) – equivalents to FAO units (in alphabetical order):

FMG – fluvi-eutric gleysol, FMm – eutric fluvisol; GLm – eutric gleysol, GLo – histo-humic gleysol; HMg – stagno-gleyic luvisol, HMm – orthic luvisol, HMl – "orthic-albic" luvisol; KMa – cambic arenosol, KMd – "typical" dystric cambisol, KMe – mollic cambisol, KMg – stagno-gleyic cambisol, KMm(a) – "moderate" dystric cambisol, KMv – calcic cambisol; LIm(q) – dystric litosol; LMm – albic luvisol, LMg – albo-gleyic luvisol; PGm – dystric planosol; PZa – ferro-orthic podzol, PZG – gleyic podzol, PZk – spodo-dystric cambisol, PZm – ferro-humic podzol, PZo – histo-humic podzol; RAk – "cambic" rendzina, RAm – "typical" rendzina; RNm(a) – "typical" ranker, RNp – "podzolic" ranker.

Woody species: Ab – *Abies alba*, Ac – *Acer pseudoplatanus & platanoides*, Al – *Alnus glutinosa & incana*, Be – *Betula pendula*, Ca – *Carpinus betulus*, Co – *Corylus avellana*, Fa – *Fagus sylvatica*, Fr – *Fraxinus excelsior*, Pa – *Padus avium*, Pc – *Picea abies*, Pi – *Pinus sylvestris*, Qu – *Quercus robur*, Sa – *Salix fragilis*, Sr – *Sorbus aucuparia*, Ti – *Tilia cordata & platyphyllos*, Ul – *Ulmus glabra*; E2 – shrub layer

Table 2. Calculated species composition for typical site conditions – beech suppression (simulation of medieval pasture)

Soil type	Height (m)	Expos.	Slope (°)	% conifer.	% br.-leav.	Species with 5% and more of presence (in descending order)
FMG	250	0	0	2	98	Fr 34, Sa 31, Al 27, Pa (E2) 65, others 8
LMg	250	0	0	36	64	Qu 47, Ab 28, Co (E2) 16, others 25
KMm(a)	250	0	0	39	61	Qu 28, Pi 18, Fa 16, Ab 15, Be 7, Pc 6, Ac 6, Co (E2) 9, others 4
HMm, HMl	250	0	0	20	80	Qu 31, Ac 13, Ca 12, Ti 12, Ab 10, kl 9, Fa 6, Pi 6, Co (E2) 29, others 10
FMm	350	0	0	31	69	Ab 22, Ac 20, Qu 18, Pc 8, Fr 8, Ti 7, Ul 6, Pa (E2) 13, Co (E2) 41, others 11
FMG	350	0	0	5	95	Fr 32, Sa 26, Al 29, Pa (E2) 52, others 13
HMm, HMl	350	0	0	42	58	Ab 24, Qu 21, Pc 12, Ac 11, Fa 8, Ti 7, Pi 6, Co (E2) 22, others 11
LMg	350	0	0	59	41	Ab 44, Qu 29, Pc 13, Co (E2) 11, others 14
KMm(a)	350	0	0	55	45	Ab 27, Qu 15, Fa 15, Pc 14, Pi 14, Be 8, Co (E2) 5, others 7
KMm(a)	350	SW	30	35	65	Qu 35, Pi 21, Fa 15, Ab 11, Be 7, Co (E2) 9, others 11
KMa	350	0	0	78	22	Pi 53, Ab 19, Be 9, Qu 7, Fa 6, Pc 6, others 0
PGm	350	0	0	66	34	Ab 48, Qu 24, Pc 14, Co (E2) 5, others 14
GLm	350	0	0	8	92	Al 49, Fr 34, Sa 8, Pa (E2) 91, others 9
PZa	350	0	0	94	6	Pi 76, Ab 14, others 10
HMm, HMl	500	0	0	55	45	Ab 30, Pc 20, Qu 14, Ac 10, Fa 9, Be 5, Co (E2) 14, others 12
KMm(a)	500	0	0	61	39	Ab 31, Pc 20, Fa 15, Pi 10, Qu 9, Be 8, others 7
KMa	500	0	0	78	22	Pi 45, Ab 24, Be 10, Pc 9, Fa 7, others 5
PGm	500	0	0	76	24	Ab 53, Pc 20, Qu 15, others 12
GLm	500	0	0	14	86	Al 47, Fr 31, Pc 7, Ab 6, Sa 5, Pa (E2) 53, others 4
RAm, RAk, KMv	500	N	30	19	81	Fa 30, Qu 23, Ac 13, Ab 12, Ti 7, Co (E2) 54, others 15
KMe	500	N	30	41	59	Ab 24, Ac 20, Fa 14, Pc 13, Qu 10, Ti 6, Co (E2) 22, others 13
KMd	500	0	0	67	33	Ab 33, Pc 21, Fa 13, Pi 13, Be 8, Qu 6, others 6
KMd	500	SW	30	57	43	Ab 23, Pi 23, Qu 15, Fa 14, Be 11, Pc 10, others 4
KMd	500	NE	30	73	27	Ab 36, Pc 28, Fa 11, Pi 10, Be 7, others 8
PZa	500	0	0	92	8	Pi 67, Ab 19, Pc 7, Be 6, others 1
LIm(q)	500	0	0	84	16	Ab 39, Pi 35, Pc 11, Be 9, others 6
GLm-GLo	500	0	0	76	24	Pc 34, Ab 22, Pi 20, Al 15, others 9
KMg	500	0	0	67	33	Ab 47, Qu 21, Pc 18, Co (E2) 13, others 14
KMm(a), PZk	700	SW	30	58	42	Ab 28, Pc 19, Fa 15, Pi 12, Be 10, Qu 8, Sr 6, others 2
KMe	700	SW	30	37	63	Fa 21, Ab 20, Ac 16, Qu 13, Pc 11, Pi 6, Co (E2) 23, others 13
KMd	700	SW	30	64	36	Ab 29, Pc 20, Pi 15, Fa 13, Be 11, Sr 6, Qu 6, others 0
PZG, PZo	700	SW	30	61	39	Pc 31, Al 24, Ab 19, Pi 11, Fr 6, Pa (E2) 33, others 9
GLm-GLo	700	0	0	86	14	Pc 47, Ab 26, Pi 13, Al 6, others 8
KMm(a), PZk	700	NE	30	72	28	Ab 38, Pc 30, Fa 15, Sr 5, others 12
KMd- shallow	700	NE	30	74	26	Ab 50, Pc 16, Fa 11, Pi 8, Be 7, Sr 5, others 3
KMg	700	0	0	88	12	Ab 60, Pc 26, others 14
PZm	850	NE	30	84	16	Pc 49, Ab 35, Fa 9, others 7
RNp-PZm (PZk)	850	NE	30	77	23	Ab 47, Pc 27, Fa 12, Sr 7, others 7
RNp-PZm (PZk)	850	SW	30	68	32	Ab 42, Pc 16, Fa 13, Pi 10, Be 10, Sr 9, others 0
PZk	850	SW	12	75	25	Pc 37, Ab 36, Fa 14, Sr 6, others 7
RNp, RNm(a)	850	SW	30	71	29	Ab 44, Pc 17, Sr 17, Pi 11, Be 10, others 1
RNp, RNm(a)	950	SW	30	71	29	Ab 40, Pc 25, Sr 20, Be 8, Pi 6, others 1
RNp-PZm	950	SW	30	70	30	Ab 40, Pc 24, Fa 12, Sr 10, Be 7, Pi 6, others 1
RNp-PZm	950	NE	30	75	25	Ab 37, Pc 36, Fa 13, Sr 8, others 6
PZm	950	0	0	83	17	Pc 52, Ab 30, Fa 10, others 8
RNp, RNm(a)	950	NE	30	80	20	Ab 39, Pc 38, Sr 15, others 8

Explanations of abbreviations used in tables

Soil type – soil units according to Morphogenetic Soil Classification System (HRAŠKO et al. 1991) – equivalents to FAO units (in alphabetical order):

FMG – fluvi-eutric gleysol, FMm – eutric fluvisol; GLm – eutric gleysol, GLo – histo-humic gleysol; HMg – stagno-gleyic luvisol, HMm – orthic luvisol, HMl – "orthic-albic" luvisol; KMa – cambic arenosol, KMd – "typical" dystric cambisol, KMe – mollic cambisol, KMg – stagno-gleyic cambisol, KMm(a) – "moderate" dystric cambisol, KMv – calcic cambisol; LIm(q) – dystric litosol; LMm – albic luvisol, LMg – albo-gleyic luvisol; PGm – dystric planosol; PZa – ferro-orthic podzol, PZG – gleyic podzol, PZk – spodo-dystric cambisol, PZm – ferro-humic podzol, PZo – histo-humic podzol; RAk – "cambic" rendzina, RAm – "typical" rendzina; RNm(a) – "typical" ranker, RNp – "podzolic" ranker.

Woody species: Ab – *Abies alba*, Ac – *Acer pseudoplatanus & platanoides*, Al – *Alnus glutinosa & incana*, Be – *Betula pendula*, Ca – *Carpinus betulus*, Co – *Corylus avellana*, Fa – *Fagus sylvatica*, Fr – *Fraxinus excelsior*, Pa – *Padus avium*, Pc – *Picea abies*, Pi – *Pinus sylvestris*, Qu – *Quercus robur*, Sa – *Salix fragilis*, Sr – *Sorbus aucuparia*, Ti – *Tilia cordata & platyphyllos*, Ul – *Ulmus glabra*; E2 – shrub layer

Table 3. Calculated species composition for typical site conditions – exclusion of spruce and silver fir (simulation of strong air pollution impact)

Soil type	Height (m)	Expos.	Slope (°)	% conifer.	% br.-leav.	Species with 5% and more of presence (in descending order)
FMG	250	0	0	0	100	Fr 34, Sa 31, Al 27, Pa (E2) 66, others 8
LMg	250	0	0	4	96	Qu 61, Fa 14, Ti 5, Ac 5, Co (E2) 21, others 15
KMm(a)	250	0	0	8	92	Fa 71, Qu 13, Pi 8, others 8
HMm, HMl	250	0	0	4	96	Fa 45, Qu 22, Ca 8, Ac 9, Ti 8, Co (E2) 20, others 8
FMm	350	0	0	1	99	Qu 21, Ac 23, Fa 21, Fr 9, Ti 8, Ul 7, Ca 5, Pa (E2) 15, Co (E2) 48, others 6
FMG	350	0	0	0	100	Fr 34, Al 30, Sa 27, Pa (E2) 55, others 9
HMm, HMl	350	0	0	4	96	Fa 58, Qu 16, Ac 9, Co (E2) 17, others 17
LMg	350	0	0	5	95	Qu 53, Fa 21, Ac 6, Be 5, Co (E2) 21, others 15
KMm(a)	350	0	0	7	93	Fa 77, Qu 8, Pi 7, others 8
KMm(a)	350	SW	30	9	91	Fa 68, Qu 16, Pi 9, others 7
KMa	350	0	0	42	58	Fa 46, Pi 42, Be 7, Qu 5, others 0
PGm	350	0	0	8	92	Qu 46, Fa 30, Pi 8, Be 7, Co (E2) 10, others 9
GLm	350	0	0	1	99	Al 52, Fr 36, Sa 8, Pa (E2) 97, others 4
PZa	350	0	0	81	19	Pi 81, Fa 13, Be 5, others 1
HMm, HMl	500	0	0	4	96	Fa 68, Qu 11, Ac 7, Co (E2) 11, others 14
KMm(a)	500	0	0	5	95	Fa 81, Pi 5, others 14
KMa	500	0	0	35	65	Fa 54, Pi 35, Be 8, others 3
PGm	500	0	0	7	93	Fa 40, Qu 35, Be 9, Pi 7, Co (E2) 7, others 9
GLm	500	0	0	1	99	Al 54, Fr 36, Sa 6, Pa (E2) 61, others 4
RAm, RAk, KMv	500	N	30	1	99	Fa 84, Qu 6, Co (E2) 15, others 10
KMe	500	N	30	2	98	Fa 74, Ac 11, Qu 6, Co (E2) 12, others 9
KMd	500	0	0	8	92	Fa 80, Pi 8, Be 5, others 7
KMd	500	SW	30	12	88	Fa 72, Pi 12, Qu 8, Be 6, others 2
KMd	500	NE	30	7	93	Fa 81, Pi 7, Be 5, others 7
PZa	500	0	0	76	24	Pi 76, Fa 17, Be 7, others 0
LIm(q)	500	0	0	44	56	Pi 44, Fa 40, Be 11, others 5
GLm-GLo	500	0	0	46	54	Pi 46, Al 35, Be 9, Sr 5, others 5
KMg	500	0	0	3	97	Qu 50, Fa 21, Ac 10, Co (E2) 30, others 19
KMm(a), PZk	700	SW	30	6	94	Fa 80, Pi 6, Be 5, others 9
KMe	700	SW	30	2	98	Fa 81, Ac 6, Qu 5, Co (E2) 9, others 8
KMd	700	SW	30	9	91	Fa 77, Pi 9, Be 6, others 8
PZG, PZo	700	SW	30	22	78	Al 48, Pi 22, Fr 12, Be 6, Pa (E2) 65, Co (E2) 6, others 12
GLm-GLo	700	0	0	49	51	Pi 49, Al 23, Sr 13, Be 12, others 3
KMm(a), PZk	700	NE	30	3	97	Fa 90, others 10
KMd- shallow	700	NE	30	6	94	Fa 84, Pi 6, Be 5, others 5
KMg	700	0	0	5	95	Fa 50, Qu 19, Be 9, Ac 8, Sr 7, Pi 5, Co (E2) 7, others 2
PZm	850	NE	30	1	99	Fa 93, others 7
RNp-PZm (PZk)	850	NE	30	3	97	Fa 89, others 11
RNp-PZm (PZk)	850	SW	30	7	93	Fa 81, Pi 7, Be 6, Sr 5, others 1
PZk	850	SW	12	1	99	Fa 92, others 8
RNp, RNm(a)	850	SW	30	21	79	Sr 33, Fa 25, Pi 21, Be 20, others 1
RNp, RNm(a)	950	SW	30	13	87	Sr 43, Fa 26, Be 17, Pi 13, others 1
RNp-PZm	950	SW	30	4	96	Fa 83, Sr 7, Be 5, others 5
RNp-PZm	950	NE	30	1	99	Fa 91, Sr 5, others 4
PZm	950	0	0	1	99	Fa 93, others 7
RNp, RNm(a)	950	NE	30	5	95	Sr 45, Fa 40, Be 10, Pi 5, others 0

Explanations of abbreviations used in tables

Soil type – soil units according to Morphogenetic Soil Classification System (HRAŠKO et al. 1991) – equivalents to FAO units (in alphabetical order):

FMG – fluvi-eutric gleysol, FMm – eutric fluvisol; GLm – eutric gleysol, GLo – histo-humic gleysol; HMg – stagno-gleyic luvisol, HMm – orthic luvisol, HMl – "orthic-albic" luvisol; KMa – cambic arenosol, KMd – "typical" dystric cambisol, KMe – mollic cambisol, KMg – stagno-gleyic cambisol, KMm(a) – "moderate" dystric cambisol, KMv – calcic cambisol; LIm(q) – dystric litosol; LMm – albic luvisol, LMg – albo-gleyic luvisol; PGm – dystric planosol; PZa – ferro-orthic podzol, PZG – gleyic podzol, PZk – spodo-dystric cambisol, PZm – ferro-humic podzol, PZo – histo-humic podzol; RAk – "cambic" rendzina, RAm – "typical" rendzina; RNm(a) – "typical" ranker, RNp – "podzolic" ranker.

Woody species: Ab – *Abies alba*, Ac – *Acer pseudoplatanus & platanoides*, Al – *Alnus glutinosa & incana*, Be – *Betula pendula*, Ca – *Carpinus betulus*, Co – *Corylus avellana*, Fa – *Fagus sylvatica*, Fr – *Fraxinus excelsior*, Pa – *Padus avium*, Pc – *Picea abies*, Pi – *Pinus sylvestris*, Qu – *Quercus robur*, Sa – *Salix fragilis*, Sr – *Sorbus aucuparia*, Ti – *Tilia cordata & platyphyllos*, Ul – *Ulmus glabra*; E2 – shrub layer

Table 4. Calculated species composition for typical stand conditions – climatic change at year 2030 (without thermophilous trees [*Acer campestre, Quercus pubescens, Ulmus laevis, U. minor*] and *Quercus petraea*)

Soil type	Height (m)	Expos.	Slope (°)	% conifer.	% br.-leav.	Species with 5% and more of presence (in descending order)
FMG	250	0	0	0	100	Fr 46, Al 26, Sa 20, Pa (E2) 46, others 8
LMg	250	0	0	1	99	Qu 74, Ca 9, Ti 6, Co (E2) 18, others 11
KMm(a)	250	0	0	3	97	Fa 53, Qu 35, Co (E2) 8, others 12
HMm, HMl	250	0	0	1	99	Qu 34, Ca 22, Fa 19, Ti 15, Ac 7, Co (E2) 23, others 3
FMm	350	0	0	1	99	Qu 26, Ca 16, Ti 13, Ac 15, Fr 11, Fa 8, Ul 6, Pa (E2) 14, Co (E2) 67, others 5
FMG	350	0	0	0	100	Fr 42, Sa 27, Al 22, Pa (E2) 57, others 9
HMm, HMl	350	0	0	2	98	Fa 33, Qu 28, Ca 14, Ti 12, Ac 8, Co (E2) 34, others 5
LMg	350	0	0	4	96	Qu 68, Fa 9, Ca 6, Ti 6, Co (E2) 31, others 11
KMm(a)	350	0	0	5	95	Fa 67, Qu 21, Co (E2) 9, others 12
KMm(a)	350	SW	30	4	96	Fa 45, Qu 44, Co (E2) 7, others 11
KMa	350	0	0	32	68	Fa 48, Pi 32, Qu 17, others 3
PGm	350	0	0	6	94	Qu 69, Fa 15, Co (E2) 17, others 16
GLm	350	0	0	0	100	Fr 45, Al 43, Sa 8, Pa (E2) 100, others 4
PZa	350	0	0	79	21	Pi 78, Fa 17, others 5
HMm, HMl	500	0	0	7	93	Fa 46, Qu 22, Ti 9, Ac 8, Ca 6, Co (E2) 36, others 9
KMm(a)	500	0	0	9	91	Fa 72, Qu 13, Pi 5, Co (E2) 7, others 10
KMa	500	0	0	39	61	Fa 47, Pi 34, Qu 10, others 9
PGm	500	0	0	20	80	Qu 52, Fa 19, Ab 16, Co (E2) 17, others 13
GLm	500	0	0	2	98	Fr 46, Al 41, Sa 9, Pa (E2) 100, Co (E2) 6, others 4
RAm, RAk, KMv	500	N	30	2	98	Fa 66, Qu 12, Ti 8, Ac 5, Co (E2) 64, others 9
KMe	500	N	30	4	96	Fa 55, Ti 11, Qu 10, Ac 10, Ca 5, Co (E2) 47, others 9
KMd	500	0	0	13	87	Fa 72, Qu 11, Pi 8, others 9
KMd	500	SW	30	10	90	Fa 61, Qu 24, Pi 9, others 6
KMd	500	NE	30	16	84	Fa 72, Ab 8, Qu 8, Pi 7, others 5
PZa	500	0	0	81	19	Pi 76, Fa 15, others 9
LIm(q)	500	0	0	56	44	Pi 44, Fa 36, Ab 11, Be 6, others 3
GLm-GLo	500	0	0	40	60	Al 46, Pi 32, Ab 8, Qu 7, Co (E2) 7, others 7
KMg	500	0	0	12	88	Qu 56, Ab 11, Ti 8, Fa 8, Ca 7, Ac 6, Pa (E2) 5, Co (E2) 53, oth. 4
KMm(a), PZk	700	SW	30	13	87	Fa 67, Qu 13, Pi 7, Ab 6, Co (E2) 5, others 7
KMe	700	SW	30	5	95	Fa 59, Qu 14, Ac 8, Ti 7, Co (E2) 38, others 12
KMd	700	SW	30	17	83	Fa 66, Qu 11, Pi 10, Ab 7, others 6
PZG, PZo	700	SW	30	22	78	Al 43, Fr 18, Pi 13, Ab 9, Qu 8, Pa (E2) 100, Co (E2) 17, others 9
GLm-GLo	700	0	0	64	36	Pi 32, Ab 29, Al 24, others 15
KMm(a), PZk	700	NE	30	18	82	Fa 74, Ab 13, others 13
KMd-shallow	700	NE	30	27	73	Fa 62, Ab 19, Pi 8, Qu 6, others 5
KMg	700	0	0	48	52	Ab 45, Qu 29, Fa 14, Co (E2) 19, others 12
PZm	850	NE	30	23	77	Fa 73, Ab 18, others 9
RNp-PZm (PZk)	850	NE	30	25	75	Fa 69, Ab 18, Pi 6, others 7
RNp-PZm (PZk)	850	SW	30	26	74	Fa 61, Ab 14, Pi 11, Be 6, others 8
PZk	850	SW	12	17	83	Fa 77, Ab 13, others 10
RNp, RNm(a)	850	SW	30	56	44	Ab 31, Pi 24, Fa 13, Be 13, Qu 11, Sr 7, others 1
RNp, RNm(a)	950	SW	30	59	41	Ab 35, Pi 21, Fa 16, Be 12, Sr 9, others 7
RNp-PZm	950	SW	30	24	76	Fa 67, Ab 15, Pi 9, Be 5, others 4
RNp-PZm	950	NE	30	23	77	Fa 72, Ab 18, others 10
PZm	950	0	0	22	78	Fa 75, Ab 17, others 8
RNp, RNm(a)	950	NE	30	64	36	Ab 50, Fa 20, Pi 10, Sr 8, Be 7, others 5

Explanations of abbreviations used in tables

Soil type – soil units according to Morphogenetic Soil Classification System (Hraško et al. 1991) – equivalents to FAO units (in alphabetical order):

FMG – fluvi-eutric gleysol, FMm – eutric fluvisol; GLm – eutric gleysol, GLo – histo-humic gleysol; HMg – stagno-gleyic luvisol, HMm – orthic luvisol, HMl – "orthic-albic" luvisol; KMa – cambic arenosol, KMd – "typical" dystric cambisol, KMe – mollic cambisol, KMg – stagno-gleyic cambisol, KMm(a) – "moderate" dystric cambisol, KMv – calcic cambisol; LIm(q) – dystric litosol; LMm – albic luvisol, LMg – albo-gleyic luvisol; PGm – dystric planosol; PZa – ferro-orthic podzol, PZG – gleyic podzol, PZk – spodo-dystric cambisol, PZm – ferro-humic podzol, PZo – histo-humic podzol; RAk – "cambic" rendzina, RAm – "typical" rendzina; RNm(a) – "typical" ranker, RNp – "podzolic" ranker.

Woody species: Ab – *Abies alba*, Ac – *Acer pseudoplatanus & platanoides*, Al – *Alnus glutinosa & incana*, Be – *Betula pendula*, Ca – *Carpinus betulus*, Co – *Corylus avellana*, Fa – *Fagus sylvatica*, Fr – *Fraxinus excelsior*, Pa – *Padus avium*, Pc – *Picea abies*, Pi – *Pinus sylvestris*, Qu – *Quercus robur*, Sa – *Salix fragilis*, Sr – *Sorbus aucuparia*, Ti – *Tilia cordata & platyphyllos*, Ul – *Ulmus glabra*; E2 – shrub layer

in the case of heavy air-pollution that disqualifies both these tree species (harmful impact on other tree species, e.g. pine, is not considered here in the interest of simplification). As a result, beech dominates practically all the Ještěd Ridge and higher locations of the Liberec Basin. Silver fir-beech wood alternates with beech-oak wood in the Sub-Ještěd Hills; beech oak-wood dominates the warmer part of the Zittau Basin.

D) The last map was made for the anticipated change of climate in 2030 according to the GISS model (a highly pessimistic scenario). The calculation included durmast oak, which was not taken into consideration in previous maps; consequently, there is generally a higher share of oak (presented table shows results w/o *Quercus petraea* for better comparability). The calculated vegetation is considerably diversified; there is clear vegetative progression, in some places having the full sequence: oak wood – oak-beech wood – beech wood – fir-beech wood. A similar situation can be found on the southern slopes of the Krušné Hory Mountains today. The maps of individual tree species representation would clearly show a high share of oak and a low share of fir on dystric planosols and other "gleyic" soils where it was significantly suppressed by pedunculate oak. Pine, which is to be expected at top elevations of Ještěd, would get up to higher elevations too. Like all other maps, this map is necessary to understand as an expression of site potential provided it remains the same. In reality the anticipated changes of climate will be so rapid that forest ecosystems will not be able to adjust to them, the more so as their key component – tree species – are strongly affected by forestry practices limiting their proliferation. Tree species will respond to the resulting stress by diminished vitality, increased propensity to damage of various type and probably premature die back. While young stands are still capable of some adaptation (if they do not dry up), older trees will often be condemned to extinction. The problem of climatic change and its impact on forests is, however, so complex that it cannot be dealt with in this paper.

E) Natural vegetation for the postglacial periods was also calculated (Pre-Boreal, Boreal, Atlantic, Sub-Boreal and older Sub-Atlantic). To reconstruct the paleoclimate, temperature and precipitation curves from the study of LOŽEK and CÍLEK 1995 were used. The calculated forest stand composition significantly diverges from what paleobotanists usually think and probably from reality as well. The biggest controversy has to do with the share of oak and spruce in the middle Holocene. Palynologically, the repeatedly attested high share of spruce from medium elevations up cannot be ecologically explained. In addition, the likely low representation of oak in late Atlantic cannot be explained in view of today's ecological and biological properties of this tree species.

DISCUSSION

The verification of the model was made in several steps. First, current potential natural vegetation was calculated for all climatic stations in this country and in other countries, and the coincidence of calculated and expected species compositions was tested. Three versions of the model with different sets of control variables were used for this step. The results of individual versions of the model differed only slightly. In view of a more realistic description of the representation of coniferous tree species, the version using the mean temperature in January as the only one to do so was used further on. The calculated species compositions with most of the climatic stations in the Czech Republic corresponded to the data in vegetation and typology maps. There is, however, no possibility to objectively compare the data, as the contents of these maps and all our views of natural vegetation in general are necessarily liable to certain error. The model from Slovakian localities, which are more diversified than the Czech ones, esp. climatically and phytogeographically, offered rather controversial results. Even more problematic were the results from most of the foreign sites, especially those situated outside Central Europe, the error growing with the distance of the evaluated site from the Czech Republic. There were probably three main reasons for unsatisfactory results: (i) different ecological nature of tree species often on the outskirts of the area, probably having some other genetic dispositions, (ii) the presence of other tree species not included in the model or not accurately defined in it (esp. Sub-Mediterranean oaks), (iii) different nature of the site variables the model could not work with, e.g. low temperature amplitude, windiness and high air humidity in the Euro-Atlantic area, dry periods and warm winters in the Sub-Mediterranean region. The fact that it was not possible to obtain acceptable results even after various corrections were used also points to the existence of these reasons.

The calculation was also made for ten primeval forests in the Czech Republic, which were documented in great detail by PRŮŠA (1985, 1999) in view of forestry and vegetation. The results were largely dependent on precisely setting edaphic variables; nevertheless, they did not diverge very much from the present state of stands on the whole. Larger discrepancies were shown with the Lanžhot primeval forest (a lowland alluvial wood), where the current species composition is partly influenced by man. A number of localities showed the already mentioned qualities of the model, that means the higher presence of oak at low elevations and on the other hand, a smaller share of spruce. The usefulness of the model for paleovegetation was tested in the locality Kameničky in the Czech-Moravian Highlands. To compare the data, interpretation of a detailed pollen diagram covering continually all of Holocene was used along with eight samples of absolutely dated ^{14}C (RYBNÍČKOVÁ, RYBNÍČEK 1998). The calculations show relative agreement with the

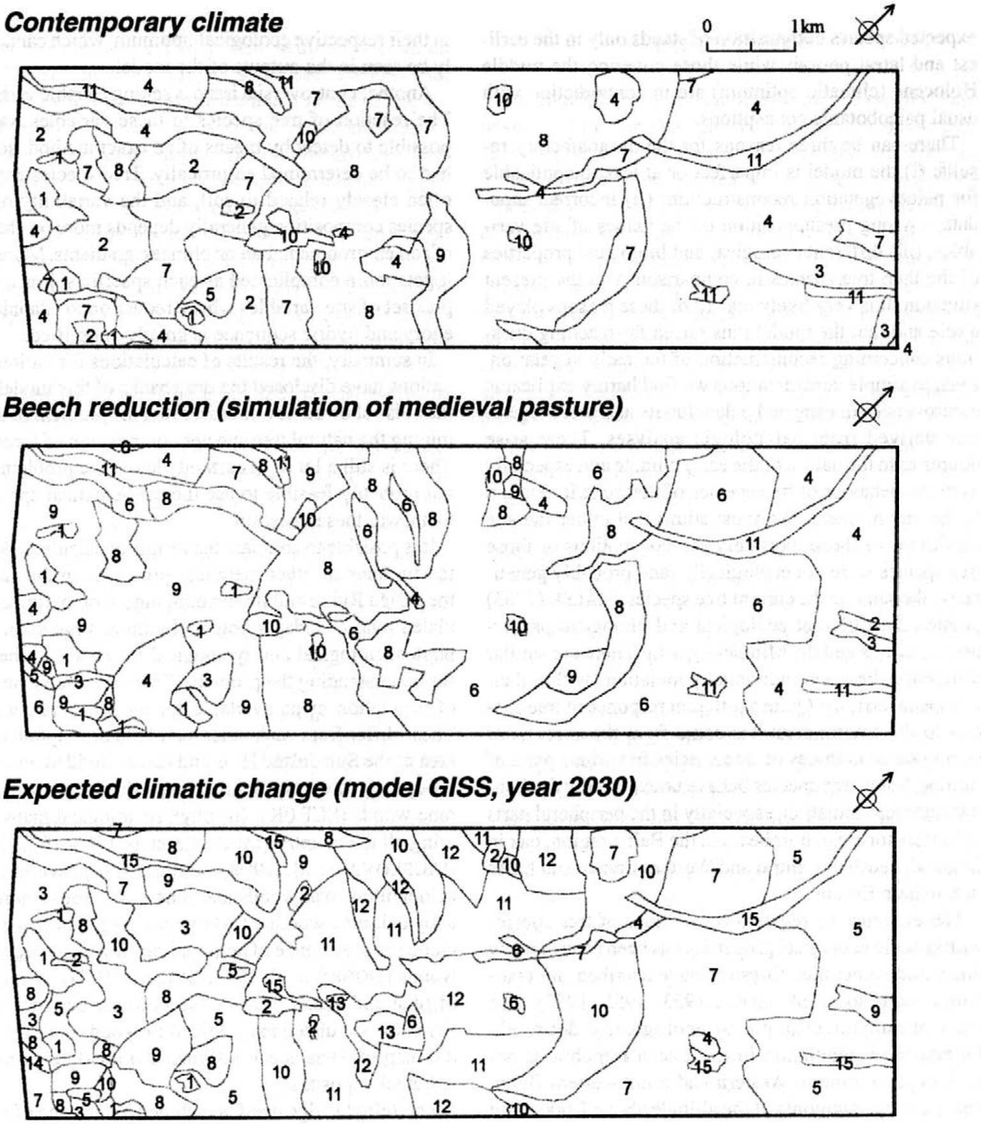

Fig. 1. Map comments

Contemporary climate: 1 – pine wood, 2 – (silver fir) pine-beech wood, 3 – (beech) silver fir-oak wood, 4 – mixed silver fir wood, 5 – beech wood with oak, 6 – mixed oak wood, 7 – beech wood, 8 – beech wood with silver fir, 9 – beech wood with spruce and silver fir, 10 – (mixed) spruce wood, 11 – ash-alder alluvial wood

Beech reduction: 1 – pine wood, 2 – mixture of pine, oak and beech (and silver fir), 3 – (beech) silver fir-oak wood, 4 – (mixed) silver fir wood, 5 – mixture of "scree trees" (maple, ash, elm, lime), 6 – (oak-beech) spruce-silver fir wood, 7 – (mixed) beech wood with silver fir, 8 – (mixed) silver fir-spruce wood, 9 – mixture of pine, silver fir, spruce (and oak), 10 – (mixed) spruce wood, 11 – ash-alder alluvial wood

Expected climatic change: 1 – pine wood, 2 – mixed pine wood, 3 – mixture of pine, oak and beech, 4 – oak wood, 5 – mixed oak wood, 6 – mixed silver fir wood, 7 – (beech) oak wood with silver fir, 8 – oak wood with beech, 9 – (mixed) oak-beech wood, 10 – beech wood with oak, 11 – beech wood, 12 – beech wood with silver fir, 13 – (oak-beech) pine-silver fir wood, 14 – mixture of "scree trees", 15 – ash-alder alluvial wood

Section through the highest part of Ještědský hřbet. Left: Podještědí Hills (about 400 m, sandstone and quaternary sediments), middle: massif of Ještěd (1,012 m, acid crystalline rocks), right: Žitavská pánev Basin (about 400 m, quaternary sediments) expected species composition of stands only in the earliest and latest periods while those covering the middle Holocene (climatic optimum) are in contradiction with usual paleobotanic conceptions.

There can be three reasons for the unsatisfactory results: (i) the model is imperfect or at least inapplicable for paleovegetation reconstruction; (ii) incorrect input data – wrong presupposition of the values of site variables; (iii) different ecological and biological properties of the then tree species in comparison with the present situation. It is very likely that all of these reasons played a role and that the model thus raised far-reaching questions concerning reconstruction of the early vegetation. Even in simple considerations we find hardly explicable controversies in expected paleoclimate and paleovegetation derived from palynologic analyses. There arise doubts as to the nature of the early climate and especially as to the behavior of tree species of that time in relation to the environment. We must admit that either the site conditions of those days defy our conceptions or those tree species were not ecologically (and probably genetically) the same as the current tree species. MÁLEK (1983) pointed out different ecological and biological properties of today's and the Middle-Ages fir. There are similar differences between individual populations within their European territory. Quite a different response of tree species to the environment has come from the analysis of ecological amplitudes of tree species in various parts of Europe. Some tree species behave unexpectedly for Central European situation, especially in the peripheral parts of the territory, e.g. hornbeam in the Baltic region, oak in England, beech in Central and Western France and limes in Southern Europe.

The existence of regional populations of tree species with specific ecological properties has been proved many times and sometimes foresters have ascribed the taxonomic value to it (SVOBODA 1953, 1955, 1957). The most prominent example of ecologically definitely formed local population in the Czech Republic is so-called upland pine in Western and Southwestern Bohemia growing commonly at the altitude above 1,000 m. In most Czech mountains the occurrence of pines ceases at 600 or 700 m, and this situation can be considered much less influenced by man. There is likely to be a number of similar cases in all of Europe and many of them may pass unnoticed. Regional ecological (genetically fixed) variety of tree species is practically impossible to cover by this model, which reduces the value of its results.

The competition mechanism used in the model (competition and dilatation exponents) is also a critical issue. Since the model does not consider vertical stratification of the stand, it does not help effectively suppress light-demanding tree species in understorey. This is most conspicuous in the representation of dwarf pine and in the mixture of oak and beech as well as in the mixture of fir and spruce with deciduous tree species. Both of these coniferous species have a tendency to create ± pure stands in their respective ecological optimum, which cannot fully be seen in the outputs of the model.

Another controversial issue is setting edaphic variables. The reaction of tree species to these variables was not possible to detect by means of an exact method, so they had to be determined empirically. Tree species are very often closely related to soil, and the variability of tree species composition generally depends more on changes of soil environment than on climatic gradients. Moreover, it gets more complicated as each specific soil is a complex set of site variables whose reduction to edaphic category and hydric sequence is greatly simplified.

In summary, the results of calculations for various situations have disclosed the drawbacks of this model, and they also showed how multifaceted the problem of determining the natural tree species composition of forests is. There is still a lot of uncertainty about the problem. It is not probably feasible to use the mathematical apparatus to answer these questions.

It is possible to compare the results of calculations with the findings of other methodic processes in the case of the Ještěd Ridge and its surroundings. Comparing a simulated map of today's potential natural vegetation with phytosociological and typological maps is most helpful for understanding the problem. There are a large number of vegetation maps available for the wider target area. These differ from each other mainly in description of the area of the Sub-Ještěd Hills and can be divided into three groups: (i) forest typological maps showing mostly acid pine woods (SLT 0K); (ii) phytosociological maps covering all the country (MIKYŠKA et al. 1968–1972; NEUHÄUSLOVÁ et al. 1998) suggest the prevalence of acidophilous oak woods and pine-oak woods (more exactly oak-pine woods); (iii) regional vegetation maps include the prevalence of acidophilous Sub-Atlantic beech woods (DOBRÝ et al. 1973; SÝKORA 1974). A mixture of pine and beech prevails (secondarily oak and silver fir) in the simulated map. Mixed fir woods are shown on the map of Pleistocene sediments (loess-like loam and colluvial deposits).

The Ještěd Ridge itself is included in the zone of beech wood where phytosociologically fir and fir-spruce beech woods also belong. The typological map suggests higher representation of spruce, and its domination at higher elevations of the Hlubocký Ridge. The simulated map shows beech as clearly dominant, with the admixture of fir and spruce at higher elevations. Spruce as a dominant tree species occurs only on underdeveloped soils in small areas, always in mixture with fir. Unlike the typological maps, its overall representation is distinctly lower.

Deciduous groves ("oak hornbeam woods") and on a higher level, acidophilous beech woods are mapped in the Zittau Basin. Forest typological maps include this area mainly in the third forest vegetation belt with beech dominating and oak mixed in. The simulated map clearly reflects soil contrasts. Mixed fir woods with growing representation of pedunculate oak at lower elevations are mapped on prevailing Pleistocene sediments covered with planosol and other "gleyic" soils. Beech woods with a small share of fir and a significant admixture of oak are calculated on the granite geest in the extrazonal sites of southern and western slopes. Deciduous groves ("oak hornbeam woods") are indicated only as transient types giving way to fir oak woods and fir beech woods.

The author made a map 1:25,000 of the target area based on interpreting the site units and phytosociological research in the field (VIŠŇÁK 2000). The legend of the map is largely made up by syntaxa designed in the Zürich-Montpellier School style – association and subassociation (42 units in all). This map in its content approximately agrees with the simulated map derived from the mathematical model.

From the paleobotanic point of view, the Sub-Ještěd Hills is the best-explored partial area. It may be deduced from only partially published results of extensive research (FIRBAS 1927) that the major tree species in the older Sub-Atlantic were fir, pine and beech. Pine cannot be considered a generally prevalent tree species in the target area. Oak was probably just a secondary tree species unlike what the popular thinking is. It is likely to have extended up to the southwestern slope of the Ještěd Ridge. Beech and fir dominated the late Holocene. Spruce was probably a locally numerous (edaphically contingent) tree species. There is very sketchy and insufficient data available for the Zittau Basin as to its paleovegetation. The dominant silver fir and spruce with a minor representation of beech is in a Sub-Boreal sample (RUDOLPH 1933) in the western part of the Liberec Basin. The interpretation of paleobotanic data concerning the older Sub-Atlantic does not basically differ from the results provided by the model. It must be said, however, that these data are very fragmentary and pertain mostly to marginal areas.

Archive documents offer an interesting comparison. They show beech as dominant with admixture of fir in the Ještěd Ridge. Occurrences of "Black Forests" are mentioned at top elevations, i.e. coniferous stands of silver-fir or spruce. These occurrences are indicated by local names like Black Mountain, Black Hill or Black Top – the main locality of these stands was, however, undoubtedly Ještěd itself. Fir and spruce, with pine, beech and oak occurring locally, have been documented as the main tree species in the Sub-Ještěd Hills since the end of the 16th century. Materials for the Zittau Basin are missing, as the forest properties described extend to the Ještěd Ridge and the Jizera Mountains. It is obvious that the condition of described forests cannot be considered relevant to today's potential natural vegetation. As elsewhere, originally more numerous beeches must have been suppressed by forest pasture (MÁLEK 1983) and by the general degradation of forest soil, which oligotrophic soils on sandstone are always prone to. A cool period called the "Little Ice Age" (1600–1850 or even earlier, SVOBODA 1995) is also in favor of fir and spruce.

CONCLUSION

The multiplicative model of natural tree species composition of the forest is relatively a useful means to evaluate partial areas in Central Europe. Its efficiency is, however, significantly decreased for these reasons: (i) the model shows the site potential regardless the dynamics of ecosystems; (ii) the model deals with tree species as individuals of homogeneous properties in all their geographical area; (iii) the soil characteristic of the environment is sketchy, and the properties of tree species in edaphic gradients were determined empirically; (iv) the competitive relationships within the model are greatly simplified. The following was confirmed in applying the model to various hypothetical sites and situations:

1. The behavior of tree species, i.e. their qualitative and quantitative participation in stands is a result of a coincidence where ecological causes make up only a part of the complex. Particularly noteworthy is the factor of variability within the species, relationships between the tree species in the stand at a time scale of developing cycles, succession and secular changes. Yet, these factors are much harder to know than a mere relationship between the tree species and the environment (habitat).
2. For this reason natural vegetation cannot be derived simply from analyzing site conditions, not even on purely floristic-phytosociologic basis. It is necessary to combine these two approaches. The paleobotanic or forest-dendrologic findings cannot be omitted either.
3. The used model simulates potential natural vegetation. It is a vegetation expression of the current site supply and does not depend on the previous development of vegetation in the particular habitat. "Developing factors", however, play a very important role in real life. Thus, the result of continuing succession and development (the preserved remains of natural forests) does not have to be identical with the meaning of the term potential natural vegetation.
4. The ecological requirements of tree species in various parts of their distribution area or individual relict sites differ, which is a result of the postglacial development. From the ecological point of view, geographically different populations of the same species cannot be seen as the only ecological individual (this is mainly true about old tree species, such as pine, birch, spruce or pedunculate oak as to their migration).
5. There are great differences in opinions as to the concept of altitudinal vegetation belts: forest typologists and geobiocenologists think in terms of continuum – the dominant species of belts are gradually replaced. Traditional phytosociology is under the influence of organismal concept and deals with clear-cut stages (oak, beech or spruce belts). Vegetation belts in the individualistic concept undoubtedly exist; however, it is not fully developed everywhere. Beech in ecologi-

cal optimum tends to create pure stands. Therefore, oak beech woods are relatively more rare than beech oak woods (it is not true for azonal sites). Beech was probably largely accompanied by fir in the past, so the beech belt was never quite common. The same is probably true for the relationship between beech and spruce. "Pure" vegetation belts, as phytosociology knows them, are often a consequence of degradation in the past, resulting in today's seemingly natural stand formations.

6. Every method used for studying the natural forest composition has certain limitations. Palynology has difficulties with interpreting pollen spectra, the inability to reliably document entomophilous tree species, dependence of the efficiency of pollen diagrams on localization and site conditions of the studied profile. The drawback of historical study is a short time the archived documents (often not numerous and not adequately specific) have been available. In most cases they document vegetation that has greatly changed. The disadvantage of phytosociology is sometimes its one-sided orientation on floristic indicators, many of which may be sub-spontaneously affected (stand and degrading stages) and may be of very different ages. On the contrary, forestry typology favors an ecological view (site research) and has a tendency to pass over phytogeographic circumstances. It is often inspired by the historical study of forests, which sometimes leads it to erroneous interpretations.
7. It seems from the analysis of habitats of some tree species in the target area, esp. hornbeam and sessile oak, that their regional absence in potentially favorable habitats is not caused by migration but by the existence of earlier ecological or cenotic barriers. These tree species were able to subsist successfully in favorable, often isolated localities, for long periods. It is probably true of beechless areas in inter-Carpathian Basins in Slovakia and for the absence of sessile oak in Southern Bohemia.
8. The postglacial development of vegetation is veiled by many uncertainties and doubts. The spreading of some formations in separate periods is at first sight contradictory to the expected climate and soils. We would expect the great expansion of mixed oak woods in most of the area of today's Czech Republic in warm and humid older Atlantic. Palynological curves, however, show the expansion of spruce, and compared to the current situation, only a little larger distribution of oak. The later existence of mixed deciduous forests of *Acer-Fraxinus* type as proposed by RYBNÍČKOVÁ (1985) has not been supported sufficiently. Uneasily explicable is also beech coming very gradually, which was probably made possible only by oscillation in precipitation and cooling in the younger Atlantic and Sub-Boreal.

The findings acquired during the study of forest composition in the area of the Ještěd Ridge are also important for forest management. They show the unambiguity of determining natural species composition using different methods and the necessity to synthesize one's approaches. The critical issues are especially edaphically "anomalous" (azonal) sites and sites affected by water as well as localities with specific mezoclimate, esp. frost affected depressions and summit areas. Also, one must not omit regional vegetation variability, behind which there are developmental and genetic circumstances.

In view of forestry, a risk of climatic changes (warming) and continuing influences of anthropogenic stressors are also a significant factor. If forest stands are to withstand all these pressures, they must be suitably physiologically equipped for it. This means preferring the tree species of potential natural composition adequate to the anticipated climate and a larger number of tree species in renewed stands. A dominant and perspective tree species in the interest area of the Ještěd Forest Administration is beech. Its share should increase not only in the Ještěd Ridge itself (at the expense of spruce), but also in the Sub-Ještěd Hills (at the expense of pine). It is desirable that beech not grow in pure stands, which usually defies the nature of natural forests, but with at least a small admixture of other tree species – ideally of fir or spruce, at lower altitudes of oak and generally of other deciduous tree species, esp. of sycamore maple. In case the climatic models are fulfilled, there would be a larger existential space for oak. Currently, however, oak is only a locally admixed tree species and growing it in pure stands is substantiated but for few exceptions. The vitality of spruce may be substantially weakened at lower elevations in the future. The areas below 500–600 m, except cold depressions and deep valleys, will be beyond the physiological amplitude of spruce in 2030 according to the GISS model. A small potential withdrawal may be expected with silver fir. Its real usefulness will probably be minimal in view of continuing difficulties of its growing.

The indispensable material for determining a target tree species composition is a forest typological map. Although it is subject to some drawbacks, it constitutes a unique set of information, which is at its scale (1:10,000) beyond comparison. Unlike vegetation (phytosociological) maps, a great advantage of typological maps is that they map sites on the level of forest type groups (SLT) and they interpret natural vegetation based on them. Mapping the sites is more objective than directly mapping the potential vegetation; therefore, typological maps are of greater value (they are less subject to errors). The phytosociological content of forest types and their groups must be continually revised and adjusted to the conditions of the particular Natural Forest Region.

The boundaries of typological units must be respected in daily practice even though whole stands or stand groups are still included in one prevailing forest type in the interest of simplification. Greater emphasis to use typological findings in forestry should be reflected in dividing the forest management units, which are ecologically too wide and are adjusted to the needs of intensive monocultural forestry focusing on spruce and pine.

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Stanovení potenciální přirozené skladby lesů pomocí matematického modelu na příkladu Ještědského hřbetu

ABSTRAKT: Pro výpočet přirozené druhové skladby lesů podle stanovištní nabídky byl vyvinut jednoduchý matematický model. Model je založen na odezvě jednotlivých druhů dřevin na klimatické a půdní charakteristiky prostředí. Pro každou dřevinu a každou ze souboru řídících proměnných jsou stanoveny hodnoty tzv. dílčí vitality. Ty jsou pak navzájem spojeny na multiplikativním principu. Ze srovnání celkových (relativních) vitalit pro jednotlivé dřeviny je pak po korekcích odvozeno potenciální zastoupení každé dřeviny na daném stanovišti. Model byl aplikován v ekologicky kontrastní oblasti Ještědského hřbetu v severních Čechách. Jeho použitelnost byla testována i na širokém souboru lokalit v České republice i v okolních zemích. Model byl vyzkoušen i pro predikci budoucí přirozené vegetace pro případ klimatických změn či při rekonstrukci vegetace v dřívějších obdobích postglaciálu. V řadě případů však výsledky výpočtů neodpovídaly očekávaným hodnotám. Je to způsobeno jednak nedokonalostí modelu, především popisu kompetičních vztahů mezi dřevinami, jednak model ukazuje i na složitost přírodních procesů, které sebelepší model nemůže z principu postihnout. Faktorem „náhodnosti" je vnitrodruhová ekologická (a genetická) variabilita dřevin, dynamický rozměr sukcese a sekulárního vývoje lesních ekosystémů a specifická povaha některých stanovištních charakteristik. Rozporuplné výsledky při rekonstrukci vegetace ve středním holocénu nastolují řadu zajímavých otázek.

Klíčová slova: přirozené složení lesů; matematický model; Ještědský hřbet; severní Čechy; potenciální přirozená vegetace; stanovištní potenciál; paleobotanika; klimatické změny

Otázka přirozeného druhového složení lesů má značný teoretický význam a je i důležitým předpokladem pro trvale udržitelné hospodaření v lesích. Názory na přirozené složení lesů ovšem nejsou jednotné. V lesnické praxi v ČR se přirozené zastoupení dřevin odvozuje z typologického systému ÚHÚL. Existují však i další přístupy, které nemusejí na konkrétních stanovištích poskytovat srovnatelné výsledky: geobiocenologie (tj. rozšíření typologického systému prof. Zlatníka dosud používaného na Slovensku), fytocenologie, paleobotanika, historický průzkum. Každá z těchto disciplín pracuje s jinými zdroji dat a na les tak pohlíží pouze z určitého úhlu své odbornosti. Teprve syntézou jednotlivých postupů lze dospět k věrohodnějším závěrům.

Zajímavým doplňkem uvedených metod může být i matematický model přirozené druhové skladby lesů. Modelů simulujících vegetační procesy a zobrazujících vegetační mozaiku v krajině byla zejména v zahraničí vyvinuta celá řada. V práci je prezentován statický model, který vyjadřuje kvantitativní složení stromového patra lesa jako funkci přírodního prostředí (stanoviště). V modelu není implementován dynamický faktor, tj. jednotlivá vývojová stadia lesního porostu a důsledky stanovištních změn tímto vývojem vyvolané. Výstupem je „stanovištní potenciál" dané lokality vyjádřený kombinací očekávaných dřevin s jejich přibližným procentuálním zastoupením. Filozofie modelu je tedy blízká koncepci potenciální přirozené vegetace (dnes běžně používané ve fytocenologickém mapování), ale i lesní typologii založené na stanovištním průzkumu. Místo do značné míry subjektivních rozhodovacích postupů je však využito matematického algoritmu a neřeší se problematika bylinného patra. Principem modelu je stanovení tzv. dílčích vitalit odpovídající jednotlivým dřevinám na konkrétním stanovišti (kombinaci stanovištních proměnných). Dílčí vitality nabývají hodnot 0 až 1. Byly odvozeny srovnáním růstových podmínek pro jednotlivé dřeviny podél gradientu stanovištních proměnných. Řídícími proměnnými, použitými v modelu, jsou průměrná teplota měsíců ledna a července, rozdíl těchto teplot, délka období s průměrnou teplotou alespoň 10 °C, podíl ročních srážek a teplot zvětšených o 10 (tzv. aridita), klimatické anomálie podmíněné vyhraněnými reliéfovými formami. Variabilita půdního prostředí je vyjádřena kombinací trofických a hydrických řad podle ZLATNÍKA (1976) ve zjemněném provedení. Hodnoty dílčích vitalit pro jednotlivé proměnné jsou spojeny na multiplikativním principu, po logaritmické transformaci. Výsledek je upraven tzv. kompetičním exponentem, který vyjadřuje rozdílnou kompetiční zdatnost jednotlivých dřevin. Získané hodnoty jsou po dalších úpravách převedeny na procenta, která vyjadřují očekávané uplatnění dané dřeviny v porostu. Model je propojen s vektorovou mapou stanovištních proměnných. Vstupními údaji jsou reliéfové kategorie (kombinace nadmořské výšky, sklonitosti a svažitosti), půdní jednotky (lze je odvodit z typologické mapy) a klimatická data pro referenční body. Většina řídících proměnných je z těchto dat vypočtena, protože jejich přímé zjišťování v terénu by bylo příliš náročné.

Popsaný model byl aplikován v oblasti Ještědského hřbetu a jeho úpatí, zahrnujících okrajové části Podještědí a Žitavské pánve. Výsledky výpočtů byly zachyceny do souboru map, v nichž je zobrazeno jak procentuální zastoupení jednotlivých dřevin, tak i lesní formace z hlediska zastoupení vůdčích dřevin. Řešily se následující případy:

1. Dnešní potenciální přirozená vegetace. Vůdčí dřevinou většiny území je buk, který do středních poloh zřetelně převažuje a teprve výše je výrazněji doprovázen jedlí (příměs do 30 %). Jedle má optimum na pseudoglejových půdách zejména v Liberecké kotlině, ale i v Podještědí. V obou těchto územích tvoří její příměs dub a buk, v menší míře lípa a smrk. Na pískovcových podkladech Ralské pahorkatiny je předpokládána směs borovice a buku, v menší míře i jiné formace. Porosty převážně smrkové či borové jsou v území celkově vzácné a jsou vždy edaficky podmíněny. Ve vrcholových polohách Ještědského hřbetu byly na chudém rankeru až litozemi vypočteny smíšené porosty smrku, jedle a jeřábu, na vyvinutých půdách je buk převažující dřevinou ještě v nadmořských výškách nad 900 m.
2. Potenciální přirozená vegetace s potlačením buku. Tato mapa simuluje vliv lesní pastvy v minulých stoletích, který znevýhodňoval buk před jedlí a smrkem (MÁLEK 1983). Vypočtené druhové skladby ukazují převahu obou uvedených jehličnatých dřevin v téměř celém Ještědském hřbetu. V Podještědí a na chudších půdách i ve vlastním hřbetu k nim přistupuje borovice. Buk si své dominantní postavení uhájil pouze na troficky nejbohatších, zejména karbonátových podložích středních poloh, kde jej doprovází dub s jedlí.
3. Potenciální přirozená vegetace s vyloučením jedle a smrku. Mapa simuluje vliv silné imisní zátěže, která obě uvedené dřeviny eliminuje. Výsledkem je převládnutí buku prakticky v celém Ještědském hřbetu a ve vyšší části Liberecké kotliny. V Podještědí se střídá boro-bučina s bukovou doubravou, také v teplejší části Žitavské pánve dominuje buková doubrava.
4. Klimatická změna k roku 2030 podle modelu GISS. Oproti první mapě výrazně vzrůstá zastoupení dubu až do středních poloh a vytváří se téměř úplný sled vegetačních stupňů, podobně jako na jižních svazích Krušných hor. Jedle a zejména smrk jsou zatlačeny, naopak větší rozšíření má borovice.

Uvedené výsledky jsou v poměrně dobrém souladu se závěry získanými jinými metodickými postupy. Při aplikaci modelu na odlehlejší území (mimo hranice ČR) tento soulad ale vždy neplatí. Rozporuplné výsledky byly získány i při simulaci vegetace z doby klimatického optima holocénu. Ukázalo se, že přirozené druhové složení lesů zdaleka není jen vyjádřením vztahu ekologicky jednoznačně definovaných dřevin k nabídce prostředí. Jednotlivé druhy dřevin představují soubory populací ekologicky (a geneticky) diferencovaných v prostoru i čase, což bylo opakovaně prokázáno provenienčními pokusy.

Při vývoji lesních porostů v minulých obdobích sehrály důležitou roli i migrace dřevin z glaciálních refugií a jejich postupné obsazování prostoru. Konečně i stanovištní podmínky konkrétních lokalit představují velmi komplexní proměnné, jejichž redukce na malý počet snadno uchopitelných „řídících proměnných" je nutně zjednodušující.

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Thinning experiment in a Scots pine forest stand after 40-year investigations

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ABSTRACT: There has been a permanent lack of experiments investigating the growth and development of pine stands as well as of convincing results. Therefore an experiment was established in a 27-years old stand of a local pine ecotype in the East-Bohemian pine region in 1957 in order to determine the effect of crown tending on the stand development and volume production compared to low tending (thinning from below) of different intensity. The investigated crown tending was founded on quality selection with determination of quality individuals and concurrent improvement of subdominant trees (plot "D"). Low thinning of medium intensity (plot "B") and high intensity (plot "C") consisted in removing subdominant trees of adequate tree classes. The experiment was evaluated after 40 years.

Keywords: stand tending; pine; increment; wood production

After World War II, strong trends of transforming and converting devastated spruce and pine monocultures were furthered (KONIAS 1951). One of the silvicultural measures directed to establishment of mixed and all-aged forests was represented by crown thinning though the current knowledge had not been favourable for that tending approach namely in pine stands (WIEDEMANN 1948). An experiment was established in 1957 in order to get more knowledge of a proper tending method in middle-age pine stands (CHROUST 1959), the results of which are topical for the present tending technology. It is so because there are efforts in the Czech forestry to tend the stands so that monocultures could be prepared to conversion to more nature-close stands. The crown thinning should be the means (ZEZULA 2000).

ISSUE

In the Czech lands similarly like in Germany the tending of even-aged pine stands was based above all on low thinnings of light to medium intensity which were preceded by interventions into the crown level in order to remove low-grade overtopping trees (PLÍVA 1987; PAŘEZ, CHROUST 1988; MUSIL 1988, etc.). Existing regulations and instructions of differentiated tending stemmed from long-term experiments and experience (BAADER 1934; WIEDEMANN 1948; ERTFELD 1960; ASSMANN 1968; MITSCHERLICH 1970–1971; DITTMAR et al. 1976, and others), which showed that the volume increment and total volume production were highest after low thinnings of low or medium intensity and after the interventions exceeding the medium level the volume production decreased by 5–10%. On the other hand, the stronger the intervention, the more the diameter increment of the main stand trees increases even though the light increment of pine is much smaller than in other species. Even such a small increase in the diameter increment is enough for the value production to increase by 5% in the thinning degree B and by 8% in the degree C (BAADER 1934; STRATMANN 1983). There is much less information on pine stand crown tending than on low tending though already SCHWAPPACH (1908) and his follower WIEDEMANN (1948) had experimented with it. The latter came to a conclusion that the crown tending in pine stands could be applied successfully as a temporary measure in the small pole stage only in order to improve the crowns of the best trees. Later the method would fail for fairly sure and untimely dieback of subdominant trees and opening up the stand. Based on further results WENK (1973) concludes that the crown interventions can come into consideration in young stands only. However MITSCHERLICH (1970–1971) brings forward the related danger. As young pine is sensitive to opening and responds by the crown extending, it may happen after an untimely release of quality canopy individuals that bottom branches will dry off and the stem form factor will decline. The more fertile the site, or in ecotypes from higher elevations the bigger that danger. In such cases the quality selection counters the aim to grow quality, which degrades in this way. Apart from this, released trees were observed to have a lower height increment than the non-released ones (MRAZEK 1996). However in older stands, from the second half of the rotation period, pine is less able to extend its crown and root system and to exploit fully the space opened by crown intervention. Therefore the light increment appears slowly and to such a small extent that it is not able to compensate the volume of cut trees and therefore increment losses occur (ASSMANN 1968). Contrary to low tending the volume increment is lower by 10% (MITSCHERLICH 1970–1971). The effect of opening manifests itself only after a long time with a longer rotation period or when some trees or stand parts are left longer than the rotation period (WAGENKNECHT 1962; RICHTER 1963; MRAZEK 1999).

A more favourable effect is expected in the variant when silvicultural operations concentrate on a limited number of the best individuals only as was presented by MICHAELIS (1907) or SCHÄDELIN (1947), or in the updated form on target trees by ABETZ (1972, 1979, 1980, 1992), MERKEL (1978), or KLÄDTKE (1990) etc. These target trees are marked visibly and permanently already in the small pole or pole stages so that the manager would not have to bother with selection of favoured trees in the following improvement felling. These individuals are expected to yield a bigger green volume and with pruning also a higher quality. Respecting the fact that the method of target trees has been applied in the last 30 years only, the forestry practice and science have not had enough convincing proofs of its effectiveness namely in pine stands. However, the results have shown so far that in order the method would be successful the opening of target trees and juvenile thinning have to get started already soon – after growing to the height of 8–12 m, and in time, during the second half of the rotation period, to apply low thinnings of medium or low intensity (ERTELD 1986; ABETZ, PRANGE 1976; SPELLMANN 1996; KILZ 1996; BURSCHEL, HUSS 1997). In the main, it represents a modified graded WIEDAMANN's (1942) tending based on the principle: in youth strongly, since the middle age weakly.

Contrary to these principles the *Programme for sustainable management in the Czech forests* (ZEZULA 1997, 2000) recommends for the pine stands tending: "to grow young stands considerably thick only with interventions by a negative selection of dominant and co-dominant trees. Low interventions should not be performed as they are supposedly harmful and economically undesirable. At older age since approximately 50 years the tending changes into positive crown and combined interventions by selecting about 100–300 target trees, the crowns of which are opened by cutting co-dominant trees away. So it is a basically contradictory recommendation to those presented in German or Czech older literature. The solution to the outlined issues of pine stands tending should be supported by the following experiment."

LOCALITY

The Pleistocene sediments are formed by fluvial gravel terraces thick 10–20 m over the chalk base in the locality of the town of Týniště nad Orlicí (50°47′ N longitude, 16°07′ E latitude). The altitude is 260 m, average annual precipitation 648 mm and average annual temperature is 8.2°C. The forest type is composed of pine-oak stands with *Vaccinium myrtillus* (1M).

OBJECT AND METHOD

A thinning comparative experiment was established in a pine stand that originated by a natural border regeneration in 1957 at its age of 27 years. The density of the small pole stand was about 7–8 thousand trees per 1 ha, stand height was about 10 m and the breast height diameter (d.b.h.) of the mean stem was 6–7 cm. The objective of the experiment was to identify how the crown tending compared with low tending of medium and higher intensity is reflected by the production qualities of the pine stand. Therefore the small pole stand was split into 3 plots sized 30 × 60 m; the low tending of medium intensity was used on the plot "B", the stronger one on the plot "C", and the crown tending with a quality selection was performed on the plot "D" (SCHÄDELIN 1947), in which promising trees were released and subdominant trees were protected. "Promising trees" were represented by codominant and intermediate trees with straight stems, smooth bark, adequately large and conical crown, and fine branching (by a formerly applied theory: with signs of stadium juvenility, NESTEROV 1951). Before the first improvement interventions 2–3 thousand of snags and drying trees (5^{th} class, Kraft) were cut away. After their removal 10 plots sized 10 × 10 m were delineated and located so that they represented the whole comparative area and could be processed statistically. Consequently the trees were numbered and measuring points were marked at the height of 1.3 m.

After measuring the trees on the plots 850 promising trees were selected and marked with a white strip. Consequently trees designed for cutting were marked by the key:

On the plot	trees of the Kraft's tree class
"B"	5, 4, (3)
"C"	5, 4, 3,(2)
"D"	in all classes by positive selection

Block observations of tree development and growth consisted in annual measurements of d.b.h., and in a periodical measurement of heights. Length, distance between the whorls, diameters at 1-m sections for volume calculations were measured in cut trees, disks were cut at breast height for ring analyses, and at the tree foot for age determination. The data were processed by common taxation and statistical methods (see below in the text).

RESULTS

STAND DENSITY – TREE NUMBERS

The stand density before the experiment was set up to range between 61 and 76 trees per 100 m². The average

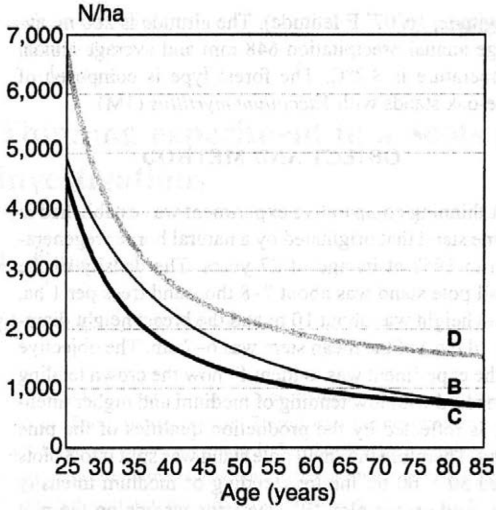

Fig. 1. Trees numbers in the compared plots depending on age fitted by reciprocal growth function

number 7,132 ± 739 trees per 1 ha was approximately twofold than the value in the Czech yield tables for yield class 4 where the stand was included (by absolute height of tree yield classification).

In setting up the experiment at the age of 27, in the first intervention 1,780 trees/ha were cut on the plot "B", 1,950 trees on the plot "C" and only 480 trees on the plot "D". So at the beginning of the experiment the stand density dropped on the plot:

„B"	to 4,380 ± 389 trees/ha	intensity 29%
„C"	to 3,420 ± 293	intensity 36%
„D"	to 5,740 ± 829	intensity 8%

The cutting intensity was highest on the plot "C", where the bulk of the subdominant trees were cut, the lowest on the plot "D", where only those trees from the dominant level that grew close to promising trees were cut. In the second thinning repeated after 2 years interventions were made also into subdominant classes because some trees had died or manifested drying up. In this second intervention on the plot "D" 2,015 trees were cut, out of it 27% dead standing trees, and the density dropped to 3,725 ± 662 trees per 1 ha. On the plots "B" and "C" in the second intervention 1,537 and 1,247 subdominant trees were cut out of the relevant tree classes, which were not removed in the previous intervention. The intensity of the second intervention was nearly equal on all plots (35–36%). The density dropped to 2,843 ± 664 trees per 1 ha and 2,173 ± 392 trees per 1 ha, respectively.

On the plot "D" in the third thinning at the age of 35 years the number of selected trees was reduced to 200

Table 1. Number of stems in the stand after thinning

Age	30	35	45	50	60
Plot					
"B"	2,843	1,912	1,624	1,229	974
"C"	2,175	1,431	1,234	988	842
"D"	3,725	2,603	2,245	1,742	1,410

as some originally selected individuals though released lagged behind in growth or were bent or broken by snow. The intervention was made at the crown level again in favour of the selected trees, and labile and dying subdominant trees were removed. On the other hand, trees possibly helping the vertical canopy were left. On the plots "B" and "C" also in the third thinning the horizontal canopy was formed. The intensity of the third intervention was lower on all three plots and dropped to 13–15%. So the decline of trees decreased after the initial steep drop (Fig. 1, Table 1).

After 40 years the number of trees on all plots was reduced by 75–78% and even in the seventies it exceeded the value of the Czech yield tables. This and other facts prove specific features of the Týniště pine ecotype (CHROUST 1989).

As the change in the number of trees on the plot in relation to age generally runs along the mirror growth curve, the course of the tree number decline in individual compartments was fitted by reciprocal Korf's growth function:

$$N(t) = \frac{1}{A\exp\left(\frac{k}{1-n}t^{1-n}\right)\frac{k}{t^n}} \quad (1)$$

DIAMETER AT BREAST HEIGHT (D.B.H.) AND DIAMETER INCREMENT (ID.B.H.)

Before the experiment was establishment on the plots "B", "C", "D", diameters at breast height ranged between 1 cm and 17 cm with the mean stem diameter about 6.6 ± 2.7 cm. When the dead trees were removed, the mean stem diameter increased to 7.2 ± 1.8 cm and the following thinnings changed the range of both the breast height diameters and mean stem diameters, depending on the

Table 2. Constants for the calculation of stem number (before thinning)

Plot	"B"	"C"	"D"
Constant *A*	5.993868	3.247669	13.290816
Constant *k*	2.244538	56.722950	1.923579
Constant *n*	1.095865	1.959075	1.081311

Acknowledgement: The constants were calculated by the SAS programme at the Department of Forest Management at the Faculty of Forestry at the Czech University of Agriculture in Prague. I thank Professor Ing. Jan Kouba, PhD., and Ing. D. Zahradník for these calculations.

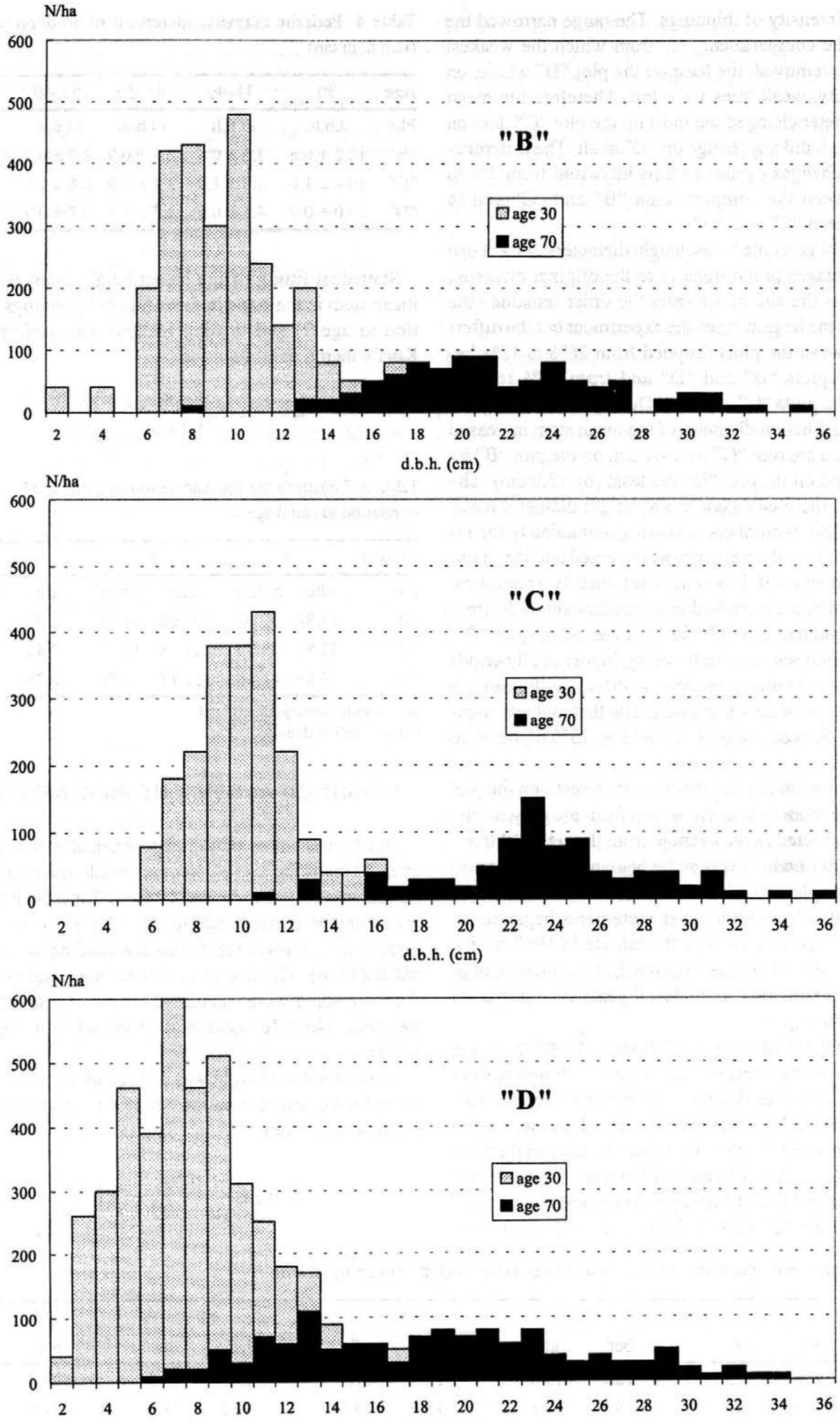

Fig. 2. Diameter structure of the 30-year old stand after thinnings and the 70-year old one before thinning on the plots "B", "C", "D"

type and intensity of thinnings. The range narrowed the most in the compartment "C" from which the weakest trees were removed, the least on the plot "D" where, on the contrary, weak trees were left. Therefore the mean stem diameter changed the most on the plot "C", less on "B", while it did not change on "D" at all. The differences in the changes of mean stems increased from 3% to 26% between the compartments "B" and "C" and to 36% between "C" and "D".

During 40 years the breast height diameters of the mean stems increased proportionally to the original diameter, therefore at the age of 70 years the order remained the same as at the beginning of the experiment but the differences between the plots dropped from 26% to 12% between the plots "B" and "D" and from 36% to 19% between the plots "C" and "D". During the 40-year period the breast height diameter of the mean stem increased the most on the plot "C" by 14.4 cm, on the plot "B" by 13.7 cm and on the plot "D" the least (by 13.0 cm). The changes in the mean stem breast height diameter result from the shift in numbers following immediately the intervention in the diameter class concerned and the diameter increment itself. It is better explained by a periodical diameter increment studied in a constant set of 30 trees of the second tree class (Table 4). It was on the plot "D", i.e. on the plot with crown thinning, higher in all periods than on the two remaining plots, so that after 40 years the mean stem breast height increment on that plot was higher by 12% than on the plot "C" and by 23% higher than on the "B".

The increase in the tree diameter increment on the plot with crown tending is obvious also from the growth ring curve constructed as the average from the set of 12 trees, the diameter of which was at the beginning of the experiment on the plot "C" 11.8 ± 1.9 cm, on "D" 9.5 ± 1.2 cm. These weaker trees with lower increments began to increase their increments after the release in 1957 so that already in the first decade they reached the increment of the stronger trees and in the last 8 years they surpassed them by 8% (Fig. 3).

The average width of growth rings in those years was 1.15 ± 0.23 mm in trees on "D", 1.06 ± 0.16 mm in trees on "C". It is obvious that the interventions into the canopy negatively influenced the increment of the mean stem. The increment on the plot "D" is smaller than on the plots "B" and "C". After 40 years of tending, i.e. at the age 70 years, mean d.b.h. of 100 large trees is nearly equal: "B" – 29.1 ± 3.9 cm, "C" – 29.8 ± 3.8 cm, "D" – 29.7 ± 2.4 cm.

Table 4. Periodic diameter increment of co-dominant trees (id.b.h. in cm)

Age	30	31–40	41–50	51–60	61–70
Plot	d.b.h.	id.b.h.	id.b.h.	id.b.h.	id.b.h.
"B"	10.2 ± 0.8	3.6 ± 0.8	2.7 ± 0.9	2.0 ± 0.9	1.6 ± 1.2
"C"	10.4 ± 1.0	3.8 ± 1.0	3.2 ± 0.9	2.6 ± 1.1	1.8 ± 0.8
"D"	10.0 ± 0.9	4.1 ± 0.9	3.7 ± 1.0	2.7 ± 0.9	2.4 ± 1.3

Statistical fitting of the breast height diameter of the mean stem in the stand before and after thinnings in relation to age (t) and tending method was performed by Korf's incremental function

$$dk = A\exp\left(\frac{k}{1-n}t^{1-n}\right)\frac{k}{t^n} \qquad (2)$$

Table 5. Constants for the calculation of mean d.b.h. in stands in relation to stand age

Constant	A		k		a	
Plot	after	before	after	before	after	before
"B"	30.84	52.63	193.60	34.34	2.39	1.89
"C"	32.59	59.79	221.68	34.77	2.43	1.88
"D"	28.85	41.06	121.17	31.06	2.26	1.88

after – after thinning, main stand
before – before thinning

HEIGHT (H) AND HEIGHT INCREMENT (IH)

The highest trees of the experimental stand reached even 13 m at the age of 30 years while the mean stand height was by 1–2 m lower (10.9 ± 0.7 m). Both top and mean height corresponds to the 4th yield class of the Czech yield tables or yield class II according to SCHWAPPACH (1896). The height increment and total height of the main stand were calculated for the tree set of the 1st tree class. No differences were observed in the top stand height.

The mean stand height was derived as a function of the mean breast height from the height curves calculated by Näslund's function

$$H(m) = \frac{d.b.h.}{(a + bd.b.h.)} + 1.3 \qquad (3)$$

Table 3. Breast height diameter (d.b.h.) of mean trees before and after thinning (d_k cm)

Age	30		40		50		60		70
Plot	bef.	aft.	bef.	aft.	bef.	aft.	bef.	aft.	bef.
"B"	8.4	9.3	12.7	13.8	16.4	17.1	19.1	19.6	22.3
"C"	9.0	9.9	13.8	14.8	18.0	18.3	21.5	21.5	24.5
"D"	7.5	7.8	11.0	11.6	13.9	14.5	16.4	16.7	19.1

bef. – before thinning
aft. – after thinning

Table 6. Constants for the calculation of height curves

Age	30	40	50	60	70
Constant *a*	0.606	0.716	0.826	0.936	1.047
Constant *b*	0.245	0.221	0.204	0.187	0.178

Table 7. Mean stand height (m)

Age	30	40	50	60	70
"B"	11.7	14.7	17.0	19.2	21.0
"C"	11.9	14.9	17.2	19.7	21.8
"D"	10.9	13.2	15.5	17.9	19.5

It is obvious from Table 7 that the top height increased by 11 m, mean height by 8.6–9.9 m during the 40-year period while the stand on the plot "C" was the highest of all even though it was highest at the beginning, too. The original average decade increment of 3.4 m dropped to 1.8 m after 40 years.

BASAL AREA AT BREAST HEIGHT (BA in m²) AND ITS INCREMENT (IBA in m²)

Basal area was calculated from the product of the statistically fitted number of trees according to formula (1) and the breast height diameter of the mean stem calculated from formula (2).

When the experiment was established, the stand basal area after removing the dead trees was 24.4 ± 0.9 m² and it was by 2.5 m² lower than indicated in the Czech yield tables. After the first two interventions repeated in the years 1957–1959 BA on the plots changed like this:

"B" by 5.1 m² to 19.3 m² (intensity 21%)
"C" by 7.7 m² to 16.7 m² (intensity 31%)
"D" by 6.6 m² to 17.8 m² (intensity 27%).

In the first 10-year period, at the age of 30–40 years when iBA usually culminates, the plot "D" had the highest absolute increment (14.5 m²) but 2.5 m² of it were trees that died within the period (19% dead trees). A similar situation was on the plot "B" (9% dead trees); so the highest increment in living trees was in the stand "C", out of which the less vital trees were removed in time. Therefore its stand basal area after 10 years amounted to 25.7 m² only, while on the plot "B" it was 29.1 m² and on "D" 29.2 m² (Table 9).

In the second period, when only one intervention was performed, the increment on all plots dropped by 25% per 10 m² on average while in living trees it was highest on the plot "C", lower on "D" and lowest on "B". The stand basal area at the age of 50 years is lowest on the plot with low thinning of higher intensity. But the original 14–15% difference between the plot "C" and the other two plots decreased to 8%.

After the thinning at the age of 50 years the ten-year increment dropped by 4% on "C", by 12% on "B" and by 23% on the plot "D" although the intervention intensity was nearly the same on all plots (15–17%). This may be explained by a different plot structure consisting of a considerably higher proportion of stronger trees on the plot with low thinning and higher intensity of previous interventions.

During the last observed period of 60–70 years 3-m wide extraction lanes were cut through the centre of each plot. In addition, dead and dying trees were removed. The periodic increment slightly increased on "C" and "D", on "D" it decreased. As a consequence, at the end

Table 8. Periodic basal area increment (iBA in m²/ha)

Age	31–40		41–50		51–60		61–70	
	w/o	w/o	w/o	w/o	w/o	w/o	w/o	w/o
Plot "B"	8.5	9.8	9.4	10.0	7.9	8.9	8.3	7.6
Plot "C"	9.0	9.0	10.2	10.2	8.1	8.1	8.5	8.8
Plot "D"	8.9	11.4	8.7	10.1	6.1	7.9	8.1	8.9

w/o – without dead trees
w – with dead trees

Table 9. Basal area (BA m²/ha)

Age	30	40		50		60		70
Stand	after	before	after	before	after	before	after	before
Plot								
"B"	19.3	29.1	24.3	34.3	28.2	37.1	29.4	38.0
"C"	16.7	25.7	21.2	31.4	26.1	34.2	30.5	39.3
"D"	17.8	29.2	23.9	34.0	28.9	36.8	31.5	40.4

after – after thinning, main stand
before – before thinning

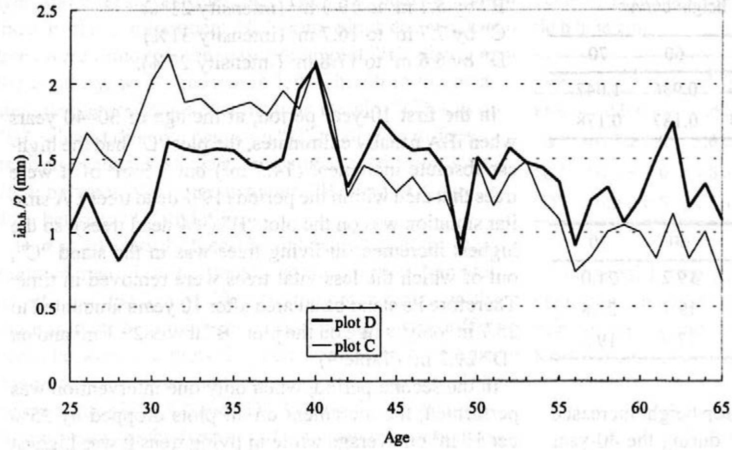

Fig. 3. Growth ring curves of 12 dominant trees from plots "C" and "D"

of the fourth decade the "D" stand overran the other two plots in stand basal area by 5–8% (Table 8).

STAND VOLUME (V) AND ITS INCREMENT (IV)

The volume of single stems (v) cut during the experiment was determined by Huber's method, and then volume yield tables were constructed according to Korsuň's (1962) method:

$$v = K.d^{(m+n\log x)}hp \tag{4}$$

where: $K = 0.023$, $m = 2.036$, $n = -0.043$, $p = 1.134$, d = d.b.h., h = height

The standing volume (m³/ha) and its development were calculated similarly like the stand basal area by formulas (1), (2), (3) and (4).

At the beginning of the experiment at the age of 27 years, when the d.b.h. of the mean stem exceeded 6 cm and the volume exceeded 0.02 m³, the stand volume was 142 m³ and was lower by about 16% than the calculations of the Czech yield tables. The highest standing volume after the first thinning was on the plot "B", lower on "D" and lowest on "C", where the intervention of highest intensity was used (28%) (Table 11). In consequence of the lower standing volume the increment in the following 10 years on this plot was by 7% lower than on the other two ones (Table 10).

However in the next period (41–50 years) the value iV on the plot "C" with more intensive thinning was higher by 2 m³ than on "B" and by 5 m³ than on "D". Despite the higher increment the standing volume lags behind by 6% on "D" and by 2% on "B" also after the second decade.

In the third period when primarily only dead trees were removed from the stands and the intervention intensity ranged from 13 to 16%, the volume increment on the plots "C" and "D" remained at the previous levels. On the other hand, it grew to 107 m³ on the plot "B". In spite of differences in 10-year increments the order of standing volume values remains the same as at the beginning of the experiment.

Only in the last observed period (61–70) both the rate of increment and standing volume changed as a consequence of cutting in the extraction lanes. The cutting in the extraction lanes affected the "B" stand to the largest extent where 68 m³ were cut, the "D" stand where 47 m³ were felled to a lower extent and to the lowest extent the "C" stand (29 m³). The intervention intensity was proportionate to the stem number within the lanes and their volume. As a result of the different intervention intensity and of the increment the order of standing volumes changed so that it was highest on "C" stand (379 m³), lower on "B" and "D" (Table 11).

In view of the quality composition of the stands based on visual assessment the trees on the plot "B" seem bet-

Table 10. Periodic volume increment (iV in m³/ha)

Age	31–40		41–50		51–60		61–70	
	w/o	w	w/o	w	w/o	w	w/o	w
Plot								
"B"	77.3	85.0	90.5	96.3	95.4	107.2	96.7	99.7
"C"	79.5	79.5	98.4	98.4	98.9	98.4	100.5	103.6
"D"	73.9	91.3	80.1	93.2	81.5	92.6	88.8	97.6

w/o – without dead trees

w – with dead trees

Table 11. Stand volume (V in m³/ha)

Age	30	40		50		60		70
Stand	after	before	after	before	after	before	after	before
Plot								
"B"	111	196	166	262	218	326	258	358
"C"	97	176	147	246	205	304	275	379
"D"	99	190	157	250	216	308	261	359

before – before thinning
after – after thinning, main stand

Table 12. Periodic basal area increment (iBA) and volume increment (iV) during 31–70 years

	iBA(m²)		iV(m³)	
	w/o	w	w/o	w
Plot				
"B"	34.5	37.3	359.9	388.2
"C"	35.8	36.1	377.3	379.9
"D"	32.6	38.3	324.3	374.7

w/o – without dead trees
w – with dead trees

ter, namely the stem purity in comparison with the plots "C" and "D". But the differences do not seem so important with respect to the overall technical quality of the stand.

SUMMARY AND DISCUSSION

In the stand with crown tending (plot "D") 850 trees were selected at the age of 27 which corresponded with the idea of a promising tree (SCHÄDELIN 1947) by their straight stem and shape of the crown. Most were codominant trees but also intermediate trees were present. After 10 years most trees of the 5th and 4th classes died and were removed (it had already happened on "B" and "C" within the previous intervention). So the vertical canopy closure and understorey could not be maintained similarly like in WIEDEMANN (1948) in the past. Because the intermediate trees though being released did not improve their vitality and some even died, the release in the third intervention in the second decade concentrated only on 200 codominant trees and 27 intermediate trees. The released codominant trees on "D" had a higher diameter increment than the parallel tree set on "C" and "D" by 8 and 14% already in the first decade. This difference increased later on (Table 4). In spite of it the d.b.h. of 100 large trees at the age 70 years is equal on all plots. A similar increase in the diameter increment in even old released pines was reported by MRAZEK (1999) in the area Ebel-Havel-Winkel.

Periodical increment at stand basal area and of the volume was highest on the plot "C" and although it increased gradually on "D", it was by 35.6 m³/ha lower after 40 years than on "D" and by 53.0 m³/ha than on "C" (Tables 10–12). The magnitude of the "loss" of volume increment in relation to the increment of the stand with more intensive low thinning corresponds with the result of WIKSTEN's Swedish experiment (1960). But in WIEDEMANN's experiments the volume increment was lower both under crown tending and low tending of higher intensity than under low tending of lower intensity. Contrary to our experiment ERTELD's and HENGST's experiments also showed the stands tended by weaker low thinnings had a higher volume increment than under stronger thinnings. Similarly DITTMAR (1966) reported, but for a short 17-year period (32–49), that with decreasing basal area the volume increment also decreased. The danger of increment losses arises namely with crown tending when codominant trees are affected by interventions in the second half of the rotation period or when the basal area is reduced from the middle age (ASSMANN 1961). With a timely density reduction in young stands and a timely transition to moderate interventions the results can be opposite (ABETZ 1972; STRATMANN 1975; BURSCHEL, HUSS 1997).

The results of the experiment which anticipated the currently adopted strategy of target trees by nearly 20 years proved the idea that it was possible to increase the target tree increment supposed they came from the 1st and 2nd tree classes and the release thinning would start at the small pole stage (ABETZ, PRANGE 1976; ERTELD 1986; BURSCHEL, HUSS 1997, and others). They also approved that the interventions into the canopy in the second half of rotation period resulted in increment losses. The experimental results and the above mentioned authors' works showed that crown tending of presented type in pine stands is not better than low tending and on the contrary, its application may result in losses of volume increment.

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Probírkový experiment v borovém porostu po 40 letech

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ABSTRAKT: Experimentů, které zkoumají vliv úrovňové výchovy na růst a vývoj borových porostů a zejména přesvědčivých výsledků, je stále nedostatek. Proto byl ve Východočeské borové oblasti v roce 1957 založen ve 27letém borovém porostu místního ekotypu pokus s cílem zjistit, jaký vliv má úrovňová výchova na vývoj porostu a jeho objemovou produkci ve srovnání s podúrovňovou výchovou různého stupně. Podstatou zkoumané úrovňové výchovy byl jakostní výběr s vyznačením kvalitních a uvolňovaných stromů se současným šetřením stromů podúrovňových (dílec „D"). Podúrovňové probírky střední (dílec „B") a silné intenzity (dílec „C") spočívaly v odstraňování podúrovňových stromů příslušných stromových tříd. Po 40 letech byl pokus vyhodnocen.

Klíčová slova: výchova porostů; borovice; přírůst; produkce dřevin

Po druhé světové válce zavládly v českém lesnictví silné tendence po přeměnách a převodech devastovaných smrkových a borových monokultur. Jedním z pěstebních opatření směřujících ke smíšeným a různověkým porostům měla být i úrovňová výchova, a to přesto, že do té doby získané poznatky nebyly pro tento způsob výchovy (zvláště borových porostů) nijak příznivé a přesvědčivé. Za účelem obohacení poznatků o vhodném způsobu výchovy borových porostů středního věku byl v r. 1957 založen experiment (CHROUST 1959), jehož výsledky jsou pro současnou pěstební techniku aktuální – to proto, že v českém lesnictví je opět snaha vychovávat porosty tak, aby monokultury mohly být připraveny na převod na porosty přírodě bližší.

Experiment byl situován do 27leté borové tyčkoviny z přirozené obnovy týnišťského ekotypu (Východočeská borová oblast, soubor LT 1 M). Cílem experimentu bylo zjistit, jak se na vývoji a růstu porostu projevuje úrovňová výchova ve srovnání s výchovou podúrovňovou slabé a silnější intenzity. Za tím účelem byla tyčkovina (hustota 7–8 tis. ks/ha, výčetní tloušťka 1–16 cm a výška 5 až 13 m) rozdělena na tři dílce, pracovně označené písmeny „B", „C" a „D". Na dílci „B" byl porost vychováván slabými podúrovňovými zásahy, na dílci „C" podúrovňovými zásahy silnějšími a na dílci „D" byl porost vychováván pozitivním výběrem úrovňovými zásahy protěžujícími cílové stromy.

V dílci „D" bylo při prvním zásahu ve 27 letech vytypováno 850 stromů/ha, které rovným kmínkem a tvarem koruny odpovídaly představám stromů nadějných. Byly to stromy převážně úrovňové, ale i vrůstavé. Po prvních deseti letech většina stromů 5. a 4. stromové třídy odumřela a byla vytěžena (na dílci „B" a „C" se tak stalo již při předcházející probírce). Vertikální zápoj a spodní etáž se proto nepodařilo udržet, podobně jako již dříve WIEDEMANNOVI (1948). Protože ani stromy vrůstavé, přestože byly uvolněny, nezvýšily svou vitalitu a některé z nich dokonce odumřely, soustředilo se uvolňování při třetím zásahu v druhém desetiletí jen na 200 stromů úrovňových a 27 stromů vrůstavých za účelem poznání jejich reakce. Uvolňované úrovňové stromy na dílci „D" již v prvním decenniu měly o 8 a 14 % větší tloušťkový přírůst než paralelní soubor stromů na dílci „C" a „B". Tento rozdíl se nadále zvětšoval (tab. 4). Podobné zvětšování tloušťkového přírůstu i u starých uvolněných borovic zaznamenal MRAZEK (1999) v oblasti Ebel-Havel-Winkel.

Periodní přírůst na výčetní kruhové základně a objemu byl ale největší na dílci „C", a přestože se na dílci „D" postupně zvětšoval, byl po 40 letech o 35,6 m^3 na ha menší než na dílci „B" a o 53,0 m^3 na ha menší než na dílci „C" (tab. 10–12). Velikost „ztráty" na objemovém přírůstu v relaci k přírůstu porostu vychovávaného podúrovňově větší intenzitou koresponduje s výsledkem pokusu WIKSTENA (1960) a DITTMARA (1966). Nebezpečí přírůstových ztrát vzniká zejména, když se snižuje výčetní základna od středního věku (ASSMANN 1961).

Výsledky experimentu potvrdily názor, že je možné zvýšit přírůst cílových stromů za předpokladu, že pocházejí z 1.–2. stromové třídy a že se s jejich uvolňováním začne již ve stadiu tyčkovin. Potvrzuje se také, že po zásazích do úrovně i v druhé polovině obmýtí dochází k přírůstovým ztrátám.

Výsledky pokusu a práce citovaných autorů ukázaly, že úrovňová výchova uvedeného typu není v borových porostech lepší než výchova podúrovňová a naopak že při její aplikaci může dojít ke ztrátám na objemovém přírůstu.

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Analysis of interspecific differences in tree root system cardinality

B. Konôpka

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ABSTRACT: In the localities Látky, Lopej, Kežmarské Žľaby and Stará Lesná, diameter at breast height (d.b.h.) as well as depth and width of tree root plates uprooted by wind were measured. Correlations between root plate measurements and d.b.h. for particular tree species in each locality were determined. The shallowest roots were found in Norway spruce, followed by silver fir and European beech. The deepest roots were found in European larch and Scots pine. Interspecific differences in the root system width were small. Root systems of spruces were significantly shallower in poorly drained site than at well-drained sites. The results proved the knowledge that pure spruce stands in poorly drained soils are the most unstable.

Keywords: root plate; soil conditions; tree stability; uprooting

Storms cause huge damage to forest stands, i.e. they most commonly break or uproot trees. PELTOLA et al. (2000) stated that in 1990, 100 million m^3 of forest cover were blown down overnight as a storm swept over Europe. Bigger damage occurred in the Christmas time of 1999 in Western and Central Europe. At that time, just in the territory of France, over 140 million m^3 of trees were blown down. In Slovakia, the worst damage by storm to forest stands in the last decade occurred in July 1996, when 1.5 million m^3 of wood was destroyed by wind in the Horehronie region, and in June 1999 – with over 1 million m^3 of trees blown down in the Považský Inovec mountains and their vicinity (KONÔPKA B. 2000).

The volume of storm damaged trees considerably differs in the particular species. These differences result from the morphological and physical properties of each tree species. Traditionally, a large part of research on mechanical stability (windfirmness) was focused on the assessment of aboveground parts of trees (e.g. LOHMANDER, HELLES 1987; SMITH et al. 1987; KONÔPKA J. 1992; VALINGER et al. 1993). However, according to my previous findings in Slovakia under unfrozen soil conditions, much more trees have been uprooted than broken by storms. Hence, further study should be focused on underground part of trees, i.e. on qualitative and quantitative evaluation of the root systems. COUTTS (1987) claimed that tree root growth and development is influenced by a number of internal and environmental factors. The most decisive are the genetic properties (internal factor) and soil conditions (environmental factor). KONÔPKA B. (1997a) found from long-term forestry records that under Slovak conditions the tree species mostly damaged by storms is Norway spruce (*Picea abies* [L.] Karst.), followed by silver fir (*Abies alba* Mill.). Medium storm damage was found on European beech (*Fagus sylvatica* L.) followed by European larch (*Larix decidua* Mill.) and Scots pine (*Pinus sylvestris* L.). Most of the other tree species growing in Slovakia are relatively resistant to storm.

The aims of this study were to evaluate the root system depth and width of some tree species, namely Norway spruce, silver fir, European beech, European larch and Scots pine, and to compare interspecific differences in root system measurements.

METHODS

Measurements of root system depth and width were done on trees uprooted by storm. Selected forest stands were in the localities Látky, Lopej, Kežmarské Žľaby and Stará Lesná. Látky and Lopej belong to the Vepor hills (Central Slovakia) while Kežmarské Žľaby and Stará Lesná belong to High Tatras (Northern Slovakia). The localities are in the fifth (fir-beech) and sixth (spruce-fir-beech) forest vegetation zones. One site (Kežmarské Žľaby) was on poorly drained soil (high water table) and the other sites were on well-drained soils. Loam and clay-loam soil types of medium depth with skeleton of 30–50% characterize the sites.

Altogether, 290 uprooted trees including 171 spruces, 49 beeches, 43 firs, 15 larches and 12 pines were measured. On the stems, diameter at breast height (d.b.h.) and on root plates (uprooted mass of roots and soil), two perpendicular diameters and maximum thickness (former

Table 1. Site characteristics and mean values of d.b.h. and root plate measurements for particular localities (± standard deviation)

Locality	Soil conditions	Tree species	Number of measured trees	d.b.h. (cm)	Root plate measures depth (cm)	Root plate measures width (cm)
Látky	loam well-drained	spruce	42	35 (± 9)	76 (± 21)	181 (± 55)
		beech	15	33 (± 6)	83 (± 17)	205 (± 40)
Lopej	loam well-drained	spruce	57	47 (± 9)	107 (± 22)	319 (± 54)
		beech	34	40 (± 10)	122 (± 24)	314 (± 58)
		fir	29	46 (± 8)	134 (± 36)	304 (± 46)
Kežmarské Žľaby	gley-loam poorly drained	spruce	40	33 (± 9)	52 (± 15)	354 (± 78)
		fir	14	37 (± 9)	84 (± 15)	250 (± 42)
Stará Lesná	gley-loam well-drained	spruce	32	35 (± 10)	63 (± 20)	254 (± 70)
		larch	15	39 (± 11)	106 (± 23)	244 (± 83)
		pine	12	37 (± 11)	118 (± 28)	265 (± 74)

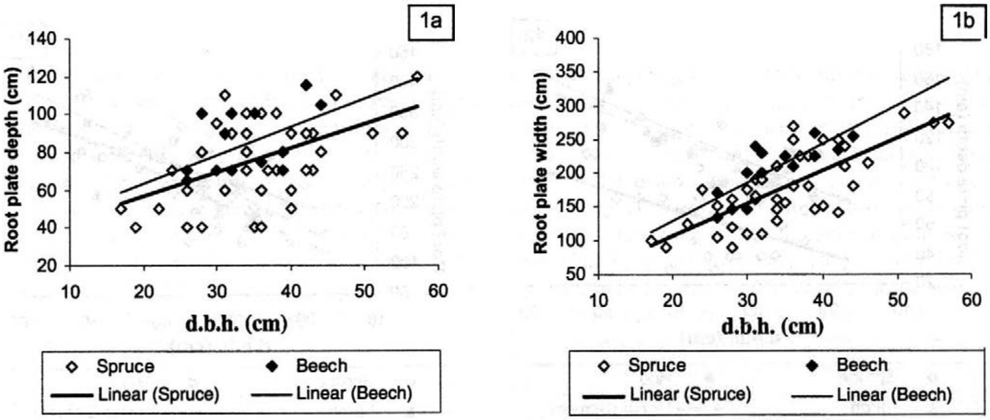


Fig. 1a,b. Interspecific differences in root plate measurements between spruce and beech in the locality Látky

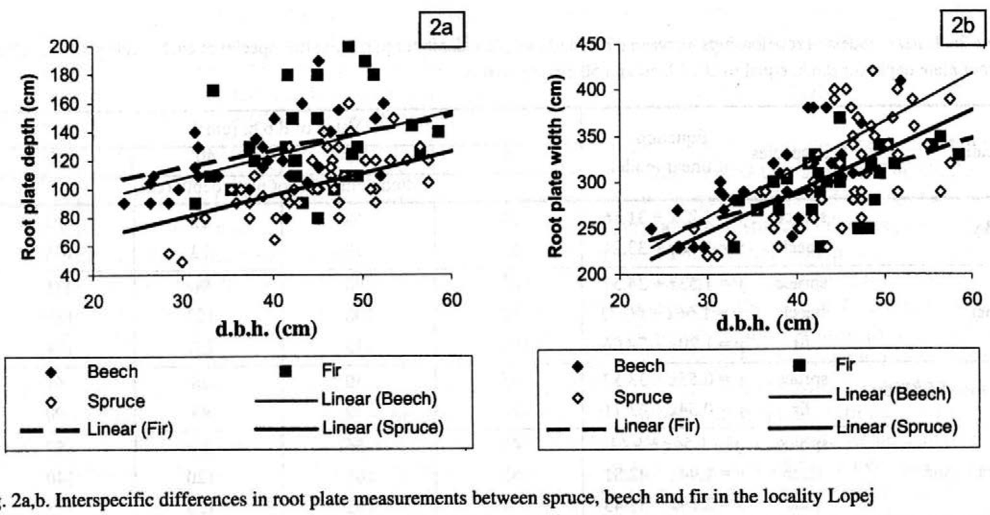
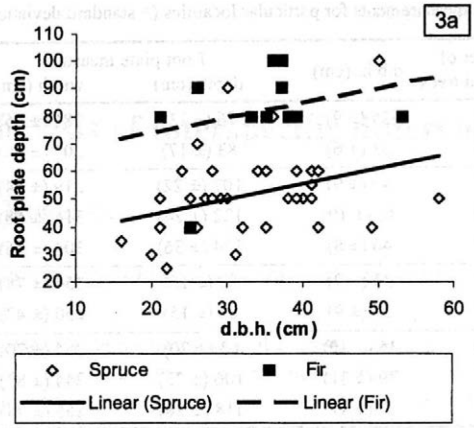


Fig. 2a,b. Interspecific differences in root plate measurements between spruce, beech and fir in the locality Lopej



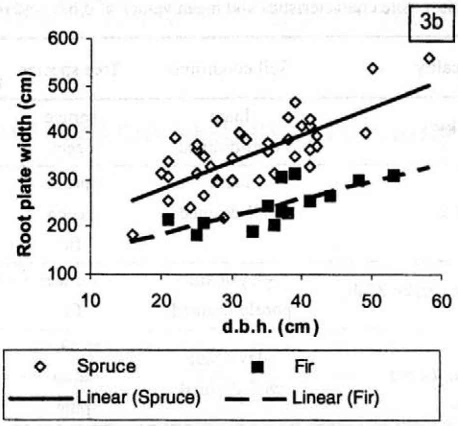
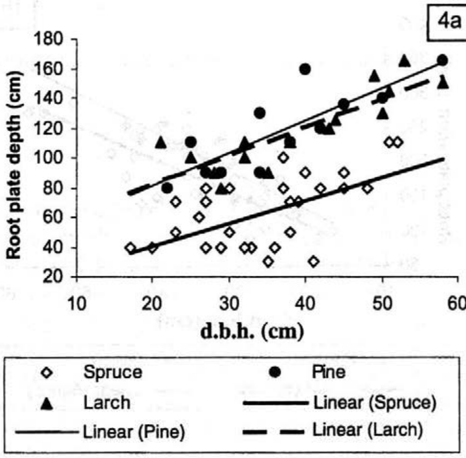


Fig. 3a,b. Interspecific differences in root plate measurements between spruce and fir in the locality Kežmarské Žľaby



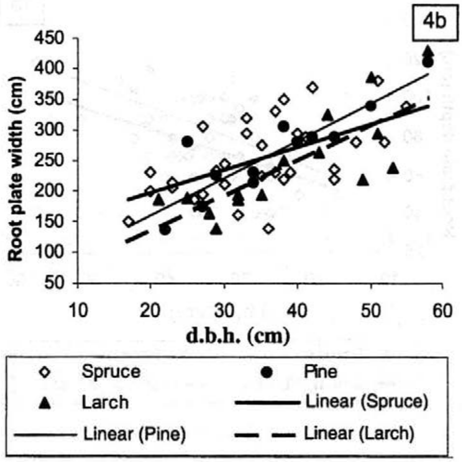


Fig. 4a,b. Interspecific differences in root plate measurements between spruce, larch and pine in the locality Stará Lesná

Table 2a. Linear models of relationships between d.b.h. and root plate depth for particular tree species at each locality. Fitted values of root plate depth for d.b.h. equal to 20, 30, 40 and 50 cm are shown

Locality	Tree species	Equation of linear model	Value of d.b.h. (cm) 20	30	40	50
			Fitted value of root plate depth (cm)			
Látky	spruce	$y = 1.27x + 31.16$	57	69	82	95
	beech	$y = 1.50x + 33.21$	63	78	93	108
Lopej	spruce	$y = 1.53x + 34.57$	65	80	96	111
	beech	$y = 1.56x + 60.72$	92	108	123	138
	fir	$y = 1.20x + 79.06$	103	115	127	139
Kežmarské Žľaby	spruce	$y = 0.55x + 33.57$	45	50	56	61
	fir	$y = 0.54x + 63.11$	74	79	85	90
Stará Lesná	spruce	$y = 1.54x + 9.61$	40	56	71	87
	larch	$y = 1.94x + 42.81$	82	101	120	140
	pine	$y = 2.19x + 37.43$	81	103	125	147

Table 2b. Linear models of relationships between d.b.h. and root plate width for particular tree species at each locality. Fitted values of root plate width for d.b.h. equal to 20, 30, 40 and 50 cm are shown

Locality	Tree species	Equation of linear model	Value of d.b.h. (cm) 20	30	40	50
			Fitted value of root plate width (cm)			
Látky	spruce	$y = 4.86x + 9.73$	107	156	204	253
	beech	$y = 5.72x + 13.53$	128	185	242	300
Lopej	spruce	$y = 1.53x + 34.57$	200	244	289	333
	beech	$y = 1.56x + 60.72$	210	262	314	366
	fir	$y = 1.20x + 79.06$	222	253	285	316
Kežmarské Žľaby	spruce	$y = 5.88x + 161.35$	279	338	397	455
	fir	$y = 3.92x + 105.07$	183	223	262	301
Stará Lesná	spruce	$y = 3.71x + 123.22$	197	235	272	309
	larch	$y = 5.81x + 16.64$	133	191	249	307
	pine	$y = 6.09x + 39.21$	161	222	283	344

depth) were measured. These measurements also characterized the mean root system width and maximum depth of root penetration in the soil. Average values of d.b.h., root plate depths and root plate widths were calculated for each site. The relationships between root plate measurements and d.b.h. were analyzed by linear correlation. Fitted values (linear model) of the dependence of root plate measurements on d.b.h. were used to evaluate interspecific differences. Linear model was used further for evaluation of water-logging influence on root system development in Norway spruce.

RESULTS

Mean values for d.b.h. of spruces at the particular sites ranged from 33 to 47 cm (Table 1). Mean root plate depth of spruces was from 52 to 107 cm, and mean root plate width from 181 to 354 cm. Mean values of d.b.h. for beeches were 33 and 40 cm, mean root plate depths were 83 and 122 cm, and mean root plate widths were 205 and 314 cm. Mean values of d.b.h. for firs were 46 and 37 cm, mean root plate depths were 134 and 84 cm, and mean root plate widths were 304 and 250 cm. Mean d.b.h. of larches was 39 cm, mean root plate depth was 106 cm, and mean root plate width was 244 cm. On pines, mean values were 37 cm for d.b.h., 118 cm for root plate depth, and 265 cm for root plate width.

Dependence of root plate measurements on d.b.h. for a particular tree species at each site is shown in Figs. 1a–4b. Based on these linear models, measurements of root plates for the values of d.b.h. equal to 20, 30, 40 and 50 cm were calculated (Tables 2a and 2b). In the Látky locality, it was found by means of a linear model that root plates of beeches were deeper by 6–15 cm and broader by 21–47 cm than those of spruces. In Lopej, beeches similarly had deeper and broader root systems than spruces. In this locality, firs had root plate depth values close to those of beeches, but beeches had broader root systems than firs. In the Kežmarské Žľaby locality, firs had root systems deeper by 29 cm than those of spruces. It was found in this locality that root plates of spruces were 96–144 cm broader than those of firs. In the Stará Lesná locality, the deepest root plates were observed in pines (81–147 cm) followed by larches (82–140 cm), roots of spruces were shallowest, measuring 40–87 cm. Differences in the root plate width between spruce, larch and pine were small.

Owing to the fact that the Kežmarské Žľaby locality was in the poorly drained site (high water table) and all the other localities were at well-drained sites, one could infer the influence of water logging on the root system development in Norway spruce. From the comparison of these two different environments, a negative effect of permanent water-logging on root system depth of Norway spruce could be stated. Contrariwise, root plate widths of spruces at the poorly drained site were significantly larger than those at the well-drained sites. These differences in the root system measurements of spruces between well-drained and poorly drained sites increased with values of d.b.h.

DISCUSSION

Distinct differences in root plate measurements were found between the studied tree species. The shallowest roots were found in spruces. Firs and beeches had significantly deeper roots than spruces. The deepest root systems were found in larches and pines. Interspecific differences in root system width were less pronounced. DAY (1950) considered the genera *Picea* and *Abies* as typically shallow-rooted and the most prone to uprooting. Most authors (e.g. HOCHTANNER 1967; RODENWALDT 1973) labeled Norway spruce as the most labile tree species under European conditions. ROTTMANN (1986) claimed that silver fir is more stable than Norway spruce, although a mixture of these two species make stands very prone to uprooting. KONÔPKA B. (1997b) found in a 60-year-old mixed forest stand that silver fir had a root system that is deeper by 20 cm than Norway spruce. Traditionally, European beech was considered to be resistant to mechanical stress caused by wind. The main reason for this assumption was that the beech wood has good physical properties, particularly a high resistance to bending and tension stress. However, large storm damage to beech forest towards the end of 1990's showed that in the case of heavy rains when soil is temporally saturated with water, followed by strong winds, stands of this species can be windthrown to a large range (KODRÍK J. 2000). On the other hand, beech admixture has a stabilizing effect in spruce and fir stands (KONÔPKA J. et al. 1980). Undoubtedly, larch and pine are important stabilizing species in regions with prevailing spruce and fir stands (ŠINDELÁŘ 1996). Interesting results were obtained by KODRÍK M. (1994), who proved the negative effect of immissions on the development of Norway spruce in the northern Slovakia.

Besides quantitative parameters of root systems (total weight and length of roots, depth and width of root penetration), qualitative parameters determine tree anchorage (COUTTS 1986). It concerns physical properties of root tissues, type of root branching and general "architecture" of the root system. The health status of roots is important because rotting can deteriorate physical properties of wood tissues considerably. FRASER (1962) suggested that *Fomes annosus* root rot reduces a tree's resistance to uprooting by 30% or more. Physical properties of roots also depend on concurrent temperature and moisture status of their tissues (SEREDA 1983). Physical properties of roots can be influenced by frequent mechanical stress, e.g. by wind. Trees are able to adapt themselves partly to this recurrent mechanical stress through morphological changes (e.g. coarsening or enhancement of specific gravity) of the most loaded parts of their bodies. JAFFE (1973) defined this kind of partial adaptation to mechanical stress with the term "thigmomorphogenesis".

The soil environment influences root development considerably. Soil texture affects the distribution of the roots, and soil consistency influences their anchoring ability (MERGEN 1954). Roots can easily penetrate sandy soils, loamy soils moderately, and clayey soils with difficulty (FRASER 1962). The most labile forest stands are in clayey soils, which do not allow root penetration to a sufficient depth, and are of low cohesion and shear strength (SMITH et al. 1987). The vertical distribution of roots hangs on soil aeration, compression, and moisture-holding capacity of the particular soil horizons. In general, relatively shallow and little spread root systems are found at fertile and moist sites where trees have sufficient water and nutrients in the upper soil layer. Contrariwise, at the poorer sites, where trees lack water and nutrients, roots must grow into a large system or penetrate to deeper horizons. Thus in general, forest stands at poor sites are more resistant to uprooting than those in good ones (VICENA et al. 1979). Maximum depth of root penetration can be reduced by excessive stoniness, shallow bedrock, clay-rich B horizon, a "plow pan", iron pan, subsurface horizon of high bulk density, high water table, or toxicity in lower horizons (SCHAETZL et al. 1989). My research also confirmed that spruces had considerably shallower roots at the poorly drained site than at the well-drained sites. An interesting finding is that root systems of firs were significantly deeper than the root systems of spruces even at the poorly drained site. In this site, spruces had considerably broader root systems than firs (root biomass of spruces in water-logged soil developed in horizontal direction more prevalently than vertical growth). ROTTMANN (1986) explained shallowness of tree root systems in poorly drained sites as a consequence of insufficient oxidation in deeper soil horizons. PYATT (1966) found that root systems of 27-year-old Norway spruces were 91–168 cm deep when growing in well-drained soils and 30–48 cm deep at poorly drained sites. His study also suggested that the thinning of trees on wet soils improves root spreading, but does not appear to increase resistance to uprooting because vertical root growth is temporarily inhibited. Similarly, KONÔPKA B. (2001) found out that root systems in mature Norway spruce stands were twice deeper at well-drained sites than at the poorly drained ones. The opposite situation was observed for root system width. Root system width was narrower by one-third of units at well-drained sites than in poorly drained ones. At poorly drained sites, stability of trees is also decreased due to low cohesion in soil as well as due to frequent occurrence of root rots (ROTTMANN 1986).

CONCLUSIONS

The parameters of tree root systems are predetermined by genetic characteristics, which govern the qualitative and quantitative differences between the particular species. Besides internal factors like genetic characteristics, root system parameters are influenced by the environment, especially by soil conditions. The results in this study proved that the root system of Norway spruce was the shallowest and most labile among the tree species investigated. Silver fir and European beech had deeper root systems. The deepest root systems were found in Scots pine and European larch. Hence, pine and larch are relatively resistant to uprooting. Interspecific differences in the root system width were less pronounced.

Permanent water logging (high water table) negatively influenced the root system depth of Norway spruce. Surprisingly, root systems of firs were significantly deeper than the root systems of spruces even of those growing in the poorly drained site. Thus, spruce at poorly drained sites are the most prone stands to uprooting. Probably, silvicultural measures (e.g. thinning) in spruce stands growing in poorly drained soils do not improve root system depth and resistance to uprooting.

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Analýza medzidruhových rozdielov drevín v mohutnosti koreňových systémov

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ABSTRAKT: Na lokalitách Látky, Lopej, Kežmarské Žľaby a Stará Lesná sa merala hrúbka $d_{1,3}$ ako aj šírka a hĺbka koreňových balov drevín vyvrátených vetrom. Sledovala sa závislosť rozmerov koreňových balov od hrúbky $d_{1,3}$ pre jednotlivé lokality a dreviny. Najplytšie korene mal smrek, po ňom nasledovala jedľa a buk. Najhlbšie koreňové systémy sa zistili pre smrekovec a borovicu. Medzidruhové rozdiely v šírke koreňových systémov boli malé. Koreňové systémy smreka boli významne plytšie na podmáčanom stanovišti než na stanovištiach nepodmáčaných. Výsledky potvrdili skutočnosť, že najlabilnejšie sú smrekové monokultúry na podmáčaných pôdach.

Kľúčové slová: koreňový bal; pôdne pomery; stabilita drevín; vývrat

Vietor poškodzuje lesné porasty najmä tým, že ich láme alebo vyvracia. Najrozsiahlejšie vetrové škody vznikli na lesoch západnej a strednej Európy na Vianoce 1999, kedy bolo len na území Francúzska poškodených okolo 140 miliónov m^3 dreva. Na Slovensku boli rozsiahle vetrové kalamity v júli 1996 na Horehroní (postihnutých bolo okolo 1,5 miliónov m^3 dreva) a v júni 1999 v Považskom Inovci a jeho okolí (1 milión m^3 dreva).

Rozdielna odolnosť proti poškodeniu vetrom (stabilita) medzi jednotlivými drevinami súvisí s rôznymi morfologickými a fyzikálnymi vlastnosťami ich nadzemných a podzemných častí. V predošlom období sa v rámci hodnotenia stability lesných porastov a drevín pozornosť sústreďovala prevažne na ich nadzemné časti. Zistilo sa však, že ak je pôda nezamrznutá, vietor dreviny častejšie vyvracia než láme. Z tohto dôvodu treba zamerať ďalší výskum hlavne na hodnotenie kvalitatívnych a kvantitatívnych znakov koreňových systémov drevín.

Na lokalitách Látky, Lopej, Kežmarské Žľaby a Stará Lesná sa na vyvrátených drevinách merali rozmery koreňových balov a hrúbka $d_{1,3}$. Látky a Lopej sa nachádzajú vo Veporských vrchoch, Kežmarské Žľaby a Stará Lesná vo Vysokých Tatrách. Kežmarské Žľaby boli na podmáčanej pôde a ostatné lokality na nepodmáčaných stanovištiach. Pôdy tu boli hlinité až ílovitohlinité, stredne hlboké, s podielom skeletu 30–50 %. Spolu sa zmeralo 290 stromov, z toho bolo 171 smrekov, 49 bukov, 43 jedlí, 15 smrekovcov a 12 borovíc. Pre každú lokalitu a drevinu sa vyrátali priemerné hodnoty meraných parametrov. Vyjadrila sa závislosť hĺbky a šírky koreňových balov od hrúbky $d_{1,3}$ pomocou lineárnej korelácie. Tieto lineárne modely sa použili na odvodenie medzidruhových rozdielov v mohutnosti koreňových systémov, ako aj na zhodnotenie vplyvu zamokrenia pôdy na vývoj koreňov smreka.

Na lokalite Látky priemerná hĺbka koreňových balov bola 76 cm pre smrek a 83 cm pre buk. Priemerná šírka koreňových balov bola 181 cm pri smreku a 205 cm pri buku. Na lokalite Lopej priemerné šírky koreňových balov boli 107, 122 a 134 cm jednotlivo pre smrek, buk a jedľu. Priemerná šírka koreňových balov bola 319 cm pre smrek, 314 cm pre buk a 304 cm pre jedľu. Na lokalite Kežmarské Žľaby boli priemerné hĺbky koreňových balov 52 cm pre smrek a 84 cm pre jedľu, pričom ich šírky boli 354 cm a 250 cm. Na lokalite Stará Lesná boli hĺbky koreňových balov pre smrek, smrekovec a borovicu rovné 63, 106 a 118 cm. Priemerné hodnoty šírky koreňových balov boli 254 cm pri smreku, 244 cm pri smrekovci a 265 cm pri borovici. Lineárne modely závislosti rozmerov koreňových balov od hrúbky $d_{1,3}$ potvrdili, že najplytší koreňový systém má smrek. Hlbší koreňový systém sa pozoroval pri jedli a buku. Najhlbšie do pôdy prenikali korene smrekovca a borovice. Medzidruhové rozdiely v šírke koreňových balov boli menej výrazné. Zaujímavý je rozdiel rozmerov koreňových balov smreka medzi podmáčaným stanovišťom na Kežmarských Žľaboch a nepodmáčanými stanovišťami. Koreňové systémy smreka boli výrazne plytšie, ale širšie na Kežmarských Žľaboch než na ostatných sledovaných lokalitách. Rozdiely v rozmeroch koreňových systémov smreka medzi podmáčanými a nepodmáčanými pôdami rástli s hrúbkou $d_{1,3}$. Jedľa mala hlbší koreňový systém než smrek aj na podmáčanom stanovišti. Smrek v zamokrenej pôde vertikálny vývoj koreňovej biomasy kompenzoval zvýšenou produkciou horizontálne orientovaných koreňov. Preto tu bol koreňový systém smreka v priemere o vyše jedného metra širší než koreňový systém jedle.

Výsledky poukázali na fakt, že smrekové porasty, hlavne ak rastú na podmáčaných stanovištiach, sú slabo ukotvené v pôde, teda aj málo odolné voči vyvráteniu. Stabilita smrečín na podmáčaných stanovištiach je zhoršená aj nižšou súdržnosťou pôdy, prípadne zvýšeným výskytom hubových ochorení koreňov. Aj napriek tomu, že jedľa má hlbšie korene než smrek, nemožno ju považovať za spevňovaciu drevinu a porasty tvorené zmesou smreka a jedle sú nestabilné.

Buk je spevňovacou drevinou, aj keď sa v ostatnom období objavili na území Slovenska pomerne rozsiahle vetrové kalamity v bučinách (spravidla išlo o kombináciu dočasného zamokrenia pôdy nadmernými zrážkami a následnej víchrice). Smrekovec a borovica sú významnými spevňovacími drevinami v oblastiach s prevahou smreka. Nemalo by sa teda na ne zabúdať pri úprave drevinového zloženia, a to hlavne na vetrom exponovaných lokalitách.

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