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Tree mechanics, hydraulics and needle-mass distribution as a possible basis for explaining the dynamics of stem morphology

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ABSTRACT: The aim of the presented work is to verify existing hypotheses which explain the control of secondary growth in diameter. Approaches which try basically to describe stem growth can be grouped into those pertaining to mechanics, hydraulics and the needle-mass distribution of the tree. It is very probable that a mechanical stress on cambial cells, due to stem bending by wind forces, is one of the central triggers for diameter growth. Simulations using an elasto-mechanical model of a 64-year old Douglas fir tree show that the "constant stress hypothesis" is not valid and that a "stress-controlled adaptive growth" cannot be regarded as a universal rule. The basic idea of the pipe model theory, the assumed constancy of the relation between the sapwood cross-sectional area and the needle mass above, turned out to be wrong. But equal tendencies for all investigated trees could indicate approaches for a modified hypothesis. Relations between the spatial needle-mass distribution and thus, the supply of assimilates and the spatial distribution of annual area growth along the stem seem to exist, but are not quite clear. Most probably, all three influences are superimposed, but the stress- or strain-controlled adaptive growth is assumed to dominate, with the exception of the crown, where requirements of water supply probably take over the control of diameter growth.

Keywords: tree mechanics; tree hydraulics; needle-mass distribution; elasto-mechanical model; diameter growth; stem morphology

In the past, numerous forest growth simulators that estimate stand development, and provide economic yield data for practical as well as scientific use, have been developed, e.g., SILVA (PRETZSCH 1992; KAHN, PRETZSCH 1997), BWIN (NAGEL 1999), MOSES (HASENAUER et al. 1995), PROGNAUS (STERBA, MONSERUD 1997). Stand prognoses are generally based on tree-individual calculated growth but, on account of the huge number of trees in a stand, the possibility of physiological, process-oriented growth modelling is very restricted. Such an approach can be found in the class of so-called functional-structural tree models (FSTM; workshops in Helsinki, 1996 [special issue of Silva Fennica, 31(3), 1997] and in Clermont-Ferrand, 1998), which simulate internal growth processes in interaction with the tree architecture, e.g., AMAPpara (DE REFFYE et al. 1997a), INCA (DIZÈS et al. 1997), LIGNUM (PERTTUNEN et al. 1998), MADEIRA (KÜPPERS, LIST 1997).

Focussing on the secondary growth in diameter, it must be stated that the responsible process chain is still largely undiscovered. Therefore, only few models try to describe diameter growth on the basis of the cambial activity (DELEUZE, HOULLIER 1998; FRITTS et al. 1999) and instead, other approaches, in FST models, too, are preferred.

Based on stem analyses, quite some time ago, it was found that there exist typical relations between the cross-sectional increment of the stem at a certain height and the living crown above (PREẞLER 1865; HARTIG 1870; LABYAK, SCHUMACHER 1954; FARRAR 1960). Founded on these observations, the simplest growth model assumes that within the crown, downwards, the area increment increases linearly and remains constant in the branch-free part of the stem (MITCHELL 1975). Analogously, DE REFFYE et al. (1997b) applied the idea that the assimilates, produced by needled stem or branch segments, are consumed by the non-needled segments below, in the way to result in equal area increments for all segments. In reality, the vertical pattern of stem-area increment is much more complex (HINCKLEY, LASSOIE 1981; FAYLE, MACIVER 1985). This is the reason why DE REFFYE et al. (1997b) developed, parallelly to the uniform approach, a distribution model for carbon allocation depending on a (empirically simulated) concentration and diffusion of assimilates. Similar considerations were made by DELEUZE and HOULLIER (1997), but the assimilate diffusion in the phloem was modelled process-oriented.

The diameter growth in the model LIGNUM (PERTTUNEN et al. 1998) is based on constraints concerning the hydraulic function of the tree stem and branches. A principal assumption is the validity of the pipe model theory (SHINOZAKI et al. 1964a,b) which postulates a proportionality between the conducting cross-sectional area of the xylem and the needle mass above.

Lastly, as a third relation, a correlation between secondary growth and the mechanical stress in the cambial cells, is stated (TIRÉN 1928; WILSON, ARCHER 1979): differences in surface stresses will be homogenised by corresponding growth reactions. Until now, this idea has only been implemented for modelling diameter growth of parts of trees (MATTHECK 1990), but not for the whole stem. FOURCAUD and LAC (1996) simulate stress-dependent growth reactions of the entire stem, but the diameter and the height growth itself are externally defined by AMAPpara tree models (BARTHÉLÉMY et al. 1995).

The present work, which was part of the results of a research project supported by the "Deutsche Forschungsgemeinschaft" (German Research Council) (GAFFREY, SLOBODA 1999), is a contribution to possible approaches for FST models to describe the dynamics of the stem, especially the diameter growth. Therefore, the change in stem form of Douglas fir (*Pseudotsuga menziesii*) was intensely studied, together with explanatory hypotheses dealing with the mechanics, the hydraulics and the needle-mass distribution of the tree.

STATUS OF KNOWLEDGE AND CONCLUSIONS

MECHANICAL APPROACHES

Many experiments give evidence for the influence of mechanical stress on plant growth (review: MITCHELL, MYERS 1995). Though not all results were consistent, it was found that *growth in diameter increases with mechanical stresses*. Interestingly, mechanical influences in times of cambial inactivity affect the growth in the following growth season (VALINGER et al. 1995; LUNDQVIST, VALINGER 1996). The induced chain of processes is still largely unknown, but the enzyme ethylene plays a central role (TELEWSKI, JAFFE 1986; TELEWSKI 1990). Among all mechanical treatments, bending shows the greatest efficiency. Torsion also increases the radial growth (QUIRK et al. 1975), whereas compression (QUIRK, FREESE 1976a) and vibration (QUIRK, FREESE 1976b) were not significant.

Normally, even at low wind speeds, *bending strain caused by wind forces dominates* over compression strain due to the weight of stem and crown. In overcrowded stands, in trees with extremely high height-diameter ratios, significant bending stresses due to their selfweight can be found (TIRÉN 1928). Then, without support of neighbouring trees, stems can buckle and break. Critical buckling loads can arise from additional crown loads (snow, ice), too (MARSCH 1989).

The classic mechanical theory of stem taper (METZGER 1893) assumes that the stem form is optimised in the way that bending stresses caused by wind are uniform all over the stem surface (*"constant stress theory"*). Then, the resulting stem form can mathematically be described by cubed diameters values, which decrease linearly upward along the stem. If further loads are taken into account, analytical solutions for the form of a stem representing a "beam of constant resistance" are no longer possible (TIRÉN 1928; YLINEN 1952). Even if the constant stress hypothesis be valid, such ideal taper forms would rarely be found because, as the forces which act on the tree do not remain constant over time, diameter growth will react adapted to the particular stresses experienced (*"adaptive growth"*) (TIRÉN 1928; WILSON, ARCHER 1979; MATTHECK 1990). Nevertheless, MORGAN and CANNELL (1994) showed that real stem forms coincide with calculated profiles, which guarantee uniform stress within a windspeed range from 2.5 to 10 m/s. Wood properties, such as, e.g., the MOE, vary in radial as well as in longitudinal direction of the stem and thus, while stress may be constant, the strain distribution might be unequal. According to YLINEN (1942), the maximum sustainable strain, and not the stress, is responsible for the mechanical failure. YLINEN (1952) spoke about the *"constant strain theory"*, rather than of a constant stress hypothesis. The latest studies, however, challenge the belief in stress or strain constancy (NIKLAS 1999; NIKLAS, SPATZ 2000). Moreover, online strain measurements on *Picea sitchensis* clearly show increasing values upward the stem (BLACKBURN 1997).

Due to the central importance of wind-induced stresses, the *need of a reliable estimation of wind forces and therefore, of including a detailed crown model, too,* exists. But one has to face a lot of difficulties concerning the determination of real wind profiles, crown sail areas and resistances. Wind-tunnel studies revealed that sail areas and drag coefficients depend on the wind speed itself (effect of streamlining) (TIRÉN 1928; YLINEN 1952; MAYHEAD 1973). Moreover, many questions of wind breakage or windthrow require, instead of viewing static wind loads, dynamic models that account for gusts and turbulences (MAYER 1985; AMTMANN 1986; GARDINER 1992, 1995; PELTOLA et al. 1993; PELTOLA 1996). Fortunately, maximum bending due to wind and thus, maximum bending stress can approximately be calculated by a static model (PELTOLA et al. 1993). For simplification, the crown is often considered to be a geometric body or area with a mass centroid on which an estimated wind force acts, or the wind forces are determined section-wise according to the needle-mass distribution (WEST et al. 1989; PELTOLA, KELLOMÄKI 1993; MORGAN, CANNELL 1994). In reference to MÖHRING (1980, 1981), who demonstrated the great importance of the branching pattern and the mass distribution of the crown for the mechanical stability of the stem, the crown with acting wind and gravity forces should be modelled as realistic as possible.

In summary, it may be said that a mechanical bending stress (to a certain extent) undoubtedly induces an increased diameter growth. Though the constant stress/strain theory/hypothesis is supported by many scientists, evidence for it is usually given only by simplified models which do not simultaneously account for a highly resolved tree geometry, distribution of wood properties and acting forces. Strain measurements rather seem to falsify this hypothesis. Thus, two prerequisites for evaluating diameter growth in response to mechanical influences, in order to reveal the tree's possible strategy of adapting resistance against failure of the stem, will be to develop a very detailed elasto-mechanical tree model and to collect the demanded input data. In this study, only the geometric information could be acquired with satisfying precision and therefore, simulated results must be interpreted with caution.

HYDRAULIC APPROACHES

Both the hydraulic hypothesis of JACCARD (1913, 1915) and the "pipe model theory" of SHINOZAKI et al. (1964a,b) assume a *proportionality between the sapwood area and the supplied needle mass above*. Consequently, the sapwood area below the crown base should remain constant. In reality, such a direct proportionality *does not exist*, as already shown by HUBER (1928). According to his studies, the relation of conducting area to needle mass ("relative conducting area" or "Huber value") increases from bottom (excluding the butt swelling) to top, especially within the crown, because a characteristic of the hydraulic system of a tree is the homogenisation of the total resistance. The size of the relative conducting areas changes in order to fulfil this hydraulic function. Whereas JACCARD could not find support for his hypothesis, the pipe model theory has met great resonance and, due to its easy applicability, has often been implied, e.g., in the LIGNUM model (PERTTUNEN et al. 1998).

Realising that the pipe model theory, as a relatively simple model, obviously does not reflect an optimal base for deriving growth models and the development of a more complex hydraulic hypothesis would require an extremely high effort in assessing conductivity data (if at all this would technically be realisable for larger trees), the aim of describing a hydraulic-oriented approach for modelling diameter growth was abandoned. Nevertheless, as statements about conductivity founded on (optically) determined sapwood areas are common in forestry and such sapwood / needle-mass ratios are already used in models, it was decided to analyse these characteristics for the Douglas fir trees, too.

APPROACHES REFERRING TO THE NEEDLE-MASS DISTRIBUTION

The "PRESSLER rule" (PREẞLER 1865) postulates a proportionality between area increment of the stem and the needle mass located above. The core of this idea amounts to the same thing as the pipe model theory. Diameter growth models, based on PRESSLER's rule, were developed by DELEUZE and HOULLIER (1997) and DE REFFYE et al. (1997a). But HARTIG (1870) had already shown that the relations are much more complex: merely within the crown, the increment of the stem cross-sectional area at a certain height is proportional to the amount of needle mass above. Concerning the distribution of the area increment in the branch-free part of the stem, the ratio of crown length to stem length and thus, the social status of the tree is responsible. But very precise stem and needle-mass analyses reveal that also within the crown no strict proportionality can be found (FUJIMORI 1970; HINCKLEY, LASSOIE 1981; FAYLE, MACIVER 1985; FUJIMORI, KIYONO 1986). Even the allocation of assimilates along the stem can differ from year to year (FAYLE, MACIVER 1985; GAFFREY 1996).

Obviously, the spatial proximity of assimilatory organs and their produced quantity of assimilates, respectively, have a significant influence on the distribution of carbon allocation in the stem. Therefore, it is to be proven whether the relations between the spatially differentiated stem-volume increment of the last year and the spatial needle-mass distribution can (mathematically) be quantified.

MATERIAL AND METHODS

The studied objects are 64-year old Douglas fir trees in a pure stand situated at Esbeek in the southern Netherlands. Several trees of this former University of Wageningen research plot were already analysed in a preceding research project (GAFFREY 1996). Now, further five trees (tree No. 104, 106, 177, 181, 231) have been examined very intensely and by application of the data of tree No. 104, an elasto-mechanical tree model was set up.

OUTER AND INNER TREE GEOMETRIES AND MASS DISTRIBUTIONS

Stem analyses with a very high resolution (GAFFREY 1995) were performed on five trees: in part, stem disks at distances of 1 m were cut off and all year rings were digitised in angle steps up to two degrees, with the aim of determining the annual ring area and thus, volume increments for eight sectors, as precisely as possible. Heartwood and sapwood areas of the stem disks and of disks of selected branches were also recorded digitally to describe the change in the conductive area. Dry masses and densities of all disks were determined, because these characteristics are fundamental input data for the elasto-mechanical tree model. With the exception of tree No. 177, the needle and branch dry masses were estimated using the (theoretically) bias-free randomised branch sampling method (GREGOIRE et al. 1995) which has slightly been modified for this purpose (GAFFREY, SABOROWSKI 1999; SABOROWSKI, GAFFREY 1999). The complete crown geometry at the level of first-order branches was assessed (branch length, base diameter, azimuth and inclination angle). In simplification, the mass centroid of the branches was estimated to be located in the middle of the branch.

DISTRIBUTIONS OF WOOD DENSITY AND OF YOUNG'S MODULUS

Within the limits of the research project, the finely resolved spatial distribution of the fresh wood density and of the modulus of elasticity (MOE) within the stem could not be measured and therefore, missing data had to be estimated.

The determined dry density of a stem disk represents an average value of the single ring densities, weighted proportionally to their areas. As Douglas fir shows a species-specific, non-linear pattern of the dependency of wood density on the cambial age (HAPLA 1985; MEGRAW 1986; JOZSA, MIDDLETON 1994), such a "horizontal" variability of density can be expressed by the following function, which represents the density ρ at a moisture content of $u = 8\%$ (GAFFREY et al. 1999):

$$\rho_8(k,\Delta\rho_i) = \frac{-6.33}{(k-10)^2 + 69.86} + 0.6 + \Delta\rho_i \qquad (\mathrm{g/cm^3})$$

$$k = \text{cambial age}$$

The density curves of different trees at the same height, as well as of different heights of the same tree, are quite similar and only differ in their vertical position. Therefore, the above function can be adjusted for each individual stem disk i by determination of the shift term $\Delta\rho_i$. As the density of fresh wood is of interest, and with a moisture content of the heartwood roughly estimated to be 30% and that of the sapwood to be 120%, correction functions which account for the wood swelling (KOLLMANN 1951) are accordingly applied.

Concerning the modelling of stress and strain in the outermost wood fibres of the stem, the modulus of elasticity E, in direction along the grain, is of greatest importance. Due to a generally assumed strong correlation between bulk density and MOE (PANSHIN, DE ZEEUW 1970; U.S.D.A. Forest Service 1989), with the use of the ring-specific density estimations, the MOE values are derived by a modified approach according to PALKA (1973):

$$E = E^* (\rho_{u^*} / \rho^*_{u^*}) \cdot [1 + a \cdot \Delta u], \; \Delta u = \min[(u - u^*), u_{\max}]$$

where E^* is the MOE at a reference density $\rho^*_{u^*}$ with moisture content u^*.

For Douglas fir, mean values $E^* = 11.5$ GPa at $\rho^*_{u^*} = 0.5$ g/cm^3 ($u^* = 12\%$) (KOLLMANN 1951) and $a = -0.01$ (PALKA 1973) were chosen, and $u_{\max} = 24\%$ is the estimated limit moisture content, above which the mechanical properties of Douglas fir wood are no longer affected. It has to be mentioned that in respect to an individual tree, the applied relations cannot claim validity (NIKLAS 1997).

MODELLING WIND FORCES

Based on the measured branch data, branch surfaces were modelled by cubic spheroids, with volumes which are directly proportional to the branch and needle masses. These solids, together with the entire stem and branch architecture, were generated and visualised with ray-tracing software, which also allows virtual orthographic photos to be taken, i.e., images without perspective distortion. With a camera axis perpendicular to the tree axis and parallel to an assumed wind direction, the projected branch spheroids represent sail areas. Virtual photos were stored as graphic files, and then the horizontal crown projections were measured using image-analysis software, with the known crown length serving as an absolute scale. (The technique of analysing virtual photos has been applied, e.g., by SINOQUET et al. [1998], to measure light interception by vegetation canopies.) Due to difficulties in differentiating single, overlapping branches, the stem was sectioned and the projection areas of all branches in each interval were united to a common sail area.

In the absence of real wind profiles, the wind speed v at a height h was estimated by $v = v_0 \cdot (h/h_0)^c$, where v_0 is the reference wind speed at height h_0, and with the parameter $c = 0.3$ for forests (HÄCKEL 1993). The wind force $F_w(h)$ acting on a sail area A (h) with a drag coefficient c_D is calculated according to $F_w(h) = 0.5 \cdot \rho_a \cdot c_D \cdot A(h) \cdot v^2(h)$. The air density ρ_a can be assumed constant with about 1.2 kg/m^3. Not constant, but a function of the wind speed, are sail area and drag coefficient, due to the streamlining effect. Based on Mayhead's experimental results (MAYHEAD 1973), the drag coefficient for Douglas fir is set to 0.5 in the case of calm and is decreased linearly to a minimum of 0.25 at a wind speed of 20 m/s. The change of the c_D value comprises the reduction of the sail area, which is held constant in the model. With respect to the branch angles, the mean height of the common sail area within a stem section is used for estimating the wind speed. Forces resulting from stem resistance against wind are relatively unimportant (PELTOLA, KELLOMÄKI 1993) and therefore neglected.

MODELLING STRESS AND STRAIN

Wind forces, stem and branch masses will bend the stem until a balance between the induced turning moments and the inner restoring moments of the stem are achieved. Moments due to wind forces are modelled by permitting the sail-area related forces to act horizontally on the stem axis at a height calculated by the average height of the insertion points of all branches within a stem section. The mass of each single branch produces its own turning moment, the individual branch angle taken into account, but the bending of branches is neglected. Stem masses are calculated with a high spatial resolution applying the estimated year ring-specific fresh densities. The values of each ring for neighbouring disks are averaged, weighted by the ring areas. To simplify the definition of zones differing in moisture content (needed for the density estimation), the number of sapwood rings is held constant along the whole stem (here: the outermost 10 rings). Fibre compression due to vertically directed stem weight is considered, too, though this effect plays only an insignificant role. As the real, irregular area shapes of the year rings, each linked with a specific MOE value, are taken as a basis for calculating restoring moments, the direction of bending must be considered. With reference to the perpendicular neutral axis a, the axial second moment of area $I_{a,i}$ of the i-th ring is defined by

$$I_{a,i} = \int_{A_i} dA \cdot d_a^2$$

with d_a being the distance of the infinitesimal area dA of ring i from a. Then the total axial second moment of area I_a and thus the structural, i.e., the weighted averaged MOE E_a of the entire stem cross section with n year rings is given by

$$I_a = \sum_{i=1}^{n} I_{a,i} \quad \text{resp.} \quad E_a = \sum_{i=1}^{n} E_i \cdot I_{a,i} / I_a$$

with M being the sum of all wind- and gravity-induced bending moments, in the state of moment equilibrium, stress $\sigma_i(d_a)$ and strain $\varepsilon_i(d_a)$ within the ith ring at a distance d_a from the neutral axis stress and strain, respectively can be calculated by

$$\sigma_i(d_a) = M \cdot d_a \cdot \frac{E_i}{\sum_{i=1}^{n} E_i \cdot I_{a,i}} \quad \text{and} \quad \varepsilon_i(d_a) = \sigma_i(d_a) / E_i.$$

Here the maximum values for the outermost fibres in the nth ring are of interest.

RESULTS

Basic data of the analysed trees are given in Table 1. Interesting is the fact that trees with more or less identical d.b.h. and height values (No. 106 and 181) can distinctly differ in needle and branch dry masses whereas, on the other hand, despite diverging stem sizes (No. 104 and 106), needle masses can be very similar.

The analyses of the dry densities do not show (or only to a certain extent) a decreasing height trend (Fig. 1), which could have been expected with increasing shares of juvenile wood. The largest tree in volume, No. 177, has a remarkably lower wood density. Very low seems to be the density directly at the base stem, at the transition of stem wood into root wood, if the single value of No. 231 is representative. The special tree of interest, No. 104, with a mean density of 0.55 g/cm³ reveals a great disk-wise variation with a minimum of 0.44 and a maximum of 0.65 g/cm³. According to the derivation of the MOE (estimation of structural MOE for fresh wood with respect to a specific bending in south-east direction, and based on wood densities), these differences are correspondingly mirrored in the MOE values, with a minimum of 9.2 GPa, a maximum of 13.9 GPa, and a mean of 12.4 GPa.

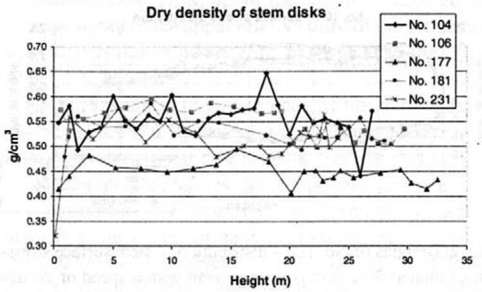

Fig. 1. Vertical distribution of wood dry density for five Douglas fir trees (bold line for tree No. 104)

MECHANICAL APPROACH

Stress distribution

The stress and strain distribution on the surface of the stem of Douglas fir tree No. 104 was simulated, assuming the conditions of a typical winter storm with a wind speed of 20 m/s above the canopy and from a north-western direction. With the estimated wind-exposed total sail area of about 27 m², the span of calculated drag coefficients ranges from 0.3 at the bottom of the crown and 0.25 at the top. The received wind load has its maximum in the stem interval from 21 m to 22 m (300 N) and constitutes in total 1,500 N.

The surface stresses of the stem, calculated for several directions, show no uniformity (Figs. 2 and 3): near the bottom, the values are relatively small, for the branchless stem slightly increasing and within the crown, they decrease remarkably. Single major deviations, esp. at the height of 16 m, can be explained by local stem thickenings. The maximum stress of ±16 MPa is still far from the risk of a fibre break: according to mean literature val-

Table 1. Basic yield data of the analysed Douglas fir trees

No.	d.b.h. (cm)	Height (m)	Needle dry mass (kg)	Branch dry mass (kg)	Stem dry mass (kg)	Total dry mass (kg)	Dry mass ratios
104	35.5	29.6	41.4	68.3	639	749	1:1.7:15.6
106	43.9	31.9	41.2	74.7	891	1,007	1:1.8:21.7
177*	58.0	> 33.5					
181	44.1	30.5	50.8	121.7	801	974	1:2.4:15.7
231	31.9	26.9	27.1	45.6	451	524	1:1.7:16.7

*Due to severe crown destruction after felling, no detailed analysis was possible

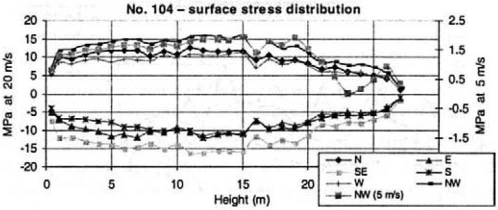

Fig. 2. Douglas fir No. 104 – distribution of stem surface stresses, simulated for a north-western wind with a speed of 20 m/s (left scale), and 5 m/s (right scale)

ues of 48 MPa ($\rho_0 = 0.47$) for the modulus of rupture (MOR) for green Douglas fir wood (KOLLMANN 1951), and taking into account a density correction as well as a reduction for regarding the whole, inhomogeneous stem (PELTOLA, KELLOMÄKI 1993), a MOR of 40 MPa seems realistic, i.e., a safety reserve of 60% would remain. The result is similar when the focus is on the strain (the figures are not shown as the strain distribution is very similar to the stress distribution). Let the general limit ε_B be 0.004 (YLINEN 1952) then, with ± 0.0014 for the estimated extrema, the safety span is 65%. As Douglas fir is susceptible to crown-top breaking at high wind speeds, these results may be inconsistent. But it must be born in mind that the model does not account for dynamic wind loading which produces much higher strain and stresses than the mean loading.

Supplementarily, the tensile stresses for the north-west direction at a wind speed of 5 m/s were calculated (Fig. 2). Compared with the graph constructed for the wind speed of 20 m/s, the curves run more or less parallel, with the exception of the crown region.

Stress reduction by growth in diameter

Assuming that within one year for a 64-year old Douglas fir, neither the change in crown geometry nor in its mass distribution is significant and therefore can be neglected, the reduction in fibre stress due to the growth in diameter is calculated. The same wind-load conditions, as described above, are chosen for tree No. 104, with the stem form being the same as the year before, and the resulting stress values taken as the basis for calculating the percentage of stress decrease (Fig. 4). Within the branch-free bole, up to a height of 16 m, the reduction is rather uniform with about 7–8%, but continuously increases within the crown and finally reaches values of 25–30%. This tendency is valid for all examined directions.

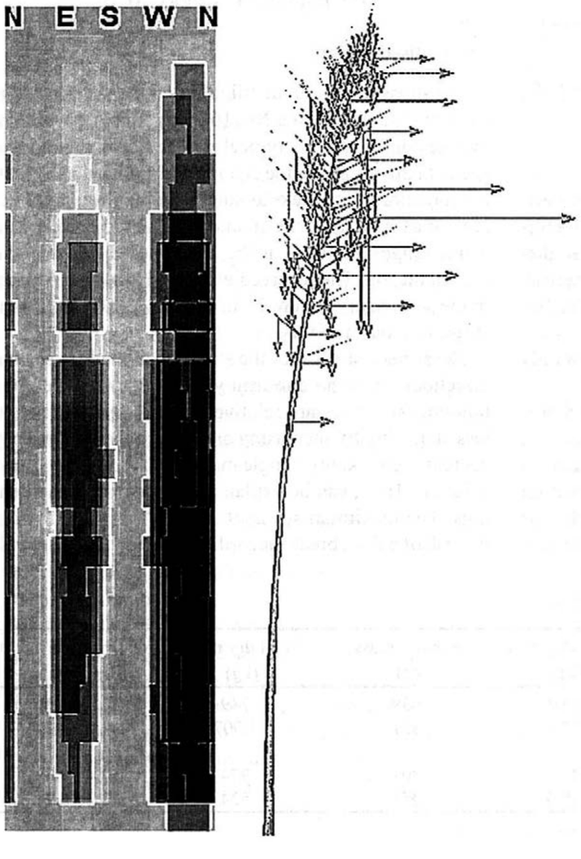

Fig. 3. Silhouette of Douglas fir No. 104, bent in a north-western storm of 20 m/s (right). View from south-west. Arrow lengths are proportional to wind and gravitational forces. Stem surface stresses transformed on rectangular grid (left). Original colour image converted to grey scale: main zone of tensile stresses between east and south and main zone of compression stresses between west and north, with shading intensity corresponding to stress values

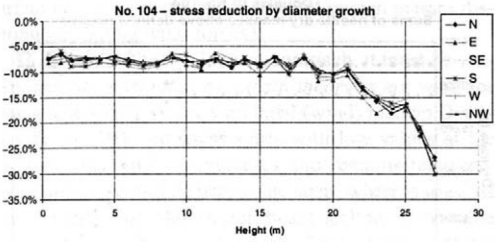

Fig. 4. Douglas fir No. 104 – stress reduction by diameter growth in the year 1997. Stresses calculated from stem geometry at the beginning and at the end of this growth period (all parameters as wind conditions, crown geometry and masses were held constant

HYDRAULIC APPROACH

For the stem, in principle, the trends of the ratios of sapwood area (digitised values for water-saturated stem disks) at a certain height and the needle mass above (oven-dry mass) are similar for all four studied Douglas fir trees (Fig. 5).

Three stem sections have to be differentiated: the butt swell with relatively high ratios, the branch-free stem with linearly decreasing values, and the crown which is characterised by a steep, exponential increase. In regard to the middle part of the tree, the graphs of trees No. 104, 181 and 231, which have comparable ratios of stem dry mass and needle dry mass (Table 1), coincide quite well. The curve of tree No. 106, with a much higher stem-/needle-mass ratio, however, runs above the other at a more or less constant distance. Statements for the stem bottom are restricted, as only for No. 231, a disk of the stem base could be analysed. As, concerning the stem's upper region, different total heights make comparisons difficult, the idea arose to first normalise height, as well as the relative conducting area. Therefore, the numerator, the sapwood area, was divided by the total sapwood volume of the tree and the denominator, the dry needle mass above the investigated stem disk, was divided by the total dry needle mass, giving the unit "cm^{-1}" for the normalised ratio. Now, below the crown, all divergences disappear, but in the upper relative third of the stem, such a uniformity does not exist (Fig. 6). Especially the values of No. 231 fall off.

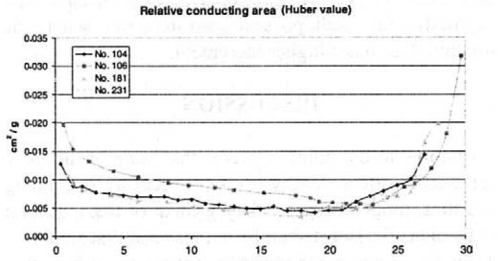

Fig. 5. Relative conducting areas (ratio of sapwood area and needle dry mass above) depending on height

An improvement in coincidence of normalised ratios can be achieved if instead of the total sapwood area, the area of the outermost five rings is used. In this case, to obtain comparable values, the conducting ring area was standardised by dividing by the total volume of exactly these five rings. (As normally the first rings contribute to most of the water conductance, SHINOZAKI et al. [1964a] already attached great importance to an analysis which refers only to these rings.) Again, it is No. 231 with under-average ratios.

Lastly, analysed for tree No. 181, the change of conductive areas within the annual stem shoots below the crown was determined. For this purpose, the differences in the sapwood area above a whorl and below the next one were calculated as percentage change per metre (to account for unequal distances between the stem disks). On average, the sapwood area decreases by 8–9% upwards within a section, but the variance is extremely great (range of change from – 36% to + 22%). A trend depending on height could not be found. In this context, the stem sapwood area below a whorl was compared with the sum of the conductive area of the branches of the whorl and of the stem directly above the whorl. There does not exist any constancy: the area sum above is about 9% higher, and again the variation from whorl to whorl is very high (range from +3% to +16%).

APPROACH REFERRING TO THE NEEDLE-MASS DISTRIBUTION

The hypothesis that the annual cross-sectional area increment depends on the needle (dry) mass, located above this position, implies the assumption of a dependency on the amount of assimilates that is imported into the stem phloem by the needled branches.

The allocation pattern which was proposed by HARTIG (1870) can be confirmed in a first, rough approximation: in tendency, predominant tree No. 177 shows an increase of ring-area growth stem downwards, whereas

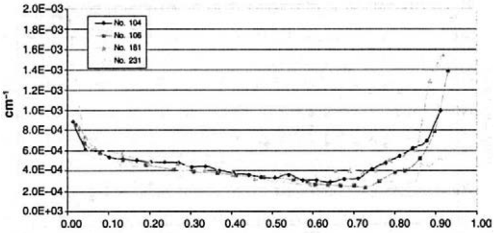

Fig. 6. Normalised relative conducting areas (ratio of sapwood area divided by total sapwood volume and needle dry mass above, divided by total needle dry mass) depending on height

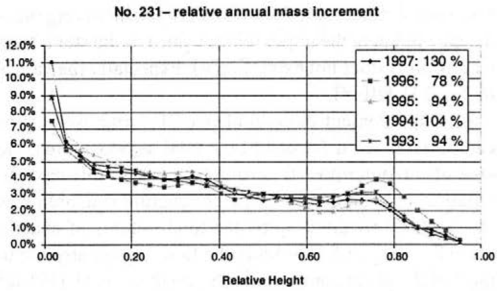

Fig. 7. Douglas fir No. 231 – relative mass increment of 30 equal-length stem sections, for each of the last five years. Percentage of total stem-mass increment related to the average increment of the last five-year period

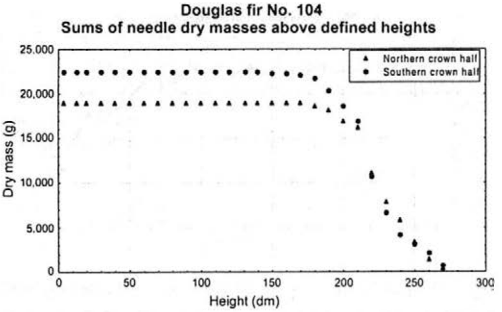

Fig. 8. Douglas fir No. 104 – needle dry masses above defined stem heights, separated for the northern ands southern crown half

No. 231, with a relatively small crown, has only a more or less constant area increment. But the pattern is much more complex, as a considerable year-by-year variation can occur. In years with favourable climatic conditions, the increased net assimilate production should be reflected in a shift towards higher shares of allocated carbon in the lower stem parts, at the expense of the upper stem region. Here, instead of the share of the unknown photosynthetic production consumed for stem growth, the increment of wood dry mass was directly regarded. Alternative calculations using the volume increment do not cause any great differences. Comparing the last five years from 1993 to 1997, separately for all trees, the stems were divided into 30 sections of equal length and for each section the mass increment was calculated as the percentage of the stem's total annual mass increment. For tree No. 231 (Fig. 7), at the height of the crown base (relative height: 0.7–0.8), the maximum of the relative increment is clearly given for the most unfavourable year 1996 (78% of the average growth in the five-year period). Moreover, it is the same year where the minimum for the stem's lower sections is found. On the other hand, a downward shift of the carbon allocation, corresponding with increasing annual growth performance and which should be most pronounced in the year 1997 (30% more growth than at average), is indistinct. In respect to the other trees, the results are even more ambiguous.

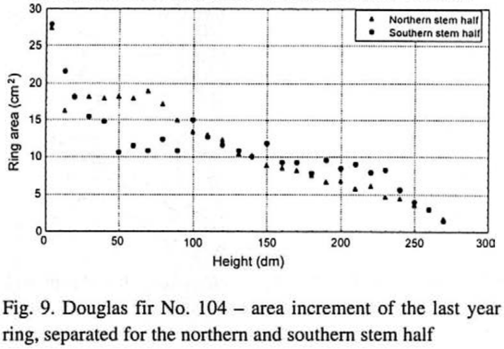

Fig. 9. Douglas fir No. 104 – area increment of the last year ring, separated for the northern and southern stem half

The influence of assimilate supply on stem growth in diameter is further proven by a more refined approach, which differentiates between eight area sectors, i.e., each sectorial annual ring increment is related to the needle mass of all those branches above, which exactly belong to the same sector. For clarity, the relations are simplified by uniting all sectors of the southern half of the tree and those of the northern half (Figs. 8 and 9). Analysed is the needle mass distribution at the time of felling (winter 1997/98) and the stem increment of the preceding growth season.

For tree No. 104, with the exception of the lowest parts of the crown (below a height of 20 m), the needle masses of both crown halves are approximately equal, confirming the optical judgement of a symmetrically developed crown. However, in the upper part of the stem, the half of the last year ring at the south-exposed side shows a significantly higher area increment. Stem downwards, this difference disappears completely, and in lower stem sections it is the northern side of the stem which shows a better growth. Unfortunately, in the other trees, the spatial distributions of wood increment in relation to the needle mass distributions follow quite other, not clear patterns. For example, tree No. 106, with an extreme asymmetric crown with three quarters of the needle mass exposed to the south, possesses no stem zone where the southern half has a higher increment.

DISCUSSION

To come to the point, it seems that none of the three approaches offers an easy-to-use concept for explaining and thus, modelling secondary growth of trees, at least of Douglas fir. But it shall be emphasised that final evidence for or against the inspected theories, or hypotheses, cannot be given because a lot of the basic input data depends on functional derivations (density and MOE distribution) or estimations (needle and branch masses distribution, acting wind forces).

In respect to the mechanical approach, it must be stated that the *constant stress/strain theory is not valid* for the whole stem. For the simulated (wind) load on Douglas fir No. 104, the stress starts with low values at the bottom, then slightly increases and remains relatively constant in the middle part of the stem, whereas towards the top, the values show a significant decline. At the same wind speed of 20 m/s, MORGAN and CANNELL (1994) calculated for *Picea sitchensis* a non-uniform stress distribution, too, but with more or less steadily decreasing stress from bottom to top. However, they do not reject the constant stress theory, because it is found to be valid within a wind speed range from 2.5 to 10.0 m/s. They argue that most trees grow in areas with an average wind speed of 5 m/s and therefore, their adaptive growth results in stress constancy exactly under these conditions. Stress simulations for the analysed Douglas fir tree at a wind speed of 5 m/s nevertheless, cannot confirm this hypothesis (Fig. 2). Answering the question on how the annual growth in stem diameter will contribute to stress reduction, it turned out that for the complete branchless stem, the values are on average 7–8% lower, whereas from the bottom to the top of the crown, they decrease by up to 30%. Certainly, as the calculations are based on the assumption of the same needle mass distribution and thus, the same wind forces, especially in the crown, the absolute percentage values will be overestimated, but, nevertheless, the general conclusion will not be affected: *diameter growth of juvenile wood* (which is found in the crown) *is apparently not (or only to a minor part) stress-induced adaptive growth*, but is, perhaps, dominantly triggered by the other function the stem has to fulfil: to guarantee a sufficient water supply corresponding to the individual demand of distinct crown parts.

Therefore, solely viewing a sapwood area/needle mass ratio and postulating its constancy without taking the hydraulic resistances into account, as is neglected by the pipe model theory, is insufficient. Moreover, e.g., it has been found for *Picea abies* (HEIMANN 1995) that, within a cross-section, the water flow velocity depends on the location of the conducting ring: first, the velocity increases by ring age, but then falls off. The observations made on Douglas fir confirm HUBER (1928), especially the steep rise of the ratio within the crown is striking. But, however, viewing the graphs (Fig. 5), some similar characteristics might offer new approaches to a quantitative description of the relation between the two variables, sapwood area and needle mass. For the branchless part of the stem, the introduction of a new, normalised ratio (Fig. 6) results in a coincidence of the graphs of all trees, including the one with a much higher ratio of stem mass to needle mass (Table 1). Still existing differences within the crown might have two explanations. On the one hand, it must be born in mind that the needle-mass distribution was only estimated and the coefficient of variation for the single whorls is on average about 20% (GAFFREY, SABOROWSKI 1999). On the other hand, as especially suppressed tree No. 231 shows a great negative deviation from the others, the normalised ratio might account for the (relative) water demand and thus, for the photosynthetic performance of the crown, relative to those of the other trees. The differences diminish if instead of the total sapwood area only the last or the last five conducting areas are examined. This is reasonable, as HUBER (1928) stated that, from a certain age onwards, for *Abies alba*, only a limited, constant number of rings essentially contribute to water conductance, and that is why SHINOZAKI et al. (1964a) focussed on the last five rings, too. For Douglas fir, the normalised ratios referring to one or to five rings are more or less identical. Further studies on trees of different age and of different social classes must show whether the relations can be generalised and what might be the dependencies between ring areas and corresponding (age-wise differentiated) needle masses.

The third approach, the trial to link the local availability of assimilates, expressed by the needle-mass distribution in the absence of any measured concentrations of photosynthesates, does not offer very usable discoveries. There are certain indications that with an increasing annual photosynthetic production, relatively more carbon is allocated in lower stem parts. Furthermore, a high local input of, e.g., the more productive southern crown half seems to result in a greater local area increment than at the opposite side of the stem. Both observations are only valid for individual trees and/or parts of the trees and/or growth periods. For instance, whereas within the crown the southern stem side is favoured for ring growth (as expected), stem downwards the conditions are reversed. According to ZIMMERMANN and BROWN (1980), a lateral transport of assimilates in the phloem is restricted and thus, less important, a possible helical whorl of the sieve cells could account for the azimuthal shift of the area increment maximum. Analyses of the spiral grain might give further insight.

Most probably, all three factors mentioned will influence the secondary growth in thickness. As the single effects overlay each other and only the result will be observable, growth analyses which try to explain and to quantify the impact of the individual triggering factors encounter fundamental problems. A certain solution may be, as has already been done, to design field experiments in which only one specific aspect, e.g., the mechanics, is pronounced. Guying trees or enlarging their instability (by attaching sand bags, for instance) will emphasise the mechanically induced cambial reactions. Girdling studies of crown parts might reveal relations between local assimilate stem input and its use for wood formation. Accompanied detailed sapwood area and needle mass analyses may complete the picture. But the present state of knowledge is that stress-induced adaptive growth seems to dominate in the branchless stem part, whereas the stem increment in the crown may be determined by hydraulic requirements.

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Mechanika, hydraulika a rozloženie ihlicovej masy ako možné postupy skúmania dynamiky kmeňovej morfológie

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ABSTRAKT: Cieľom príspevku je overenie hypotéz, ktoré vysvetľujú sekundárny hrúbkový rast. Postupy opisujúce hrúbkový rast sú založené na mechanickom alebo hydraulickom princípe alebo na rozložení ihlicovej hmoty stromu. Je veľmi pravdepodobné, že mechanické pnutie kambiálnych buniek, spôsobené silou vetra, je jedna z najdôležitejších príčin hrúbkového rastu. Simulácie pomocou elasto-mechanického modelu 64-ročných duglasiek vyvracia platnosť „teórie konštantného pnutia", následkom čoho ani „teória adaptívneho rastu" nemôže byť prijatá ako pravidlo. Základná myšlienka „Pipe Model teórie", ktorá vychádza z konštantnej relácie medzi priečnou plochou bele a od nej vodou zásobovanej listovej masy, sa ukázala ako neplatná. Rovnaká tendencia všetkých skúmaných stromov však umožňuje formuláciu pozmenenej hypotézy. Relácie medzi priestorovým rozložením ihlicovej masy, a tým aj množstvom asimilátov, a priestorovým rozložením plošného prírastku po kmeni sa javia pravdepodobné, nie však jasné. Pravdepodobne sa všetky tri vplyvy prekrývajú, pričom pnutím spôsobovaný adaptívny rast dominuje s výnimkou oblasti koruny, kde sa pre hrúbkový rast ako najdôležitejší ukazuje vodný režim.

Kľúčové slová: stromová mechanika; stromová hydraulika; rozloženie ihlicovej hmoty; elasto-mechanický model; hrúbkový rast; kmeňová morfológia

Pri stromových rastových modeloch, ktoré spájajú najmä stromovú štruktúru a funkciu ("functional-structural tree models": mimoriadne vydanie časopisu Silva Fennica, *31*(3), 1997), je pre popis dynamiky kmeňovej morfológie dôležité poznať význam funkčných požiadaviek kmeňa pre jeho sekundárny hrúbkový rast. Pri nedostatku presnejších znalostí procesov, ktoré riadia kambiálne delenie, sa modeluje rast hrúbky na vyššej úrovni abstrakcie v závislosti od mechanického námáhania (napr. FOURCAUD, LAC 1996), hydraulických hodnôt (napr.

PERTTUNEN et al. 1998) alebo v závislosti od rozloženia ihlicovej hmoty (napr. MITCHELL 1975; DE REFFYE et al. 1997b). V tejto práci, ktorá bola podporovaná nemeckou grantovou agentúrou Deutsche Forschungsgesellschaft (GAFFREY, SLOBODA 1999), bolo skúmané, do akej miery sú tieto tri postupy vhodné pre popis hrúbkového rastu duglasky (*Pseudotsuga menziesii*).

Pri mechanickom aspekte sa vo všeobecnosti ukazuje, že hrúbkový rast je podporovaný predovšetkým ohybným pnutím (napr. MITCHELL, MYERS 1995). Rozšírená je hypotéza, že kmeňové zóny s relatívne vysokými hodnotami pnutia vykazujú zvýšený, „adaptívny" rast (TIRÉN 1928; WILSON, ARCHER 1979; MATTECK 1990), ktorého cieľom je vyrovnávanie tohto pnutia ("constant stress theory/hypothesis": METZGER 1893). Výsledky z poslednej doby vnášajú však pochybnosti o konštantnosti pnutia v reálnych situáciách zaťaženia (BLACKBURN 1997; NIKLAS 1999; NIKLAS, SPATZ 2000). Podľa hydraulického postupu zabezpečuje hrúbkový rast podľa JACCARDA (1913, 1915) resp. podľa „Pipe-Model teórie" (SHINOZAKI et al. 1964a,b) proporcionalitu medzi priečnou plochou bele a od nej vodou zásobovanej listovej masy. Výhrady voči takémuto konštantnému vzťahu vzniesol už HUBER (1928). Nakoniec je pozorovaná závislosť rozloženia prírastku kmeňovej plochy od rozloženia ihlicovej masy (PREẞLER 1865; HARTIG 1870), pričom prírastkový vzor môže byť veľmi komplexný a závislý od klimatických faktorov (FAYLE, MACIVER 1985).

K preskúmaniu týchto troch vzťahov boli vykonané detailné analýzy na štyroch 64-ročných duglaskách z monokultúry v Esbecku v Holandsku. Pri veľmi podrobných kmeňových analýzach boli určené štruktúry vnútorných ročných kruhov ako aj bele a jadrových oblastí. Korunová geometria bola zistená pre všetky vetvy prvého rádu, vetvová a ihlicová sušina bola odhadnutá metódou RBS (GAFFREY, SABOROWSKI 1999). Jeden strom (č. 104 bývalej skusnej plochy Univerzity Wageningen) bol vybraný pre konštrukciu elasticko-mechanistického modelu pre simuláciu rozloženia pnutia na povrchu kmeňa v rôznych zaťažovacích situáciách. Informácie o rozložení hmoty kmeňa, potrebné pre tieto simulácie, boli odhadnuté individuálne vyrovnanými a od kambiálneho veku nezávislými frekvenčnými funkciami (GAFFREY et al. 1999). Na týchto frekvenčných hodnotách, špecifických pre ročný kruh a korigovaných odhadnutými vlhkosťami, spočívajú ohybno-elastické modely, ktoré sú potrebné pre popis elastického správania.

Sily vetra boli vypočítané diferencovane pre jednotlivé korunové sekcie za predpokladu zvyčajných vetrových profilov. K výpočtu plachtových plôch boli použité virtuálne fotografie kolmo k smeru vetra nasmerovaných výrezov korún, ktoré boli vytvorené pomocou Ray-tracing-Software a následne zmerané obrazovo-analytickými postupmi. Pri simulácii zaťaženia boli zohľadnené okrem priamo na kmeň pôsobiacich síl vetra a gravitačných síl kmeňovej masy aj momenty jednotlivých vetví.

Pri simulácii mechanického správania duglasky č. 104 pri typických víchricových situáciách (vietor zo severozápadu s rýchlosťou 20 m/s) dosahuje namerané vetrové zaťaženie koruny silu asi 1 500 N. Vypočítané povrchové pnutia nie sú konštantné (obr. 2 a 3): tieto sú v prízemnej oblasti relatívne malé, ľahko stúpajú v bezvetvovej časti kmeňa a podstatne klesajú v korunovej oblasti. Maximálne dosiahnutá hodnota ± 16 MPa je ďaleko vzdialená od hodnoty ± 40 MPa, ktorá je považovaná za okamih zlomu vlákna. Pri pozorovaní naťahovania, resp. stláčania namiesto pnutia vlákna bol dosiahnutý rovnaký výsledok. (Treba však zdôrazniť, že bol modelovaný iba statický vetrový model. V skutočnosti nastávajú podstatne vyššie dynamické zaťaženia, ktoré môžu už pri podstatne menších rýchlostiach vetra spôsobiť škody.) Ak sa vypočíta dosahované napätie pri rovnakej situácii pre kmeň z predchádzajúceho roku, je možné určiť hrúbkovým prírastkom vyvolaný pokles napätia. Ukázalo sa, že ten je v bezvetvovej časti kmeňa relatívne konštantný, v korunovej časti smerom k vrcholu rastie, a týmto protirečí myšlienke adaptívneho rastu.

Pri hydraulickom postupe sa ukázalo, že pomer priečnej plochy bele a ihlicovej masy nad miestom merania nie je nikdy konštantný, jeho priebeh je ale pre všetky stromy veľmi podobný (obr. 5). Prízemná časť kmeňa vykazuje vysoké hodnoty, v bezvetvovej časti kmeňa nasleduje kontinuálny takmer lineárny pokles a v korune veľmi silný nárast. Strom č. 106 vykazuje v porovnaní s ostatnými tromi duglaskami jednoznačne vyššie hodnoty v podkorunovej oblasti. Pri dvojnásobnom normovaní, delení priečnej plochy bele celkovým objemom bele kmeňa a ihlicovej hmoty nad pozorovanou výškou kmeňa celkovou ihlicovou masou, ako aj voľbou relatívnych výšok, je dosiahnutá pre všetky stromy podstatne lepšia kongruencia kriviek (obr. 6). Iba kmeň č. 231 s ľahko utlačenou korunou vykazuje v hornej oblasti výrazne menšie normované pomery.

Vzťahy medzi stavom koruny (a tým ihlicovej hmoty) a rozložením plošného prírastku kmeňa, ako ich popisuje HARTIG (1870), je možné pozorovať iba čiastočne a aproximatívne. Pri nadúrovňovom strome č. 181 rastie podľa HARTIGA plošný prírastok v bezvetvovej časti kmeňa s klesajúcou výškou. Pri úrovňovom strome, ako napr. č. 231, sa nachádza lokálne prírastkové maximum v korunovej časti (čo má platiť pre podúrovňové stromy), v bezvetvovej časti kmeňa plošný prírastok smerom k báze rastie tiež – aj keď pomalšie. Ak je väčšia ihlicová masa a tým pre prírastok kmeňa vyššie dispozitívne asimilačné množstvo dôvodom pre ukladanie asimilačnej hmoty v spodných kmeňových oblastiach, tak by mal tento vzťah platiť aj v klimaticky veľmi výhodných rokoch s vysokou asimilačnou produkciou. Pre skúmané stromy však toto nie je možné jednoznačne potvrdiť.

Pre popis a modelovanie hrúbkového rastu pre sledované duglasky je možné konštatovať, že mechanická hypotéza, ktorá vychádza z adaptívneho rastu k dosiahnutiu konštantného pnutia, bola potvrdená nanajvýš v bezvetvovej časti kmeňa, aj to iba aproximatívne, v korunovej časti však nie. V korunovej časti je pravdepodobne dominantný vodný režim, ktorý podnieťuje podstatne vyšší hrúbkový prírastok a tým prírastok na vodivej ploche. V každom prípade nebola potvrdená „Pipe-Model teória“, ktorá popisuje konštantný pomer plochy bele k zásobovanej ihlicovej hmote. Ostáva preskúmať, či sú relatívne normované pomery invariantné, t.j. či sú nezávislé od druhových alebo stanovištných vplyvov. Ak by sa toto potvrdilo, ponúkal by sa na tomto mieste hydraulický postup modelovania prírastku, závislý od ihlicovej hmoty. Pesimistickejšie je možné hodnotiť priamy vzťah medzi rozložením ihlicovej hmoty a kmeňového prírastku. Dôvodom tohto môže byť, že vzťah medzi ihlicovou hmotou a pre kmeň dispozitívnych asimilátov nie je, ako je tvrdené, lineárny. Je potrebné zhodnotiť, či všetky tri pozorované faktory nemajú spoločný vplyv na hrúbkový rast.

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The Milešice virgin forest after 24 years (1972–1996)

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ABSTRACT: Detailed measurements were repeatedly made in 1972 and 1996 in the Nature Reserve Milešice virgin forest in order to study developmental changes of the virgin forest stand. Standing and lying trees were plotted in maps and repeatedly measured and forest types were mapped together with developmental stages and condition of natural regeneration. Phytocoenological relevés were made, soil pits digged out and described, directional photographs provided. Field surveys and results from 1972 and 1996 were processed according to the same methodology. The results demonstrated a long-term acidification of soils and a gradual return of the forest community indirectly affected by man back to the developmental trajectory of the natural forest. The return is characterized by the development of a more complex stand structure and a finer stand texture, by the gradually increasing volume of both live and dead timber and by the gradual differentiation of advance growths.

Keywords: dynamics; monitoring; virgin forest

Repeated measurements of mensurational, typological and stand characteristics were made across the whole area of the Milešice virgin forest Nature Reserve (NR) in 1996. The works were conducted as a part of the long-term project *Research of developmental dynamics of virgin forest reserves in the Czech Republic*, resolved by a group of experts within activities run by the Agency for Nature Conservation and Landscape Protection of the Czech Republic, Branch Brno (AOPK), and link up with detailed investigations made by Ing. Eduard Průša, CSc., and Dr. Ing. František Pišta in 1972. They try to cover developmental changes in the territory under study, to derive from them the general laws of development and to provide a competent groundwork for the area management.

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HISTORY

The today's virgin forest resulted from a fusion of two large stands of different age and was gradually reduced to the present size of hardly 9 hectares (Fig. 1 and Table 1). In the year 1858, its south-eastern part consisted of Stand 30f whose age was ranging from 60–120 years and which could not be considered a virgin forest. Nevertheless, the stand arised from the natural regeneration of the original virgin forest, which is evidenced by the corresponding mixture of tree species and by the tree age-span of more than sixty years (Pišta, Průša 1974). The low age of the stand results from the fact that the stand grows partly on ecologically unstable water-logged soil where even stands in the natural forest suffer from periodical windfalls.

Here, the classical stage of disintegration due to age did not fully develop but the disintegration occurred due to abiotic agents (wind on water-logged soils).

In 1856, when the forest district was first subjected to the Saxon method, the Milešice virgin forest was taking up 32.92 morgens, i.e. nearly 19 hectares. In the period from 1891–1930, total fellings made in the virgin forest amounted to 1,357 solid meters of timber. There were no more fellings made in the virgin forest since the time.

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Table 1. Development of the Milešice virgin forest from 1858 according to forest management plans (Pišta, Průša 1974)

Marking	Year	Acreage	Stand description	Age	Note
30a	1858	32 morgens, 920 six feet	SM, JD, BK, several KL	virgin forest	
30f		5 morgens, 760 six feet	SM, JD, BK	60–120 years	
30a	1869	24 morgens, 1,330 six feet	SM, JD, BK, several KL	virgin forest	
30f		5 morgens, 760 six feet	SM, JD, BK	70–130 years	
17i	1881	4.99 ha	SM, JD, BK, several KL	virgin forest	gaps at "Nebenschneite"
17k		3.68 ha	SM, individually JD, several KL	80–140 years and younger	
17i	1891	4.99 ha	SM, JD, several BK, few KL	virgin forest	
17k		2.73 ha	SM, individually JD, several BK	90–150 years and younger	occasional breakages
17i	1900	5.34 ha	(SM+JD) 7, BK 3	virgin forest	
17k		2.73 ha	SM 7, JD 2, BK 1, individually and in groups	100–160 years	heavy water-logging in the south-eastern edge
17i	1908	5.34 ha	SM 4, individually and in groups JD 3, BK 3, SM + BK undergrowth	virgin forest	Stocking 0.7/0.8. Per 1 ha 100 m^3 hard, 400 m^3 soft, in total 2,670 m^3. Larger gaps with SM undergrowth.
17c		2.73 ha	SM 7, individually and in groups JD 2, BK 1	100–150 years	Stocking 0.9/0.8. Per 1 ha 50 m^3 hard, 500 m^3 soft, in total 1,501 m^3.
17c	1920	8.07 ha	SM 6, individually and in groups JD 2, BK 2, SM + BK undergrowth	122–162 years, upper part virgin forest	Stocking 0.8/0.9. Per 1 ha 80 m^3 hard, 400 m^3 soft. Total 645 m^3 hard, 3,228 m^3 soft; in total 3,873 m^3.
17c	1950	7.98 ha	SM 5, JD 3, BK 2	180 years	nature reserve
4b	1965	8.84 ha	SM 58, JD 05, BK 33, KL 04	200 years	Per 1 ha 473 m^3. Total 2,890 m^3 conif., 1,924 m^3 decid., in total 4,814 m^3. Regeneration missing due to red deer. The stock includes standing dead trees – SM 103, JD 21, BK 54, KL 2 m^3.

Explanatory notes:
SM – Norway spruce (*Picea abies*)
JD – silver fir (*Abies alba*)
BK – European beech (*Fagus sylvatica*)
KL – sycamore maple (*Acer pseudoplatanus*)
"Nebenschneite" = secondary cleared boundary line (compartment line)

Large-scale clear fellings were used in the last century to cut out the surrounding forests of natural species composition, the subsequent stands were later severely damaged by bark stripping and those situated westwards of the virgin forest were destroyed by wind in 1956 (PIŠTA, PRŮŠA 1974).

The virgin forest was a part of the original Schwarzenberg game enclosure which was in use until 1960 with the fence having had suffered a considerable damage due to extensive wind breakages already some time ago. The restored game preserve started to be operated once again from 28 September 1976 (on a larger area than the original enclosure) and at the same time, the Milešice virgin forest was fenced as an enclave amidst the preserve. The preserve restoration was preceded by disagreement on the part of the Šumava Protected Landscape Area Administration, the then regional centre of the state care of historical monuments and nature protection in České Budějovice, which pointed out that it is useless to build a game preserve with the intensive rearing of red deer in the area with the permanent natural occurrence of this game and naturally with enormous losses on forest stands. The viewpoint was not accepted and the fencing of the virgin forest inside the preserve became the only possible solution for its preservation.

Development of the virgin forest is summarized in Table 1.

The virgin forest was proclaimed National Nature Reserve by the Decree of the Ministry of Education No. 186/48 of 23 January 1948.

At checking the virgin forest on 14 September 1958, the conservator of nature protection J. Jiřík found out that the reserve is in a good condition and pointed out that it is a serious competitor to the Boubín virgin forest. According to the check-up elaborate of 1962, the protection of this territory was cancelled by the Decree of the Ministry of Education No. 29.368/65-V2 of 5 July 1965 as recommended by natural scientists (PIŠTA, PRŮŠA 1974). The recommendation of the screening committee composed of natural scientists reads as follows: "... to close down (the reserve) and to decide in its place after a detailed research whether the Zátoňská hora Mt. should be protected as an example of flowery beech stand in the region of Central Šumava ..." (MÍCHAL, PETŘÍČEK 1998). The viewpoint not only did not take into account the virgin forest value from aspects other than just botanical (e.g. the valuable object from the viewpoint of the developmental dynamics of the whole community), but entirely neglected the fact that it is situated within a large complex of most frequently occurring groups of forest types (GFT) of the whole Šumava Mts. (e.g. in contrast to the much better preserved Boubín virgin forest which however does not represent the main forest types in the Šumava Mts.). A major part (89%) of the Milešice virgin forest is situated on the GFT Acidic Spruce-Beech, which takes up 22.8% of the whole natural forest range 13 – the Šumava Mts. and the Novohradské hory Mts. (PLÍVA, ŽLÁBEK 1986), and shows naturally poor species composition as a site; however, this does not mean it should not deserve protection.

The issue of a new enunciation of the national nature reserve was once again opened in the years 1972–1973 and the development indicated that the official proceedings would not take long (URBAN 1975).

However, the repeated enunciation was made by the Decree of the Ministry of Culture of the Czechoslovak Republic No. 14505/89-SOP of 21 December 1989, when the National Nature Reserve was officially declared on an area of 9.63 hectares.

METHODOLOGY

The whole revision was made on the basis of detailed maps and calculations recording the condition of the virgin forest in the year 1972 (PIŠTA, PRŮŠA 1974) with making use of a modified methodology of the field investigations and assessment of collected data (VRŠKA 1997). The tree layer was revised and the map was completed with records on all trees which achieved d.b.h. of 10 cm in the period under study. Newly fallen trees were plotted in the map, too. Callipered were all trees of d.b.h. greater than 10 cm with their characteristics being re-

Table 2. Changes in the chemism of soils in the period 1972–1996

PTP number	1					
Horizon	*A02*	Of	*A03*	Oh	*A1/2*	Ae
Horizon thickness (cm)	*3–9*	3–7	*9–15*	7–12	*15–25*	12–20
Year	*1972*	1996	*1972*	1996	*1972*	1996
pH – H_2O	*4.95*	4.0	*4.60*	3.4	*4.85*	3.6
pH – KCl	*3.24*	3.0	*3.21*	2.6	*3.60*	2.8
Cox (%)	*16.20*	34.61	*14.10*	22.94	*5.70*	8.75
Nt (%)	*1.87*	1.61	*1.81*	1.10	*0.32*	0.47
C:N	*8.7*	21.5	*7.8*	20.9	*17.8*	18.6
Al + H (me/100 g)	–	9.5	–	9.1	–	10.6
CEC (me/100 g)	–	22.9	–	16.5	–	12.1
S = CEC – (Al + H)	–	13.4	–	7.4	–	1.5
BS = V (%)	–	58.8	–	45.0	–	12.6

Explanatory notes: Cox – percentage of oxidizable carbon; Nt – total nitrogen content; Al + H – exchangeable aluminium and hydrogen; CEC – cation exchangeable capacity; S – immediate content of exchangeable bases (Ca, Mg, K, Na, Fe, Mn); BS – degree of sorption complex saturation; me – milliequivalent

Table 3. Changes in the chemism of soils in the period 1972–1996

PTP number		2		
Horizon	*A03*	Of/Oh	*A*	Ae
Horizon thickness (cm)	*3–7*	3–7	*7–20*	7–20
Year	*1972*	1996	*1972*	1996
pH – H_2O	*3.79*	3.7	*3.90*	3.9
pH – KCl	*3.15*	3.0	*3.29*	3.2
Cox (%)	*25.20*	21.57	*6.84*	2.58
Nt (%)	*1.46*	1.38	*0.32*	0.19
C:N	*17.3*	15.6	*21.4*	13.6
Al + H (me/100 g)	–	7.9	–	9.3
CEC (me/100 g)	–	12.6	–	10.5
S = CEC – (Al + H)	–	4.7	–	1.2
BS = V (%)	–	37.2	–	11.2

corded (dead standing tree, stub, etc.), and the lying trees were characterized for three stages of disintegration. About 160 trees were measured for height in order to design the height flow sheets as a groundwork for the volume calculations. The mensurational calculations were made with the use of the volume tables issued by Lesprojekt (1952).

The undergrowths were mapped, in which trees did not reach d.b.h. of 10 cm as at the date of the measurement, and a new mapping was made of the developmental stages and their phases.

Samples of upper humus horizons were taken from 4 soil pits on permanent typological plots (PTP) (3 PTPs in the virgin forest and 1 PTP on a parallel plot in the cultivated spruce stand) for chemical, biochemical and microbiological analyses in order to assess changes in the soil (chemical analysis). The biochemical and microbiological analyses were not made before and they mostly serve as a comparison material for other repeated investigations. All soil analyses were performed in accredited laboratories of AOPK CR – Branch Brno. The terminology and designation of soil horizons and soil subtypes was reworked to the valid soil classification system used by Institute of Forest Management (ÚHÚL) (MACKŮ, VOKOUN 1993). The changes were assessed by using the currently available methods of comparison (REJŠEK 1999). The results of soil analyses made in 1972 are taken over from PIŠTA and PRŮŠA (1974). Sampling for the analyses was made in the same period as in 1972; nevertheless, the comparison of results from analyses depending more on the precipitation status (total nitrogen content) should be considered informative. With the respect to the size of the material, the authors present only some paedological data.

Phytocoenological relevés were repeated on all 4 PTPs for circular areas of 25 m in diameter (i.e. ca. 490 m²), which link up with the phytocoenological relevés made in 1972 (PIŠTA, PRŮŠA 1974). The terminology of plants was unified (DOSTÁL 1989). At working out the phytocoenological relevés, the classification of tree species synusia made use of the stratification scale according to Zlatník (RANDUŠKA et al. 1986), the classification of herbs made use of the Braun-Blanquet combined scale of abundance and dominance, modified and refined by Zlatník (RANDUŠKA et al. 1986). The herb synusia was assessed by using the ecological groups of plant species (EGS) (PLÍVA, PRŮŠA 1969). The mathematical data processing was not made due to a limited number of the phytocoenological relevés and hence low conclusive evidence.

There were 11 directional photographs made for repeated photographing, whose place and direction were plotted in the detailed map of trees.

The original maps were digitalized in the geographic information system (GIS TOPOL) by using a special software for the generation of virgin forest maps, designed by Mgr. Dušan Adam. Following analyses were made by using these digital maps and associated databases. The programme facilities used were currently available softwares FOXPRO, MS Excel, MS Word. The phytocoenological relevés were assessed by means of the programme TYP, developed a the Department of Forest Botany, Dendrology and Typology, Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry in Brno (MZLU).

NATURAL CONDITIONS

Localization and wider territorial relations

The Nature Reserve of Milešice virgin forest is situated about 4.5 km eastwards of the village Kubova Huť

Table 4. Changes in the chemism of soils in the period 1972–1996

PTP number			3			
Horizon	*A02*	Of	*A03*	Oh	*A1/A2*	Ae
Horizon thickness (cm)	*3–5*	3–5	*5–8*	5–8	*8–18*	8–20
Year	*1972*	1996	*1972*	1996	*1972*	1996
pH – H_2O	*3.75*	3.8	*3.40*	3.4	*3.58*	3.6
pH – KCl	*2.99*	2.9	*2.72*	2.6	*3.13*	2.8
Cox (%)	*26.40*	37.78	*30.90*	23.49	*8.40*	7.39
Nt (%)	*1.86*	1.30	*1.72*	1.06	*0.36*	0.27
C:N	*14.2*	29.1	*18.0*	22.2	*23.3*	27.4
Al + H (me/100 g)	–	7.1	–	8.3	–	12.4
CEC (me/100 g)	–	18.1	–	12.3	–	14.8
S = CEC – (Al + H)	–	11.0	–	4.0	–	2.4
BS = V (%)	–	61.0	–	32.4	–	16.1

(Prachatice district), in the territory of the Protected Landscape Area Šumava, amidst the forest stands managed by the enterprise Lesy České republiky, s.p. (Forests of the Czech Republic, s.p.). Organizationally, the area belongs in the forest enterprise Boubín residing in Vimperk, forest district Mlynářovice residing in Volary, Stand 226 B. It is a part of the game enclosure Boubín and its total aligned area according to the digital map is 8.86 ha.

The whole territory is to be found in Forest Region 13 – Šumava (PLÍVA, ŽLÁBEK 1986). Biogeographic regionalization: sub-province Hercynian, biogeographic region 1.62 – Šumava (CULEK et al. 1995).

Geomorphological conditions

The altitude of the Milešice virgin forest Nature Reserve ranges from 1,070–1,125 m and its terrain is formed by a slightly inclined flat slope with eastern aspect. The slope is not articulated by any stream incisions or other terrain forms.

Geological conditions

The geological structure of the territory is simple. Parent rock is biotitic paragneiss. The parent rock grain is rather coarse here, and dark coloured by biotite. By weathering, it generally provides deep soils, sufficiently rich in nutrients and loamy-sand, skeletal soils in the basement (PIŠTA, PRŮŠA 1974).

Climatic conditions

Average monthly precipitations (mm) in the period 1901–1950, Station Horní Vltavice, Kubova huť, altitude 1,003 m (KOLEKTIV 1961):

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
58	61	49	63	88	98	112	96	69	61	51	61

Year	IV–IX	X–III
867	526	341

Average monthly precipitations (mm) in the period 1901–1950, Station Lenora, Zátoň, altitude 790 m (KOLEKTIV 1961):

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
49	47	41	54	74	84	102	83	61	57	50	55

Year	IV–IX	X–III
757	458	299

Average monthly temperatures (°C) in the period 1901–1950, Station Kvilda, altitude 1,058 m (KOLEKTIV 1961):

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
–5.3	–4.5	–1.3	2.7	8.2	11.1	12.9	12.2	8.7	4.4	–0.5	–3.7

Year	IV–IX
3.7	9.3

The region belongs in the cold zone – CH6 (QUITT 1974).

TYPOLOGICAL RELATIONS AND THEIR CHANGES

Acidic Spruce-Beech with hair-grass – 6K1 (7.87 ha, 88.8%)

Prevailing on the whole area under study with the exception of its south-eastern portion. Site conditions are characterized on PTP 1 (Table 2), PTP 3 (Table 4), and on the parallel PTP (Table 5).

Description of the soil profile on PTP 1 – under spruce:

Ol	– 0–3 cm	– sward formed by wavy hair-grass, leaf litterfall,
Of	– 3–7 cm	– black-brown, nearly decomposed organic litterfall,
Oh	– 7–12 cm	– decomposed organic litterfall, dark brown, moist,
Ae	– 12–20 cm	– dark grey-brown, sandy, very weakly skeletal, loose,
Ep	– 20–27 cm	– grey-brown, loamy-sand, weakly skeletal, loose,
Bhs	– 27–38 cm	– dark brown-reddish, loamy-sand, loose,
Bs	– 38–70 cm	– rusty dark brown melting into ochre with increasing depth, loamy-sand, loose,
Bs/Cd	– 70 m	– yellow-brown, loamy-sand, skeletal, settled, moist.

Soil subtype is Humus Podzol, soil kind loamy-sand, humus sub-form thick mor moder. Active soil reaction significantly decreased in all three repeatedly measured horizons (Table 2). While all three horizons could be classified as medium acidic in the year 1972, the prevailing present classification is strongly acidic and in the case of

Table 5. Changes in the chemism of soils in the period 1972–1996

PTP number				Parallel				
Horizon	*A01/A02*	Ol + Of	*A03*	Oh	*A1*	Ae	*A2*	Ep
Horizon thickness (cm)	*0–5*	0–5	*5–8*	5–8	*8–13*	8–13	*13–20*	13–21
Year	*1972*	1996	*1972*	1996	*1972*	1996	*1972*	1996
pH – H_2O	*3.76*	–	*3.54*	–	*3.30*	3.6	*3.57*	3.9
pH – KCl	*2.89*	–	*2.26*	–	*2.69*	2.9	*2.99*	3.3
Cox (%)	*32.10*	36.84	*29.10*	21.65	*12.90*	6.57	*6.42*	6.70
Nt (%)	*1.75*	1.52	*1.67*	0.99	*0.61*	0.24	*0.32*	0.29
C:N	*18.3*	24.2	*17.4*	21.9	*21.1*	27.4	*20.1*	23.1
Al + H (me/100 g)	–	4.9	–	8.7	–	6.8	–	11.8
CEC (me/100 g)	–	15.0	–	15.2	–	7.9	–	13.0
S = CEC – (Al + H)	–	10.1	–	6.5	–	1.1	–	1.2
BS = V (%)	–	67.6	–	42.9	–	13.5	–	8.9

Table 6. Biochemical characteristic of soils

Milešice 12. 8. 1996	PTP number	1	2	3	Parallel
	Horizon	Ae	Ae	Ae	Ae
Respiration	(mg CO_2.100 g/h)	1.43	3.37	3.69	3.97
Ammonization	(mg NH_4^+.100 g/h)	0.00	0.00	0.00	9.22
Nitrification	(mg NO_3^-.100 g/h)	0.75	1.49	1.42	0.66
Cellulose decomposition	%	3.84	5.81	0.49	0.23

horizon Oh even very strongly acidic. Potential soil exchangeable reaction of all three horizons ranged within the interval of strongly acidic soils in the year 1972 and the year 1999 also showed a significant decrease. Horizon Of is ranging on the dividing line between strongly acidic and very strongly acidic, other horizons are classified as very strongly acidic (Table 2). All measured horizons exhibit an increased percentage of oxidizable carbon. In terms of its content, the forest floor horizons can be classified as very strongly humose, horizon Ae as strongly humose. The forest floor horizons showed a mild decrease in total nitrogen; yet they are classified as soils with a very high content of Nt. In contrast, horizon Ae exhibits an increased Nt content and can be classified as the preceding horizons – soils with the very high content of Nt. The upper humus horizons are sorptionally saturated (Of) or slightly unsaturated (Oh), horizon Ae being highly saturated, however. Actual content of exchangeable basic cations is very low. Respiration activity is medium and its value is lowest of all PTPs under study. This is a good evidence to the highest content of humus both in the mineral soil and in the forest floor horizons.

PTP 3 – under the mixture of beech and spruce:

Ol – 0–3 cm – leaf and needle litterfall, no vegetation,
Of – 3–5 cm – partly decomposed detritus with distinguishable litterfall residues, loose,
Oh – 5–8 cm – decomposed organic litterfall, brown-black, moist,
Ae – 8–20 cm – coffee brown, loamy-sand, crumbly, loose,
Bvs – 20–32 cm – ochre to yellow-reddish, sandy, skeletal, loose.

Soil subtype is Cryptopodzol Oligotrophic, soil kind loamy-sand to sandy soil (basement), humus sub-form thick mor moder. Active soil reaction hardly changed in all three repeatedly measured horizons (Table 4) and can be still classified as strongly acidic in the case of horizon Of and horizon Ae, and very strongly acidic in horizon Oh. As compared with the year 1972, the potential exchangeable soil reaction dropped by about a tenth of pH (horizons Of, Oh), and by three tenths of pH in the case of horizon Ae (Table 4). Despite the slight decrease, horizons Of and Oh can still be classified as very strongly acidic with horizon Ae having recorded a transition from the group of strongly acidic soils into the group of very strongly acidic soils. The forest floor horizons exhibit both up and down fluctuations in the representation of oxidizable carbon, which still range within the group of very strongly humose soils (horizon Of increase and horizon Oh decrease). The mild decrease in horizon Ae makes it possible to classify the horizon as strongly humose, similarly as in the year 1972. Forest floor horizons remain in the group of soils with the very high Nt content and horizon Ae shifted into the group of soils with the high Nt content (originally very high). Horizon Of is sorptionally saturated, horizon Oh is slightly unsaturated, horizon Ae is sorptionally highly unsaturated. Actual content of exchangeable basic cations is very low in all studied horizons. Respiration activity is high.

Parallel PTP in spruce pure stand at the northern edge of the reserve:

Ol – 0–3 cm – undecomposed coniferous litterfall,
Of – 3–5 cm – partly decomposed needle litterfail with recognizable original structure,
Oh – 5–8 cm – decomposed organic litterfall, brown-black, moist,
Ae – 8–13 cm – brown to greyish, sandy, moist,
Ep – 13–21 cm – light grey, sandy to loamy sand, moist,
Bhs – 21–28 cm – dark brown, loamy-sand, loose, weakly skeletal,
Bs – 28–38 cm – reddish to ochre, sandy, loose, medium skeletal.

Soil subtype is Humus Podzol, soil kind loamy-sand to sandy soil (in the base direction), humus sub-form thick mor moder. Active soil reaction exhibited a mild increase in the horizons Ae and Ep (Table 5); however, in the case of horizon Ae a transition was recorded from the group of very strongly acidic soils into the group of strongly acidic soils and horizon Ep remains classified as strongly acidic although the soil reaction improved. The increased pH values were also recorded for the potential exchangeable reaction (Table 5). Horizon Ae still shows (even with the increased value) a very strongly acidic reaction and horizon Ep can be classified as strongly acidic thanks to the increased pH. Oxidizable carbon increased in the horizon Ol+Of and dropped in horizon Oh; yet, the two forest floor horizons can be classified as very strongly humose. The value dropped to half in horizon Ae (from 12.90 to 6.57) and shifted the horizon into the group of strongly humose soils. The eluvial horizon Ep remained unchanged and is classified as strongly humose. All horizons recorded a mild decrease of total nitrogen. In spite of the fact, all horizons of the forest floor remain in the group with the very high Nt content. Horizon Ae can now be classified as a horizon with the high Nt content similarly as the eluvial horizon Ep (both with originally very high contents). The saturation of sorption complex is markedly decreasing with the increasing

Table 7. Phytocoenological table – Summary

1972 1996	Forest type	6K1		6S1		6K1		6K1	
	PTP number	1		2		3		P	
Tree class	Cover (%) *1972*	*80*		*65*		*?*		*?*	
	1996	40		5		70		70	
I	*Abies alba*	*10*	.	.	.	.	.	.	.
	Picea abies	*30*	.	.	.	.	.	.	.
II	*Abies alba*	*5*	.	*15*	.	.	20	.	.
	Fagus sylvatica	*1*	.	*15*	.	.	10	.	.
	Picea abies	*10*	30	*40*	.	.	30	.	70
III	*Fagus sylvatica*	*25*	20	.	.	.	10	.	.
	Picea abies	.	.	.	.	.	.	.	+
IV	*Picea abies*	.	.	.	5	.	.	.	.
	Sorbus aucuparia	.	+	.	.	.	.	.	.
V_{1a}	*Abies alba*	.	.	.	–	.	.	.	.
	Fagus sylvatica	.	+	.	+	.	.	.	.
	Picea abies	.	–2	.	+	.	.	.	+
	Sorbus aucuparia	.	+	.	.	.	.	.	.
V_{1b}	*Abies alba*	.	–	.	–	.	+	.	.
	Acer pseudoplatanus	.	–	.	.	.	.	.	.
	Fagus sylvatica	–	+	.	+	.	–	.	.
	Picea abies	–	.	.	–	.	–	.	+
	Sorbus aucuparia	–	.	.	–	.	.	.	.
V_2	*Abies alba*	.	.	.	.	.	–	.	.
	Fagus sylvatica	–	+	.	+	.	+	.	.
	Picea abies	–	–	.	–	.	–	.	+
EGS	Cover of non-woody undergrowth synuzia (%) *1972*	*50*		*90*		*?*		*?*	
	1996	80		95		5		10	
4/5	*Festuca rubra*	.	.	–	.	.	.	.	.
4/13	*Brachypodium sylvaticum*	.	+	.	+	.	.	.	.
5/6	*Athyrium filix-femina*	–	–	.	.	.	.	.	.
7/9	*Vaccinium myrtillus*	.	–	.	–	.	.	–	.
7/11	*Nardus stricta*	–	1	*–3*	–2	.	.	.	.
8	*Acetosella vulgaris*	–	+	–	1	.	.	.	.
9/8	*Agrostis tenuis*	*1*	.	*–2*	.	.	.	.	.
9	*Avenella flexuosa*	*–3*	–4	*1*	–3	.	1	–	1
9	*Carex pilulifera*	–	.	.	1	.	–	.	.
9	*Luzula luzuloides*	+	–2	.	–2	.	.	.	.
9	*Maianthemum bifolium*	–	–2	.	1	.	1	.	.
10/3	*Galium pumilum*	.	1	.	+	.	.	.	.
10/5	*Gymnocarpium dryopteris*	–	–	.	.	.	.	.	.
10	*Dryopteris carthusiana*	.	.	.	.	.	.	–	.
10	*Dryopteris dilatata*	.	1	.	.	.	+	.	.
10	*Oxalis acetosella*	*1*	1	*–2*	–2	.	+	–	.
10	*Rubus idaeus*	.	+	.	–	.	.	.	.
10/17	*Prenanthes purpurea*	–	.	.	.	.	.	.	.
11	*Agrostis stolonifera*	.	+	.	1	.	.	.	.
11	*Carex pallescens*	.	.	–	.	.	.	.	.
11	*Juncus effusus*	.	.	–	.	.	.	–	.
11	*Vignea ovalis*	–	+	.	1	.	.	.	–
12	*Deschampsia cespitosa*	+	.	*–3*	+	.	.	–	.
14	*Cardamine amara*	.	.	.	.	.	.	–	.
15	*Vignea cinerea*	.	.	.	.	.	.	*1*	+
16/15	*Carex nigra*	.	+	.	+	.	.	.	.
17/9	*Lycopodium annotinum*	.	–	.	–	.	.	.	.
17/10	*Soldanella montana*	–	.	.	.	.	.	–	.
17/11	*Calamagrostis villosa*	–	+2	*1*	.	.	+	*–3*	1
17	*Homogyne alpina*	–	–	.	.	.	.	.	.
17	*Luzula sylvatica*	–	.	–	.	.	.	.	–

Explanatory notes:
1) in all phytocoenological relevés, the left value in the columns (*in italics*) is data from 1972 (Pišta, Průša 1974) and the right value is data from 1996
2) in 1996, relevés were taken on 12 July
3) tree class (Randuška et al. 1986)
4) EGS – ecological group of plant species (Plíva, Průša 1969)

depth (the part beneath the eluvial horizon was not measured), which corroborates the occurring process of podzolization. The horizon Ol+Of is sorptionally saturated; Oh slightly unsaturated, Ae highly unsaturated, Ep extremely unsaturated. Actual content of exchangeable basic cations is very low. Respiration activity is high.

The communities of herb synusia, naturally poor in species, responded to the opening on PTP 1 which is at the stage of disintegration by increased total herb coverage (Table 7). Dominant position is still kept by the species *Avenella flexuosa* from EGS 9 – mildly moist, nutrient-poor. Species with originally only marginal representation such as *Luzula luzuloides*, *Maianthemum bifolium* (both species EGS 9) and *Calamagrostis villosa* from EGS 17/11 – sub-alpine/alternately moist show a higher representation thanks to the better light conditions. In contrast, the parallel plot exhibits an increased canopy density of the tree layer (spruce), to which the community responded mainly by a severe drop in the representation of the species *Calamagrostis villosa*.

Fresh Spruce-Beech with oxalis and turfted hair-grass – 6S1 (0.47 ha, 5.3%)

Scattered on four plots – mild depressions; forms a transition to water-affected soils in the eastern portion of the reserve; however, soils in this site are not water-affected. The herb layer and soil conditions are characterized on PTP 2.

Description of soil profile on PTP 2:

Ol	– 0–3 cm	– continuous turf with wavy hair-grass, leaf litterfall,
Of/Oh	– 3–7 cm	– decomposed organic litterfall, brown-black, moist,
Ae	– 7–20 cm	– dark brown, at some places melting into greyish-brown, crumbly, moist,
Bvs	– 20–35 cm	– reddish to ochre, sandy-loam, loose, moist, weakly skeletal.

Soil subtype is Cryptopodzol Mesotrophic suggesting the transition to Cryptopodzol Oligotrophic, soil kind sandy soil, humus sub-form sod moder. Active soil reaction hardly changed in the two repeatedly investigated horizons (Table 3) and can still be classified as strongly acidic. Potential exchangeable soil reaction decreased in the comparison with the year 1972 by about a tenth of pH and still remains strongly acidic (Table 3). The forest floor horizon Of/Oh shows a slight fall in the value of oxidizable carbon but is still classified as very strongly humose. The decrease of the value in horizon Ae also means a shift into the group of humose soils (originally strongly humose). Total nitrogen content in the forest floor horizon Ol/Of is very high and remains nearly un-

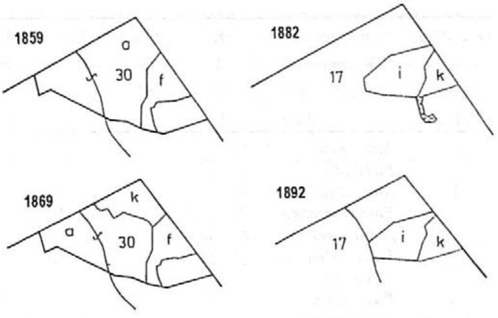


Fig. 1. Historical development of area of Milešice virgin forest

changed in the period under study. Horizon Ae exhibits a decreased percentage representation from 0.32 to 0.19% and its content of total nitrogen is now classified as high (originally very high). The forest floor horizon is sorptionally slightly unsaturated, horizon Ae is highly unsaturated. Actual content of exchangeable bases is very low. Respiration activity is high.

The ongoing disintegration of the main tree layer (stage of disintegration) and related very favourable light conditions together with the game pressure eliminated by fencing facilitated a further species differentiation of the herb layer on the PTP 2 under study. The dominant species is now *Avenella flexuosa* – EGS 9 – mildly moist, nutrient-poor, accompanied by the former dominant *Nardus stricta* from EGS 7/11 – very nutrient-poor, alternately moist; other species occurring in the site are *Luzula luzuloides* (EGS 9 – mildly moist, nutrient-poor) and *Oxalis acetosella* (EGS 10 – fresh, medium-nutrient). The originally dominant species of *Deschampsia cespitosa* from EGS 12 – moist, medium-nutrient, disappeared nearly totally and was replaced by the above mentioned species. The number of species increased from the original 11 to 15.

Fresh Spruce-Fir with oxalis – 6O1 (0.11 ha, 1.3%)

Takes up a small continuous plot in the south-eastern portion of the area and represents a transition between communities unaffected by water and permanently water-logged sites with water table reaching nearly to the top of the soil profile, particularly in periods with abundant precipitations.

Water-logged Fir-Spruce with cane – 7G3 (0.41 ha, 4.6%)

Consists of two plots in the south-eastern portion of the reserve, in its lowest parts. Soils are permanently water-logged with water table reaching up to the soil surface, particularly in spring periods. Soil subtype is peat gley. Opened parts in this site are overgrown with continuous *Calamagrostis villosa*, the regeneration of tree species (spruce) occurs only on lying stems.

MENSURATIONAL CHARACTERISTICS AND THEIR CHANGES

Tree layer changes in the reserve in the period under study are illustrated in Tabs. 8–15 and Figs. 2–10. The assessment is made by the respective tree species and by the mapped developmental stages.

Virgin forest in general

The developmental trend in the reserve is characterized by the long-term withdrawal of fir, which did not stop even after fencing the reserve (Figs. 2, 6), by the general ageing of beech population (Fig. 6) with the missing young generation, and by a more favourable age (and diameter) pattern of the spruce population. At the same time, the development of a new (youngest) beech generation has been started, be it just individually spread seedlings. Fig. 6 still does not record the coming regeneration (spruce and beech) which has not yet reached the measured dimensions.

The total number of live trees in the reserve slightly increased in the period 1972–1996 from 2,021 to 2,092 similarly as the stem volume of live trees which increased from 4,216 to 5,024 m^3 (Tables 8, 9). Conspicuous is the increase in the amount of dead timber, which doubled both in terms of tree number and basal area. Here the tree dying especially shows in the already developed stage of disintegration and also the fact that no dead wood is taken out from the fenced reserve. The increasing values of all hectare indicators (Table 9) clearly signal the developmental trend towards a better utilization of the growing space in the reserve, which was originally blocked by the heavy pressure of red deer.

Norway spruce *(Picea abies)*

All indicators of absolute values exhibit a gradual mild increase of spruce in the reserve (Figs. 7–9) the trend being given by the growing up new generation of spruce in the eastern portion of the reserve and by only individual (not massive or whole-area) dying of the most sizeable (oldest) individuals, particularly in the central and southern parts of the reserve.

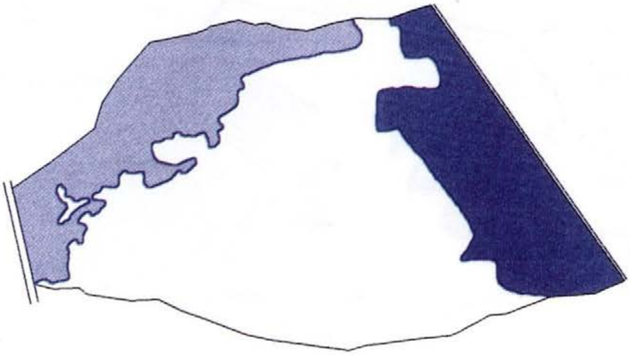
The relative representation does not signal this unambiguous trend (Fig. 2). Especially the representation by the volume of live stems shows a decrease of the relative representation from 56.1 to 54.2% despite its increase from 2,366 m^3 to 2,722 m^3. The seeming discrepancy results from a more pronounced increase of the stem volume in beech since the species exhibits a culmination of the volume increment in the trees of the main storey.

The distribution of tree numbers in diameter classes was slightly improved; yet there are not enough trees in the diameter classes 1 and 2. Nevertheless, the present trend of development suggests that even this unfavourable situation will be gradually levelled out.

European beech *(Fagus sylvatica)*

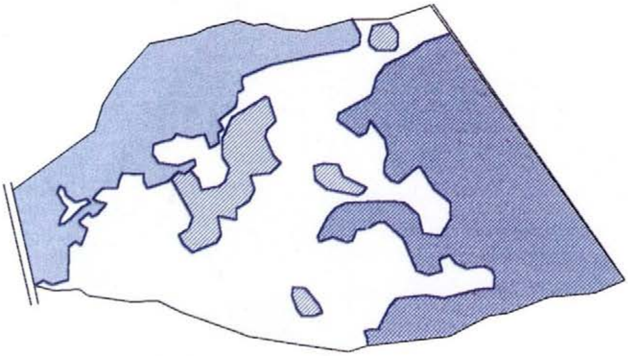
Beech is the second main tree species in the reserve. At a very mild decrease in the number of live trees (from 687 to 648) it exhibits increased basal area and stem vo-

MILEŠICE – VÝVOJOVÁ STADIA 1972 (Pišta et Průša)



■	stadium dorůstání	1,80 ha
▒	stadium „optima“ - zralosti	1,70 ha
□	stadium rozpadu	5,36 ha
	CELKEM	8,86 ha

MILEŠICE – VÝVOJOVÁ STADIA 1996



▨	stadium dorůstání - fáze dožívání	2,66 ha
▒	stadium „optima“ - zralosti	1,70 ha
□	stadium rozpadu	3,95 ha
▨	stadium rozpadu - fáze zmlazování	0,55 ha
	CELKEM	8,86 ha

TopoL 22. 9. 1999

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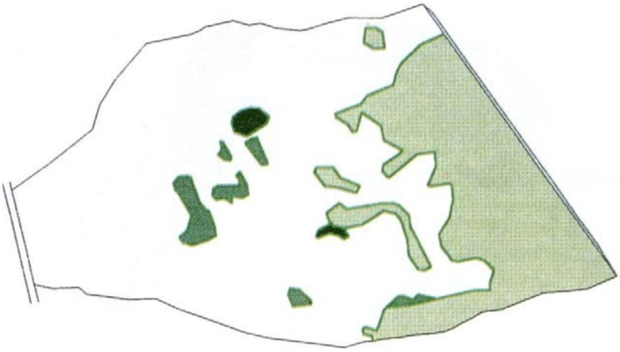
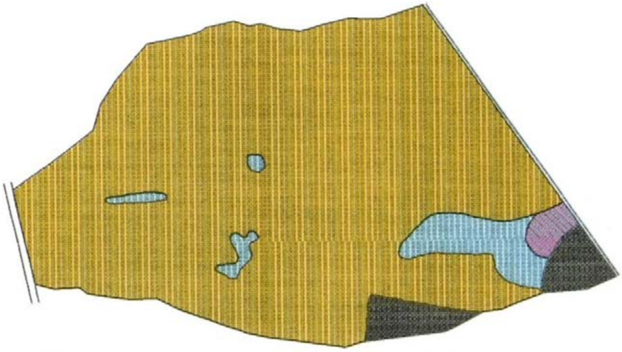
AOPK ČR, det. prac. Brno, Dr. T. VRŠKA a kol. 1999

MILEŠICE – ZMLAZENÍ 1996



■	smrk do 0,5 m	0,07 ha
▩	smrk 0,5 - 1,5 m	0,19 ha
▢	smrk 1 - 6 (převažuje 4 m)	2,31 ha
	CELKEM	2,57 ha

MILEŠICE – TYPOLOGICKÁ MAPA



▥	6K1 – kyselá smrková bučina metlicová	7,87 ha
▥	6S1 – svěží smrková bučina šťavelová s metlicí trsnatou	0,47 ha
▨	6O1 – svěží smrková jedlina šťavelová	0,11 ha
■	7G3 – podmáčená jedlová smrčina třtinová	0,41 ha
	CELKEM	8,86 ha

Topol. 22. 9. 1999

1 :5000

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MILEŠICE 1972-1996

Legend:

● Norway spruce - Picea abies

◑ silver fir - Abies alba

○ European beech - Fagus sylvatica

⊕ sycamore maple - Acer pseudoplatanus

⊗ European mountain ash - Sorbus aucuparia

—⊖ fallen tree - hard

- - ⊖ fallen tree - half-rotten

·······⊖ fallen tree - disintegrated

—+⊖ windthrow

●4 diameter class 4 = 35-44 cm

● live trees, that reached d.b.h. = 10 cm in the period 1972-1996

● trees, that died in the period 1972-1996

♉ forked tree

♉ forked tree with stub

☊ live tree with stilt roots

♁ fracture

♁ stub

∅ dead standing tree

\+ stump

⋀⋁ forest type boundary line

⋀⋁ boundary line of groups of natural regeneration in 1996

◯ ▪4 permanent typological plot

MILEŠICE - stand texture in 1972

Legend:

■	stage of growth	1,80 ha
□	stage of optimum	1,70 ha
□	stage of disintegration	5,36 ha
	TOTAL	8,86 ha

MILEŠICE - natural regeneration in 1996

Legend:

■	Norway spruce (Picea abies) 10 ... 0 - 0,5m	0,07 ha
▩	Norway spruce (Picea abies) 10 ... 0,5 - 1,5m	0,19 ha
░	Norway spruce (Picea abies) 10 ... 1 - 6m (prevailing 4m)	2,31 ha
	TOTAL	2,57 ha

MILEŠICE - stand texture in 1996

Legend:

▩	stage of growth, phase of expiration	2,66 ha
□	stage of optimum	1,70 ha
□	stage of disintegration	3,95 ha
▨	stage of disintegration, phase of regeneration	0,55 ha
	TOTAL	8,86 ha

MILEŠICE - forest types

Legend:

▥	6K1 - Acidic Spruce-Beech with Deschampsia cespitosa	7,87 ha
▥	6S1 - Fresh, Nutrient-medium Spruce--Beech with Deschampsia cespitosa	0,47 ha
▧	6O1 - Nutrient-medium Spruce-Fir with Oxalis acetosella	0,11 ha
■	7G3 - Wet Fir-Spruce with Calamagrostis villosa	0,41 ha
	TOTAL	8,86 ha

Topol. 5.1.2001

MILEŠICE – ZMLAZENÍ 1996

MILEŠICE – POROSTNÍ MAPA

Stadium rozpadu – fáze zmlazování. Absence výplně růstového prostoru v pokročilém rozpadu je ve srovnání s předcházejícím obrázkem zcela evidentní – The absence of the filler of the growth space in the advanced stage of disintegration is quite evident compared with previous picture. European beech starts to regenerate on the empty areas (not visible in this picture). Stage of disintegration – natural regeneration phase

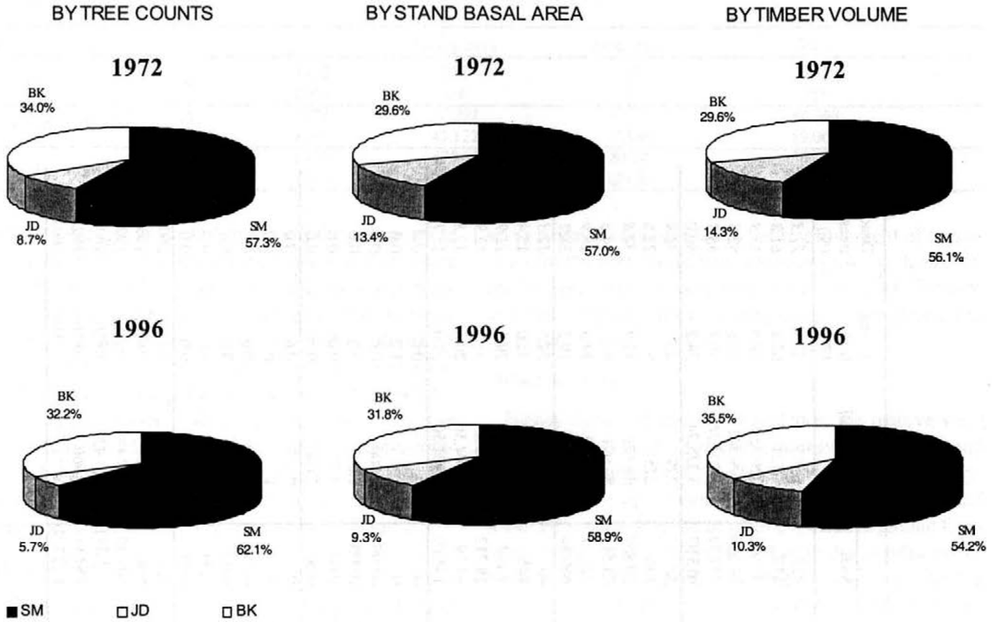
Počátek stadia rozpadu. Na podmáčených stanovištích v jihovýchodní části území se přirozená obnova převážně uplatňuje na padlých kmenech a při eliminaci nadměrných stavů jelení zvěře se na prosvětlených plochách dostavuje okamžitě – At wet stands in the south-eastern part of the study area, natural regeneration takes place mainly on fallen tree trunks. Natural regeneration comes immediately on open areas if excessive stock of red deer is lowered

Stadium „optima"– zralosti. Pomístně jednotlivě odumírající stromy v hustém korunovém zápoji stále nezajišťují dostatečný světelný požitek potřebný pro přežití jejich nové generace – Stage of "optimum" – maturity. Separate dying trees in the dense canopy closure still do not ensure sufficient light for their new generation to survive

Stadium rozpadu s opožděně počínající fází zmlazování. Rozvinutý rozpad hlavní etáže v době před oplocením (1976) umožnil rozvoj souvislých nárostů *Calamagrostis villosa*, které dnes brzdí přirozenou obnovu – Stage of disintegration with delayed beginning natural regeneration phase. Expanding disintegration of the main storey in the period before fencing (1976) enabled developing of continuous *Calamagrostis villosa* growths that block the natural regeneration nowadays

Stadium rozpadu – fáze zmlazování. Podrost smrku v pozadí je 20 let regenerující skupina dříve tlumená silným okusem, v popředí nové nárosty. Při silné účasti buku v hlavní etáži je v podrostu buk zastoupen sporadicky jednotlivými semenáčky – Norway spruce undergrowth in the background is the group regenerating for 20 years, formerly suffering from intensive browsing; there is new advance regeneration in the front. European beech creates only a very small part of undergrowth (separate seedlings) although it forms the important part of the main storey. Stage of disintegration – natural regeneration phase

Stadium rozpadu – fáze zmlazování, v pozadí postupně přecházející do stadia dorůstání. Buk v souvislých nárostech smrku zcela chybí, neboť byl totálně zkousáván jelení zvěří před oplocením, zatímco smrk lépe přežíval v bonsajovité formě a rychleji zregeneroval – European beech is totally missing in continuous spruce advance regeneration because it was totally browsed by red deer before fencing. Norway spruce – on the contrary – survived better in the dwarfed "bonsai form" and regenerated more quickly. Stage of disintegration – natural regeneration phase in the transition into stage of recruitment in the background



Legend: SM – Norway spruce (*Picea abies*), JD – silver fir (*Abies alba*), BK – European beech (*Fagus sylvatica*)

European mountain ash (*Sorbus aucuparia*) and sycamore maple (*Acer pseudoplatanus*) are joined with European beech (*Fagus sylvatica*) (their portion < 1%)

Fig. 2. The representation of living trees by species in per cent on the whole area

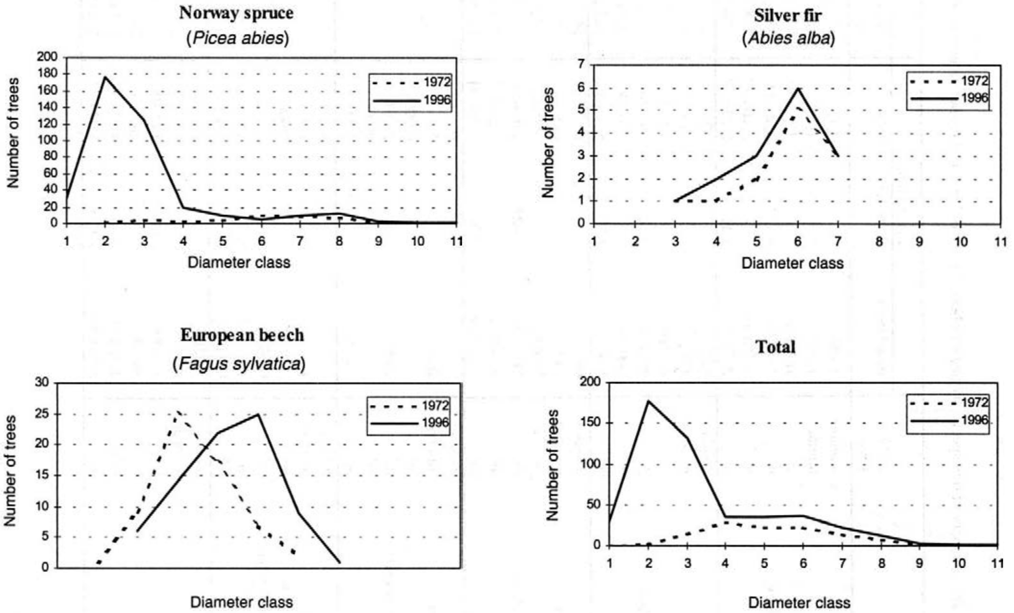


Fig. 3. The number of living trees in diameter classes in main tree species – stage of growth

Table 8. The summary of tree species by tree numbers, stand basal area and timber volume on the whole area

	1972 1996	Living trees			Dead trees				Virgin forest total	Living trees (%)	Dead trees (%)
		intact trees	fractures	total	dead standing trees	stubs	fallen	total			
Norway spruce (*Picea abies*)	*number*	*1,158*		*1,158*	*157*		*74*	*231*	*1,389*	*57.3*	*71.3*
	number	1,296	2	1,298	162	52	209	423	1,721	62.1	61.8
	m^2	*188.450*		*188.450*	*9.451*		*22.549*	*32.000*	*220.450*	*57.0*	*53.3*
	m^2	224.609	0.102	224.711	13.557	14.161	46.912	74.630	299.341	58.8	52.8
	m^3	*2,366.42*		*2,366.42*	*138.91*		*298.83*	*437.74*	*2,804.16*	*56.1*	*58.3*
	m^3	2,720.66	1.11	2,721.77	150.75	34.87	428.35	613.97	3,335.74	54.2	50.0
Silver fir (*Abies alba*)	*number*	*176*		*176*	*30*		*23*	*53*	*229*	*8.7*	*16.4*
	number	118	1	119	38	43	75	156	275	5.7	22.8
	m^2	*44.310*		*44.310*	*5.129*		*15.740*	*20.869*	*65.179*	*13.4*	*34.8*
	m^2	35.380	0.196	35.576	11.137	12.771	24.607	48.515	84.091	9.3	34.3
	m^3	*600.98*		*600.98*	*74.06*		*143.25*	*217,31*	*818.29*	*14.3*	*28.9*
	m^3	518.45	1.20	519.65	161.26	41.80	266.38	469.44	989.09	10.3	38.2
European beech (*Fagus sylvatica*)	*number*	*687*		*687*	*16*		*24*	*40*	*727*	*34.0*	*12.3*
	number	643	5	648	11	29	65	105	753	31.0	15.4
	m^2	*97.640*		*97.640*	*1.830*		*5.341*	*7.171*	*104.811*	*29.6*	*11.9*
	m^2	118.870	0.801	119.671	1.217	5.474	11.521	18.212	137.883	31.3	12.9
	m^3	*1,248.71*		*1,248.71*	*22.69*		*73.10*	*95.79*	*1,344.50*	*29.6*	*12.8*
	m^3	1,749.37	8.04	1,757.41	16.89	14.63	112.57	144.09	1,901.50	35.0	11.7
Sycamore maple (*Acer pseudoplatanus*)	*number*			*0*				*0*	*0*	*0.0*	*0.0*
	number	26		26				0	26	1.2	0.0
	m^2			*0.000*				*0.000*	*0.000*	*0.0*	*0.0*
	m^2	2.097		2.097				0.000	2.097	0.5	0.0
	m^3			*0.00*				*0.00*	*0.00*	*0.0*	*0.0*
	m^3	25.46		25.46				0.00	25.46	0.5	0.0
European mountain ash (*Sorbus aucuparia*)	*number*			*0*				*0*	*0*	*0.0*	*0.0*
	number	1		1				0	1	0.0	0.0
	m^2			*0.000*				*0.000*	*0.000*	*0.0*	*0.0*
	m^2	0.008		0.008				0.000	0.008	0.0	0.0
	m^3			*0.00*				*0.00*	*0.00*	*0.0*	*0.0*
	m^3	0.04		0.04				0.00	0.04	0.0	0.0
Total	*number*	*2,021*	*0*	*2,021*	*203*	*0*	*121*	*324*	*2,345*	*100.0*	*100.0*
	number	2,084	8	2,092	211	124	349	684	2,776	100.0	100.0
	m^2	*330.400*	*0.000*	*330.400*	*16.410*	*0.000*	*43.630*	*60.040*	*390.440*	*100.0*	*100.0*
	m^2	380.964	1.099	382.063	25.911	32.406	83.040	141.357	523.420	100.0	100.0
	m^3	*4,216.11*	*0.00*	*4,216.11*	*235.66*	*0.00*	*515.18*	*750.84*	*4,966.95*	*100.0*	*100.0*
	m^3	5,013.98	10.35	5,024.33	328.90	91.30	807.30	1,227.50	6,251.83	100.0	100.0

Table 9. Hectare indices – total

Milešice			Living trees	Dead trees	Total
Trees per 1 ha	(ind.)	*1972*	*228*	*37*	*265*
		1996	236	77	313
Stand basal area per 1 ha	(m^2)	*1972*	*37.291*	*6.777*	*44.068*
		1996	43.122	15.940	59.062
Timber volume per 1 ha	(m^3)	*1972*	*475.86*	*84.74*	*560.60*
		1996	567.08	138.55	705.63

lume (Table 8, Figs. 7–9). This indicates the culmination in the main storey of disintegration stage and a lower number of individuals at the stage of growth (sparsely scattered trees with enough growing space and with the spruce undergrowth). Regarding the gradual dying of trees in the main storey, beech shows an increased number of dead trees in the period under study, and analogically also an increased volume of dead timber in the reserve (Table 8). The curve of tree number representations in the diameter classes (Fig. 6) corroborates the general ageing of the beech population with the absence of young generation in the diameter classes 1 and 2.

Silver fir (*Abies alba*)

The long-term trend of fir withdrawal continued in the period under study (1972–1996). Fir exhibits a drop in all measured parameters (Figs. 7–9, Table 8). The total number of trees fell from 176 to 119 (Table 8) and the situation is even worse with respect to the fact that the dying occurred especially in the diameter classes 3, 4, 5 and 6, i.e. not in the oldest trees. The fencing of the reserve certainly contributed to the improvement of conditions for the survival of new advance growths; however, the fir population is very weakened with poor fertility, and has not been able of creating a new viable generation up to now.

Other species

Newly appeared species recorded in the reserve were sycamore maple (*Acer pseudoplatanus*) – 26 trees and European mountain ash (*Sorbus aucuparia*) – 1 tree. Sycamore finds employment as an interspersed species and it can be expected on the basis of experience gained from other reserves in similar sites that under conditions of eliminated game impact on arising advance growths it is going to find an employment also in the regeneration of tree species (VRŠKA et al. 1999).

Comparison by stages of development

All stages of development are recorded by means of relatively representative curves of tree frequencies in the diameter classes (Figs. 3–5).

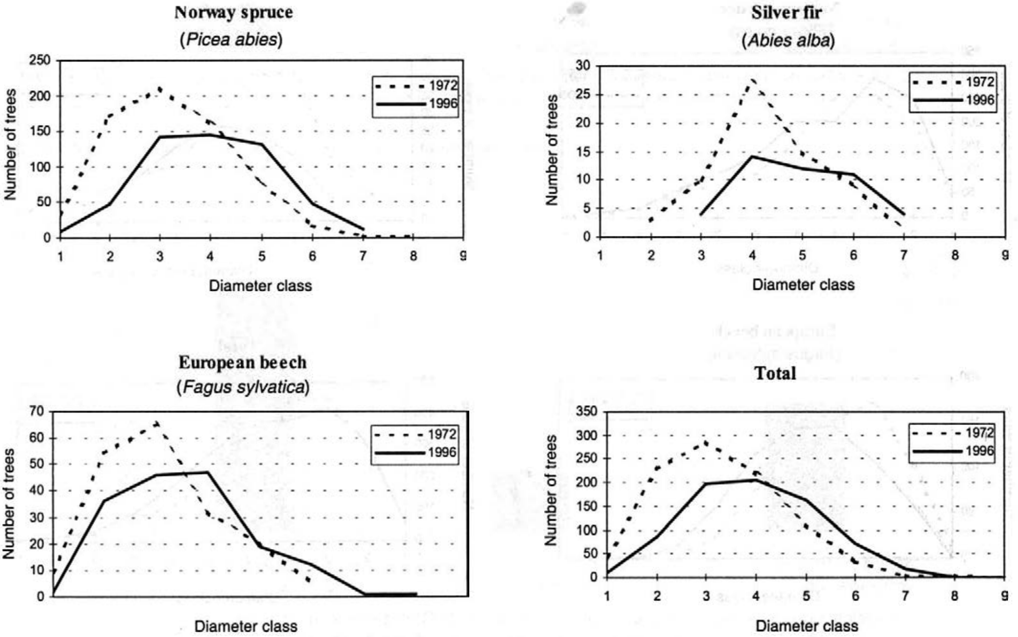
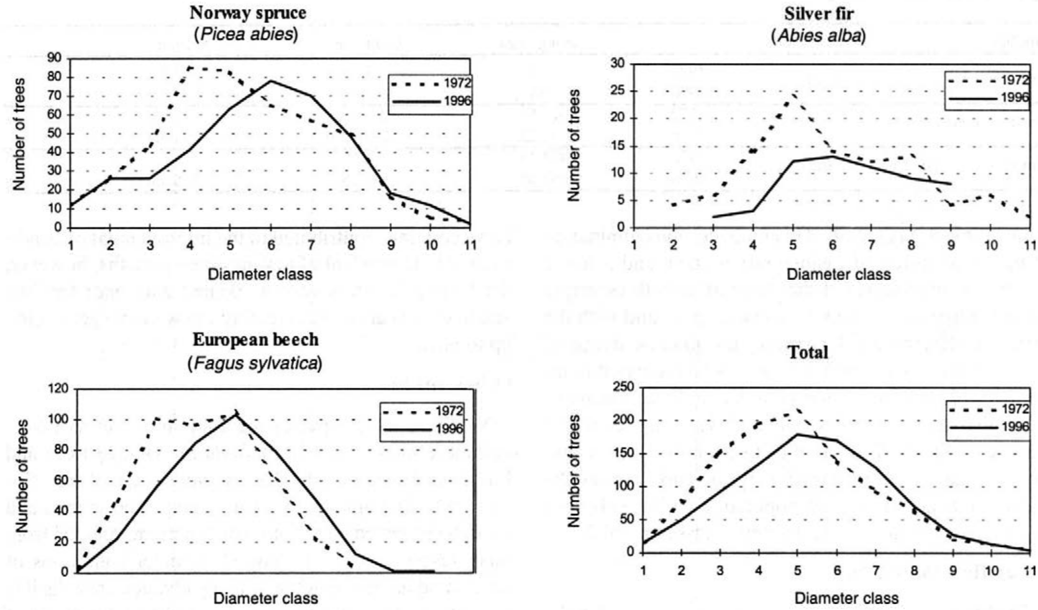


Fig. 4. The number of living trees in diameter classes in main tree species – optimum stage

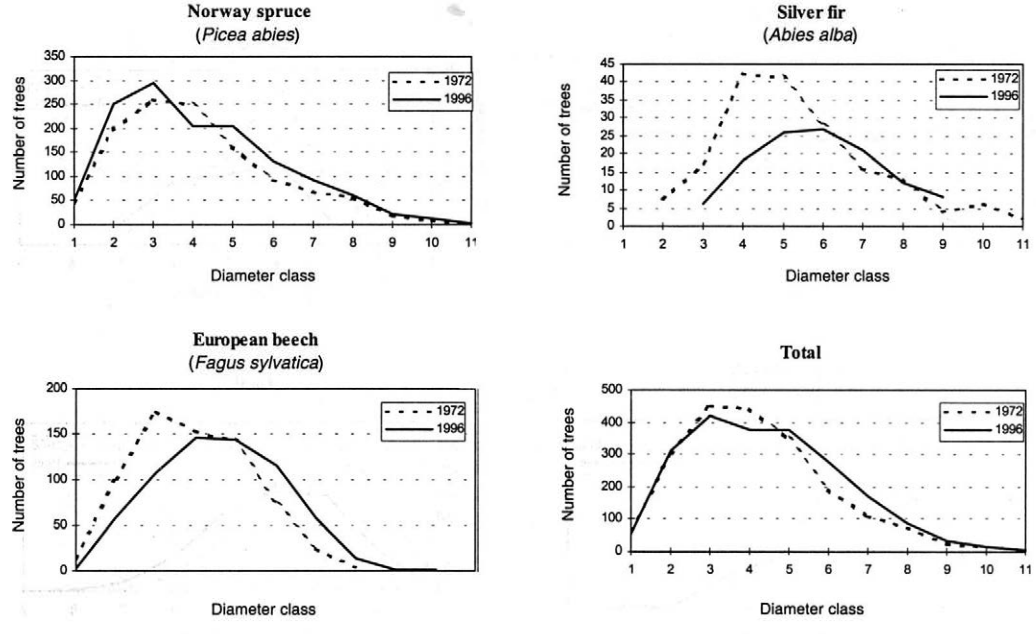

Norway spruce (*Picea abies*)

Silver fir (*Abies alba*)

European beech (*Fagus sylvatica*)

Total

Fig. 5. The number of living trees in diameter classes in main tree species – stage of disintegration

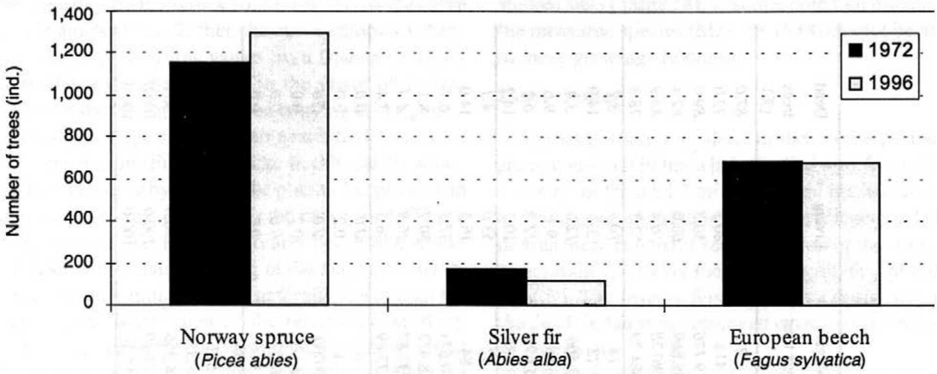

Norway spruce (*Picea abies*)

Silver fir (*Abies alba*)

European beech (*Fagus sylvatica*)

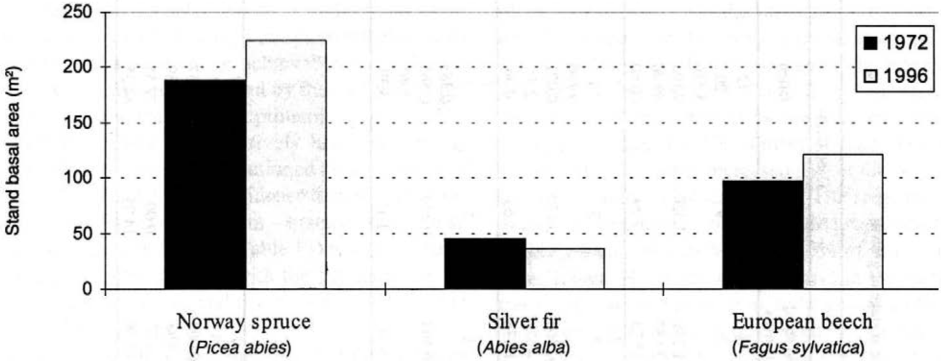
Total

Fig. 6. The number of living trees in diameter classes in main tree species – virgin forest total



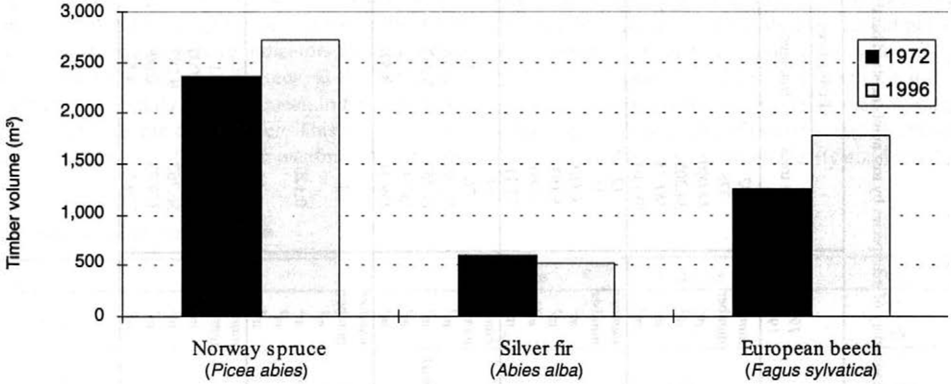
European mountain ash (*Sorbus aucuparia*) and sycamore maple (*Acer pseudoplatanus*) are joined with European beech (*Fagus sylvatica*) (their portion < 1%)

Fig. 7. Changes in numbers of living trees in main tree species



European mountain ash (*Sorbus aucuparia*) and sycamore maple (*Acer pseudoplatanus*) are joined with European beech (*Fagus sylvatica*) (their portion < 1%)

Fig. 8. Changes in stand basal area of living trees in main tree species



European mountain ash (*Sorbus aucuparia*) and sycamore maple (*Acer pseudoplatanus*) are joined with European beech (*Fagus sylvatica*) (their portion < 1%)

Fig. 9. Changes in timber volume of living trees in main tree species

Table 10. The summary of tree species by tree numbers. stand basal area and timber volume at stage of growth

		Living trees			Dead trees				Virgin forest total	Living trees (%)	Dead trees (%)
	1972 1996	intact trees	fractures	total	dead standing trees	stubs	fallen	total			
Norway spruce *(Picea abies)*	*number*	*42*		*42*	*8*		*12*	*20*	*62*	*36.5*	*87.0*
	number	378		378	7	9	20	36	414	80.3	72.0
	m²	*14.000*		*14.000*			*5.176*	*5.176*	*19.176*	*50.7*	*89.9*
	m²	34.205		34.205	1.241	4.320	9.103	14.664	48.869	60.0	82.4
	m³	*181.38*		*181.38*	*29.50*		*69.40*	*98.90*	*280.28*	*50.4*	*88.9*
	m³	381.07		381.07	15.33	7.29	80.60	103.22	484.29	52.7	78.3
Silver fir *(Abies alba)*	*number*	*12*		*12*	*1*		*1*	*2*	*14*	*10.4*	*8.7*
	number	15		15	3	3	1	7	22	3.2	14.0
	m²	*3.310*		*3.310*			*0.196*	*0.196*	*3.506*	*12.0*	*3.4*
	m²	5.183		5.183	0.864	0.770	0.071	1.705	6.888	9.1	9.6
	m³	*46.00*		*46.00*	*4.20*		*2.75*	*6.95*	*52.95*	*12.8*	*6.2*
	m³	77.11		77.11	12.74	5.65	0.36	18.75	95.86	10.7	14.2
European beech *(Fagus sylvatica)*	*number*	*61*		*61*			*1*	*1*	*62*	*53.0*	*4.3*
	number	76	1	77	3	2	2	7	84	16.3	14.0
	m²	*10.290*		*10.290*			*0.385*	*0.385*	*10.675*	*37.3*	*6.7*
	m²	17.253	0.283	17.536	0.393	0.479	0.565	1.437	18.973	30.7	8.1
	m³	*132.47*		*132.47*			*5.40*	*5.40*	*137.87*	*36.8*	*4.9*
	m³	259.31	4.57	263.88	5.31	1.11	3.39	9.81	273.69	36.5	7.4
Sycamore maple *(Acer pseudoplatanus)*	*number*			*0*				*0*	*0*	*0.0*	*0.0*
	number	1		1				0	1	0.2	0.0
	m²			*0.000*				*0.000*	*0.000*	*0.0*	*0.0*
	m²	0.126		0.126				0.000	0.126	0.2	0.0
	m³			*0.00*				*0.00*	*0.00*	*0.0*	*0.0*
	m³	1.66		1.66				0.00	1.66	0.2	0.0
Total	*number*	*115*	*0*	*115*	*9*	*0*	*14*	*23*	*138*	*100.0*	*100.0*
	number	470	1	471	13	14	23	50	521	100.0	100.0
	m²	*27.600*	*0.000*	*27.600*	*0.000*	*0.000*	*5.757*	*5.757*	*33.357*	*100.0*	*100.0*
	m²	56.767	0.283	57.050	2.498	5.569	9.739	17.806	74.856	100.0	100.0
	m³	*359.85*	*0.00*	*359.85*	*33.70*	*0.00*	*77.55*	*111.25*	*471.10*	*100.0*	*100.0*
	m³	719.15	4.57	723.72	33.38	14.05	84.35	131.78	855.50	100.0	100.0

The stage of growth (Tables 10, 11, Fig. 3) has the curve peak in Diameter Class 2; then the curve exhibits a sharp fall and dwells on very low values from Diameter Class 4 upwards the reason being trees in the phase of expiration. Spruce shows a generally true copying of the general curve of this stage since it is an absolute dominant of the new generation (Fig. 10) unlike beech and fir which are represented only by trees in the phase of expiration in the main stand storey. Comparing the curves of 1972 and 1996 we can see that it is particularly beech that shows the process of population ageing at the stage of growth. The mean hectare indicators are naturally lower than the average for the whole area of the reserve under study with the exception of the total number of live trees which is higher (great amount of young individuals). Here we always have to bear in mind that the number of trees includes only trees with d.b.h. = 10 cm and more.

The stage of optimum – maturity (Tables 12, 13, Fig. 4) slowly and evenly approaches its culmination (which can take as long as other 50 years). The general curve of tree frequencies in the diameter classes is flatter in the comparison with the year 1972 and more symmetrical towards the centre of diameter range achievable in local sites (Fig. 4). A similar trend is shown by the individual species represented at the stage of optimum – maturity. The curve of fir exhibits an excessively heavy flattening, which is given by the above mentioned disintegration of the remaining population. An evidence to the coming culmination of the stage of optimum – maturity can be also seen in the hectare indicators (Table 13) where the number of trees slightly dropped with the simultaneous increase of their basal area and reserve which amounts to 757 m^3 in the live trees.

Similarly as the stage of optimum – maturity, the stage of disintegration (Tables 14, 15, Fig. 5) clearly "profiled" itself in the period under study. The curves of frequencies in the diameter classes shifted towards higher diameter classes (Fig. 5) and the species populations reach maximum dimensions achievable in the local sites. Fir is dying markedly faster than spruce and beech, which maintain a fitted curve up to the highest dimensions achievable. The mean hectare indicators are lower than total average in the number of trees, at the same time exceeding very slightly the total mean in terms of basal area and stem volume of live trees. This is a good evidence to the presence of trees with maximum size for the studied sites (Table 14); absolute potential dimensions of the measured species (MACAR 1988) cannot be met with in these growing conditions.

Dead timber

The total volume of dead timber in the period under study increased in the whole studied area from 751 m^3 to 1,228 m^3 or from 84.7 m^3 to 138.6 m^3 per hectare (Tables 8, 9) the trend suggesting a more developed and in terms of area more extensive representation of the stage of disintegration and partly the stage of growth – phase of expiration. The reserve fencing plays a positive role since the dead timber is not removed even from marginal parts of the reserve.

All three developmental stages are very practically represented by the amount of the dead timber. The number of dead trees at the stage of growth increased from 13 to 28 per hectare (Table 11), and the volume of dead stems increased from 61.8 m^3 to 73.2 m^3 per hectare, which indicates the dying of voluminous sizeable trees in the phase of expiration. On the other hand, the volume of 85 m^3 falls upon 168 dead trees at the stage of optimum – maturity (Table 13). Here, it is mainly the intermediate trees of medium size (Tree Class III), which cannot survive the long-term shading by the fully enclosed main storey (Tree Class II). The number of dead trees and the volume of dead timber increased also at the stage of optimum – maturity (Tables 12, 13). The stage of disintegration is characteristic of the highest proportion of dead timber which amounts here to 31.5% of live stem volume. Tables 14, 15 show an increase in the number of trees and dead timber volume in the period under study. It follows out from the ratio between the number of trees and the volume of stems (dead) that the trees in question are of larger size (average 2.73 m^3 per stem).

The greatest volume of dead timber in the reserve exhibits spruce (614 m^3). Its percentual representation by tree number, basal area and stem volume is very even (Table 8), which is a good evidence of its long-term regular representation in the tree species composition of the reserve. By contrast, fir exhibits all values of percentual representation of dead trees more than twice higher than in live trees. This is most pronounced in the difference between the representation of tree species by stem volume where fir has 10.3% of live trees and 38.2% of dead trees within the reserve, which clearly confirms the per-

Table 11. Hectare indices – stage of growth

Milešice			Living trees	Dead trees	Total
Trees per 1 ha	(ind.)	*1972*	*64*	*13*	*77*
		1996	261	28	289
Stand basal area per 1 ha	(m^2)	*1972*	*15.333*		*15.333*
		1996	31.694	9.892	41.586
Timber volume per 1 ha	(m^3)	*1972*	*191.92*	*61.81*	*253.73*
		1996	402.07	73.21	475.28

Note: Data on stand basal area in dead standing trees in 1972 are missing and therefore this table is not complete

Table 12. The summary of tree species by tree numbers. stand basal area and timber volume at optimum stage

	1972 1996	Living trees intact trees	 fractures	 total	Dead trees dead standing trees	 stubs	 fallen	 total	Virgin forest total	Living trees (%)	Dead trees (%)
Norway spruce (*Picea abies*)	*number*	*671*		*671*	*124*		*14*	*138*	*809*	*72.7*	*80.7*
	number	524	1	525	118	14	83	215	740	70.8	75.4
	m^2	*61.010*		*61.010*	*2.940*		*1.689*	*4.629*	*65.639*	*70.3*	*56.5*
	m^2	74.312	0.031	74.343	4.368	1.328	6.331	12.027	86.370	72.8	60.7
	m^3	*713.36*		*713.36*	*26.84*		*21.43*	*48.27*	*761.63*	*68.8*	*52.1*
	m^3	907.78	0.25	908.03	40.70	2.10	42.57	85.37	993.40	70.6	59.1
Silver fir (*Abies alba*)	*number*	*65*		*65*	*19*			*19*	*84*	*7.0*	*11.1*
	number	45		45	15	11	17	43	88	6.1	15.1
	m^2	*9.420*		*9.420*	*1.760*			*1.760*	*11.180*	*10.8*	*21.5*
	m^2	9.047		9.047	1.987	1.053	1.744	4.784	13.831	8.9	24.2
	m^3	*132.88*		*132.88*	*21.16*			*21.16*	*154.04*	*12.8*	*22.8*
	m^3	128.91		128.91	26.62	2.00	12.30	40.92	169.83	10.0	28.3
European beech (*Fagus sylvatica*)	*number*	*187*		*187*	*8*		*6*	*14*	*201*	*20.3*	*8.2*
	number	163	1	164	3	7	17	27	191	22.1	9.5
	m^2	*16.410*		*16.410*	*0.495*		*1.312*	*1.807*	*18.217*	*18.9*	*22.0*
	m^2	18.190	0.126	18.316	0.094	0.982	1.916	2.992	21.308	17.9	15.1
	m^3	*190.24*		*190.24*	*5.17*		*18.10*	*23.27*	*213.51*	*18.4*	*25.1*
	m^3	244.44	0.45	244.89	0.87	3.13	14.18	18.18	263.07	19.0	12.6
Sycamore maple (*Acer pseudoplatanus*)	*number*			*0*				*0*	*0*	*0.0*	*0.0*
	number	8		8				0	8	1.1	0.0
	m^2			*0.000*				*0.000*	*0.000*	*0.0*	*0.0*
	m^2	0.448		0.448				0.000	0.448	0.4	0.0
	m^3			*0.00*				*0.00*	*0.00*	*0.0*	*0.0*
	m^3	4.87		4.87				0.00	4.87	0.4	0.0
Total	*number*	*923*	*0*	*923*	*151*	*0*	*20*	*171*	*1,094*	*100.0*	*100.0*
	number	740	2	742	136	32	117	285	1,027	100.0	100.0
	m^2	*86.840*	*0.000*	*86.840*	*5.195*	*0.000*	*3.001*	*8.196*	*95.036*	*100.0*	*100.0*
	m^2	101.997	0.157	102.154	6.449	3.363	9.991	19.803	121.957	100.0	100.0
	m^3	*1,036.48*	*0.00*	*1,036.48*	*53.17*	*0.00*	*39.53*	*92.70*	*1,129.18*	*100.0*	*100.0*
	m^3	1,286.00	0.70	1,286.70	68.19	7.23	69.05	144.47	1,431.17	100.0	100.0

Table 13. Hectare indices – optimum stage

Milešice			Living trees	Dead trees	Total
Trees per 1 ha	(ind.)	*1972*	*543*	*101*	*644*
		1996	436	168	604
Stand basal area per 1 ha	(m^2)	*1972*	*51.082*	*4.821*	*55.903*
		1996	60.091	11.649	71.740
Timber volume per 1 ha	(m^3)	*1972*	*609.69*	*54.53*	*664.22*
		1996	756.88	84.98	841.86

manent withdrawal of fir in the reserve. Beech has an opposite trend than fir for all values of species representation and its percentual values for live trees are more than double if compared with those for dead trees.

DEVELOPMENT OF STAND STRUCTURE AND TEXTURE

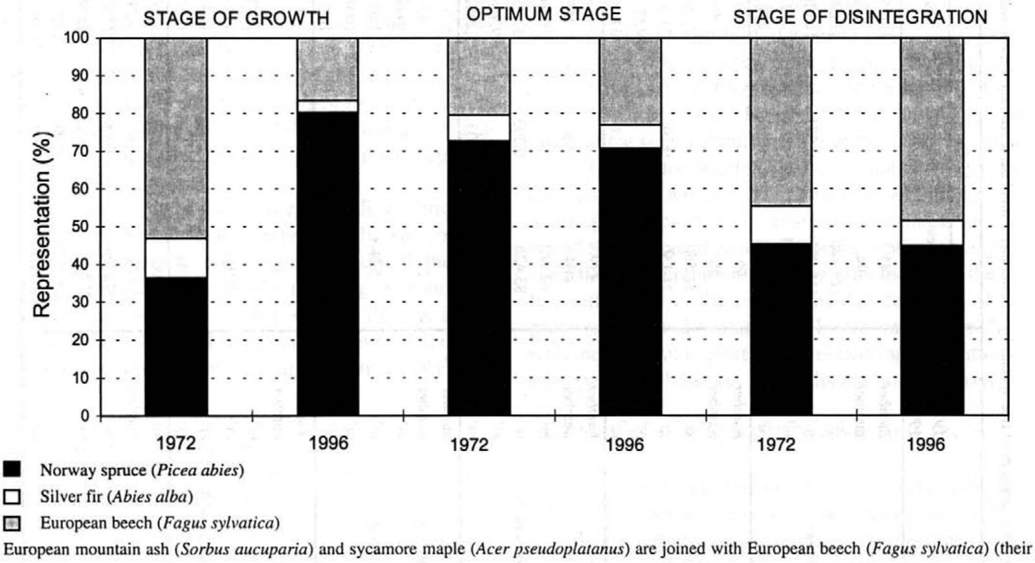
Development of natural regeneration

Development of natural regeneration in the period 1972–1996 is recorded only in one map in the coloured enclosure. In 1972, the reserve was not fenced yet and there was no regeneration of tree species due to the severe pressure of red deer. After fencing in 1976, a gradual regeneration occurs, which is however not so fast as in the forest stands of lower altitudes the reason being climatic conditions.

The eastern part of the reserve shows a gradually growing new generation of spruce (interval 1–6 m) in which a certain percentage of trees already reached the measured d.b.h. The group was recorded as early as in 1972 but its area was smaller, which is corresponded to by the continual increase of height from the western edge of the group towards the eastern edge. The average age of taller individuals in the group is about 30 years although the tree rings at d.b.h. do not reach the mentioned values – the advance growths were bitten off by game at a smaller height.

New regeneration groups arised in the course of the studied period in the central part of the area which is classified (similarly as in 1972) into the stage of disintegration. In 1996, all newly arisen plots exhibited the occurrence of spruce, beech seedlings were found only very rarely as individuals, fir seedlings were not found at all. This certainly relates to the shorter period of spruce fertility in local conditions and in the case of fir also to the fact that the number of fructifying individuals rather decreased in the period under study.

There is a very good precondition now in the fenced reserve for the further development and differentiation of natural regeneration – not only that of spruce.



European mountain ash (*Sorbus aucuparia*) and sycamore maple (*Acer pseudoplatanus*) are joined with European beech (*Fagus sylvatica*) (their portion < 1%)

Fig. 10. Changes of representation by living tree counts at developmental stages in the period 1972–1996

Table 14. The summary of tree species by tree numbers, stand basal area and timber volume at stage of disintegration

		Living trees			Dead trees				Virgin forest total	Living trees (%)	Dead trees (%)
	1972 1996	intact trees	fractures	total	dead standing trees	stubs	fallen	total			
Norway spruce (*Picea abies*)	*number*	*445*		*445*	*25*		*48*	*73*	*518*	*45.3*	*56.2*
	number	394	1	395	37	29	106	172	567	44.9	49.3
	m²	*113.440*		*113.440*	*6.511*		*15.684*	*22.195*	*135.635*	*52.5*	*54.2*
	m²	116.093	0.071	116.164	7.949	8.513	31.478	47.940	164.104	52.1	46.2
	m³	*1,471.68*		*1,471.68*	*82.57*		*208.00*	*290.57*	*1,762.25*	*52.0*	*53.1*
	m³	1,437.81	0.86	1,438.67	94.72	25.48	305.18	425.38	1,864.05	47.6	44.7
Silver fir (*Abies alba*)	*number*	*99*		*99*	*10*		*22*	*32*	*131*	*10.1*	*24.6*
	number	58	1	59	20	29	57	106	165	6.7	30.4
	m²	*31.580*		*31.580*	*3.369*		*10.415*	*13.784*	*45.364*	*14.6*	*33.7*
	m²	21.150	0.196	21.346	8.286	10.949	22.792	42.027	63.373	9.6	40.5
	m³	*432.10*		*432.10*	*48.70*		*140.50*	*189.20*	*621.30*	*15.3*	*34.6*
	m³	312.43	1.20	313.63	121.90	34.15	253.71	409.76	723.39	10.4	43.1
European beech (*Fagus sylvatica*)	*number*	*439*		*439*	*8*		*17*	*25*	*464*	*44.7*	*19.2*
	number	404	3	407	5	20	46	71	478	46.3	20.3
	m²	*70.940*		*70.940*	*1.335*		*3.644*	*4.979*	*75.919*	*32.8*	*12.2*
	m²	83.426	0.393	83.819	0.730	4.013	9.039	13.782	97.601	37.6	13.3
	m³	*926.00*		*926.00*	*17.52*		*49.60*	*67.12*	*993.12*	*32.7*	*12.3*
	m³	1,245.62	3.03	1,248.65	10.71	10.39	95.00	116.10	1,364.75	41.3	12.2
Sycamore maple (*Acer pseudoplatanus*)	*number*			*0*				*0*	*0*	*0.0*	*0.0*
	number	17		17				0	17	1.9	0.0
	m²			*0.000*				*0.000*	*0.000*	*0.0*	*0.0*
	m²	1.524		1.524				0.000	1.524	0.7	0.0
	m³			*0.00*				*0.00*	*0.00*	*0.0*	*0.0*
	m³	18.93		18.93				0.00	18.93	0.6	0.0
European mountain ash (*Sorbus aucuparia*)	*number*			*0*				*0*	*0*	*0.0*	*0.0*
	number	1		1				0	1	0.1	0.0
	m²			*0.000*				*0.000*	*0.000*	*0.0*	*0.0*
	m²	0.008		0.008				0.000	0.008	0.0	0.0
	m³			*0.00*				*0.00*	*0.00*	*0.0*	*0.0*
	m³	0.04		0.04				0.05	0.00	0.0	0.0
Total	*number*	*983*	*0*	*983*	*43*	*0*	*87*	*130*	*1,113*	*100.0*	*100.0*
	number	874	5	879	62	78	209	349	1,228	100.0	100.0
	m²	*215.960*	*0.000*	*215.960*	*11.215*	*0.000*	*29.743*	*40.958*	*256.918*	*100.0*	*100.0*
	m²	222.201	0.660	222.861	16.965	23.475	63.309	103.749	326.610	100.0	100.0
	m³	*2,829.78*	*0.00*	*2,829.78*	*148.79*	*0.00*	*398.10*	*546.89*	*3,376.67*	*100.0*	*100.0*
	m³	3,014.83	5.09	3,019.92	227.33	70.02	653.89	951.24	3,971.16	100.0	100.0

Table 15. Hectare indices – stage of disintegration

Milešice			Living trees	Dead trees	Total
Trees per 1 ha	(ind.)	*1972*	*183*	*24*	*207*
		1996	164	65	229
Stand basal area per 1 ha	(m²)	*1972*	*40.291*	*7.641*	*47.932*
		1996	41.579	19.356	60.935
Timber volume per 1 ha	(m³)	*1972*	*527.94*	*102.03*	*629.97*
		1996	563.42	177.47	740.89

Stand structure

Historical development of the stand under study – especially the long-term location within the game enclosure – had a negative influence on the development of stand structure. The oldest parts (central and southern) are slightly differentiated in terms of structure – spruce with beech and fir (Tree Class II) in the main storey and individually interspersed intermediate individuals (Tree Class III). The situation lasts long (since times before the year 1972) due to the absence of the natural regeneration.

The eastern portion is enriched with a continuous layer of trees in the interval 1.3 m – 1/2 main storey height (Tree Class IV) with the main storey (Tree Class II) having a lower stand density than that in the central and southern parts. As to the structure, this part is most diverse and nearest to natural forest. Its development is very dynamic, particularly after the reserve fencing, and a further development can be anticipated towards an even more diverse structure (terminal phase of the stage of optimum – maturity).

The northern part of the reserve has the simpliest structure. It is formed by a continuous layer of spruce with interspersed beech at the main level (Tree Class II) and with several interspersed dominant individuals of spruce and beech (Tree Class I), surviving from the former generation of trees. This portion of the area was most probably artificially regenerated since its height is very uniform and the development of the existing spruce generation was not differentiated by the gradually opening main storey of old trees.

In general, a greater stand structure differentiation occurred in the period under study with the eastern part being now structurally more complex and with the central and southern parts gradually reaching the condition, in which a pre-requisite exists (provided that the severe pressure of red deer is absent) that the development will proceed from the very beginning to a structurally more complex formation. The structurally simpliest northern part will differentiate as late as with the gradual opening of the main storey which lets the light and heat into the groundfloor parts of the stand thus facilitating the development of a new tree generation.

Table 16. Biggest living trees in the reserve in 1996

Species	d.b.h. (cm)	Height (m)
Norway	73	**45**
spruce	**105**	37
Silver	80	**40**
fir	**87**	32
European	54	**37**
beech	**68**	28

Stand texture

The stand texture was markedly refined in the period under study (1972–1996), which was made possible thanks to the permanent fencing of the reserve, which brought to a stop the "blocking" of the structural and textural development of the area. The eastern part is at the stage of growth – phase of expiration. In 1972, a prevailing portion of the area was classified as a stage of growth (without the phase of expiration) because there was no greater disintegration occurring in the dominant level. In 1996, the area of this stage was not only larger (from 1.80 ha to 2.66 ha), but also more diverse (see maps in the coloured enclosure).

The same trend – increasing texture diversity – is also exhibited by the area of the original stage of disintegration (5.36 ha in 1972). The present stage of disintegration has an area of mere 3.95 ha (with a much more articulated edge) and there are new groups of regeneration phase gradually arising within the area of the original stage of disintegration (0.55 ha in 1996), i.e. the new advance growths succeed in developing viable groups which have sufficient light supply for further growth.

Nearly without any change is on the other hand the group at the stage of optimum – maturity. Due to its uniformity (structure, species, age) the group did not exhibit any changes in terms of stand structure with the area remaining unchanged (1.70 ha) and the articulation of edges and the number of groups (1) being kept in the original condition. Differentiation can be anticipated in the future either due to the precocious disintegration of the group (abiotic and consequently biotic reasons), or along with the physical expiration of the existing generation of trees (which is however a very distant time horizon).

GENERAL ASSESSMENT AND DISCUSSION

The soil conditions did not exhibit any particularly significant changes; active and exchangeable reaction fluctuated from the original values into both directions. There are still very strongly acidic and strongly acidic soils prevailing in the reserve. The upper soil horizons are strongly to very strongly humose. Soils in the reserve are saturated to mildly unsaturated in terms of sorption, and even highly unsaturated with the increasing depth. Actual content of exchangeable basic cations is very low. The entire area exhibits a decrease in tree species synusia coverage, the phenomenon which was responded to by an increasing coverage of the herb layer and by a greater species differentiation. Changes in the representation and coverage of herb synusia species are determined by species with very similar site requirements (determinants of slightly moist up to fresh, or nutrient-poor up to nutrient-medium sites) and no significant fluctuations.

The long-term withdrawal of fir in the reserve continues. The spruce population gets more uniform even in terms of age (and diameter), and its development is stabilized. The beech population shows signs of general ageing and some spontaneous regeneration can be seen to occur as late as in the 90s by individually interspersed seedlings among the dominant spruce. The total number of trees in the area under study slightly increased similarly as the volume of live stems. Rather pronounced is the increase of dead timber – namely in terms of tree number and basal area, which was doubled in the comparison with the year 1972. Average hectare indicators of mensurational variables unambiguously suggest a better utilization of the tree layer growing space in the reserve.

The stand structure differentiation is a permanent phenomenon in the reserve with the eastern part of the reserve exhibiting a particularly differentiated structure and the developmental trend approaching the terminal phase of the stage of growth.

The studied area is passing through a period of the creation of a finer (and thus more complex) stand texture. The beneficial influence of the reserve fencing is obvious with the prevention of permanent "blocking" of the tree layer development, particularly represented by browsing on the natural regeneration. The number of developmental stages and phases is increasing and the boundaries between the stages last longer thanks to the developing diversity, which contributes to general stability and even development of the entire reserve.

The historical development outlined the ways, intensity and temporal dimensions of affecting the area under study. The long-term influencing of the stand development, particularly its location amidst the game enclosure resulted in the disturbance of natural developmental cycles of the individual tree species, in the pronounced simplification of stand structure and texture, and in a total breakage of the continuous age distribution of the populations of respective tree species. The conversion of neighbouring stands into unstable spruce monocultures (in addition to the standard attributes of unstableness – MÍCHAL 1992 – here even more destabilized by red deer barking) is a reason to a greater unstableness of the whole extensive forest complex to biotic agents (particularly to *Ips typographus*). The knowledge about the dynamics and composition of forest communities (MÍCHAL, PETŘÍČEK 1998) in the spruce-beech forest altitudinal vegetation zone indicates that the stands can develop more complex stand formations which are often shifted up to the terminal phase of the stage of growth in terms of their development, i.e. the formations in which the growing space of tree species is filled to maximum with individuals of different species (spruce, beech, fir, sycamore), different age and different social position in the stand (Tree Classes I–V).

The reserve's development recorded in the period 1972–1996 suggests a fast spontaneous return to the mentioned attributes of forest stands on the described sites. An unambiguously positive measure was the repeated fencing of the reserve, without which one could hardly speak of a spontaneous and by-man-unaffected development in the game enclosure (notwithstanding § 29, letter g), Act No. 114/1992 Gaz. on nature and landscape conservation). From the viewpoint of the further development in the reserve, there is a potential danger of the eight-toothed spruce bark beetle (*Ips typographus*) gradation in neighbouring spruce monocultures, which would generate a much greater pressure on the existing population of Norway spruce in the reserve than in the mixed natural forests on larger areas. A fast sanitation of trees infested with the spruce bark beetle is therefore most desirable in these unstable monocultures since the 9 hectares of the reserve unaffected by man will never make it possible to envisage a normal functioning of the current processes of self-regulation in the natural forests on the described sites.

Despite the so far unfavourable development of the population of silver fir and the present absence of natural regeneration, there are possibilities now for its regeneration (favourable light conditions at the stage of disintegration, protection of seedlings from browsing). An opportunity offers itself to study a probable spontaneous return of the species into the reserve's forest community. An active care of its genepool and adequate representation in the stands should be resolved in the neighbouring stands of the commercial forest with the reserve itself serving as a reference plot on which the spontaneous development of tree species occurs with all its attributes.

Beech which is permanently finding its place in the new generation of tree species – although at low numbers – does not need any special care in the reserve.

CONCLUSIONS FOR FUTURE DEVELOPMENT OF THE AREA

With respect to the unique character of the Milešice Virgin Forest Nature Reserve as a natural forest situated in the most important sites of the Šumava Mts. (Bohemian Forest), its developmental tendencies and potential risks of leaving the present trajectory of development, the following measures have been proposed:

- To maintain the fencing in perfect condition, to make fast repairs in parts damaged by fallen trees.
- To do no interventions into the reserve's development (no underplanting, selection of advance growths, felling for any purpose, etc.).

- To carry out structural measures in stands adjacent to the reserve (226A, 222C1/2, C3) in order to support a more diverse stand texture.
- To underplant fir (in groups) at mildly opened places in stands adjacent to the reserve with active protection against browsing; to introduce beech into gaps; to regenerate spruce from its natural regeneration.
- To carry out consistent sanitation of trees infested by eight-toothed spruce bark beetle (*Ips typographus*) in neighbouring spruce monocultures and thus protect the reserve from the unnaturally severe pressure of this biotic agent.

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ABSTRAKT: V letech 1972 a 1996 bylo v přírodní rezervaci Milešický prales provedeno opakované podrobné měření za účelem sledování vývojových změn pralesovitého porostu. V mapě byly zobrazeny a opětovně měřeny stojící i ležící stromy, mapovány lesní typy, vývojová stadia a stav přirozeného zmlazení. Dále byly provedeny fytocenologické zápisy, vykopány a popsány půdní sondy a zhotoveny směrové fotografické záběry. Venkovní šetření i zpracování výsledků z let 1972 a 1996 byly provedeny podle stejné metodiky. Výsledky prokázaly dlouhodobé okyselování půd a postupný návrat člověkem nepřímo ovlivňovaného lesního společenstva na vývojovou trajektorii přírodního lesa. Tento návrat je charakterizován tvorbou složitější porostní struktury a jemnější porostní textury, postupným nárůstem objemu živého i odumřelého dřeva a postupnou diferenciací nárostů.

Klíčová slova: dynamika; monitoring; prales

Půdní poměry nedoznaly závažnějších změn, aktivní i výměnná půdní reakce se pohybovaly obousměrně od původních hodnot. V rezervaci stále převažují velmi silně kyselé a silně kyselé půdy. Svrchní půdní horizonty jsou silně až velmi silně humózní. Půdy v rezervaci jsou ve svrchních horizontech sorpčně nasycené až mírně nenasycené, s přibývající hloubkou postupně až vysoce nenasycené. Okamžitý obsah výměnných bazických kationů je velmi nízký. Celoplošně došlo k poklesu pokryvnosti synuzie dřevin, na což reagovalo bylinné patro zvýšením pokryvnosti a větší druhovou diferenciací. Změny v zastoupení a pokryvnosti druhů synuzie bylin jsou determinovány druhy s velmi podobnými stanovištními nároky – mírně vlhká až čerstvá/chudá až středně bohatá stanoviště – a nedochází k žádným výrazným výkyvům.

Pokračuje dlouhodobý ústup jedle v rezervaci. Populace smrku je věkově (i tloušťkově) vyrovnanější a vývojově stabilizovaná. Populace buku celkově stárne a teprve v devadesátých letech 20. stol. dochází ke spontánnímu zmlazení buku jednotlivě vtroušenými semenáčky mezi dominantním smrkem. Mírně se zvýšil celkový počet stromů ve sledovaném území stejně jako objem živých kmenů. Výrazný je nárůst odumřelého dřeva – zejména počtu stromů a výčetní základny, který činí dvojnásobek hodnoty z roku 1972. Průměrné hektarové ukazatele dendrometrických veličin jednoznačně poukazují na lepší využití růstového prostoru dřevinného patra v rezervaci.

Trvale dochází k diferenciaci struktury porostu a zejména východní část rezervace je strukturálně velmi diferencovaná a vývojový trend spěje k terminální fázi stadia dorůstání.

Sledovaná plocha prochází obdobím tvorby jemnější (a tedy složitější) textury porostu. Zcela prokazatelně je i zde vidět kladný vliv oplocení rezervace a zamezení trvalého „blokování" vývoje dřevinného patra, zejména okusem přirozeného zmlazení. Zvětšuje se počet skupin různých vývojových stadií a fází, díky utvářející se členitosti se prodlužují hranice mezi stadii, což přispívá k celkové stabilitě i vývojové vyrovnanosti celé rezervace.

Historický vývoj naznačil způsoby, intenzitu i časové dimenze ovlivnění sledovaného území. Dlouhodobé ovlivnění vývoje porostu, zejména jeho poloha uprostřed obory pro jelení zvěř, způsobily narušení přirozených vývojových cyklů jednotlivých druhů dřevin, výrazné zjednodušení porostní struktury i textury a zpřetrhání kontinuálního věkového rozložení populací jednotlivých druhů dřevin. Přeměna okolních porostů na labilní smrkové monokultury (kromě standardních atributů lability – MÍCHAL 1992 – zde ještě více destabilizované loupáním jelení zvěře) je příčinou větší lability celého rozsáhlého lesního komplexu vůči biotickým činitelům (zejména *Ips typographus*). Z poznatků o dynamice a složení lesních společenstev (MÍCHAL, PETŘÍČEK 1998) ve smrkobukovém lesním vegetačním stupni vyplývá, že porosty dokážou vytvářet složitější porostní útvary, často vývojově posunuté až do terminální fáze stadia dorůstání. Tedy útvary, kdy růstový prostor dřevin je maximálně vyplněn jedinci různých druhů (smrk, buk, jedle, klen), různého věku, různého sociálního postavení v porostu (stromové třídy I–V).

Vývoj rezervace zachycený v periodě 1972–1996 naznačuje, že dochází k rychlému spontánnímu návratu k uvedeným atributům lesních porostů na popisovaných stanovištích. Jednoznačně pozitivním krokem bylo opětovné oplocení rezervace, bez něhož nelze v oboře hovořit o samovolném, člověkem neovlivněném vývoji (nehledě na § 29, písm. g zákona 114/1992 Sb., o ochraně přírody a krajiny). Z hlediska dalšího vývoje rezervace je významné potenciální nebezpečí gradace populace lýkožrouta smrkového (*Ips typographus*) v okolních smrkových monokulturách, která by vytvořila mnohonásobně větší tlak na dosavadní populaci smrku v rezervaci, než by bylo možné ve smíšených přírodních lesích na větších rozlohách. Proto je nanejvýš žádoucí provádět v těchto labilních monokulturách rychlou asanaci aktivních kůrovcových stromů. Necelých 9 ha plochy rezervace v člověkem narušeném stavu v žádném případě neumožňuje kalkulovat s fungováním běžných autoregulačních pochodů v přírodních lesích na popisovaných stanovištích.

I přes dosavadní nepříznivý vývoj populace jedle bělokoré nyní vznikají možnosti pro její obnovu (vhodné světelné podmínky ve stadiu rozpadu, ochrana semenáčků před okusem), a tím se nabízí možnost sledovat možný spontánní návrat této dřeviny do lesního společenstva v rezervaci. Aktivní péče o její genofond a zastoupení v porostech by tak měla být řešena v okolních porostech hospodářského lesa a samotná rezervace by měla sloužit jako referenční plocha, na které probíhá spontánní vývoj dřevin se všemi jeho atributy.

Buk, který se sice v malém množství, ale trvale uplatňuje v nové generaci dřevin, nevyžaduje v rezervaci zvláštní péči.

Vzhledem k jedinečnosti PR Milešický prales jako objektu přirozeného lesa na plošně nejvýznamnějších stanovištích Šumavy, jeho vývojové tendenci a potenciálním rizikům vybočení ze současné vývojové trajektorie, je navrženo:

- udržovat oplocení v bezvadném stavu, rychle opravovat poškozené části po pádu stromů,
- nezasahovat do vývoje rezervace (neprovádět žádné podsadby, selekce nárostů, těžby za jakýmkoliv účelem apod.),
- v porostech přiléhajících k rezervaci (226 A 1, 222C1/2, C3) provádět strukturální zásahy za účelem tvorby složitější porostní struktury,
- v jemně prosvětlených místech porostů přiléhajících k rezervaci provádět podsadbu jedle (v hloučcích) s aktivní ochranou proti okusu, v kotlících vnášet buk, smrk obnovovat z přirozeného zmlazení,
- v okolních smrkových monokulturách provádět důslednou asanaci stromů napadených lýkožroutem smrkovým (*Ips typographus*) a chránit tak rezervaci vůči nepřirozeně vysokému tlaku tohoto biotického činitele.

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Production and vertical distribution of fine and small roots in Japanese black pine on sandy soil

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ABSTRACT: Fine and small root biomass, its vertical distribution and production was investigated in two Japanese black pine (*Pinus thunbergii* Parl.) stands of different age growing on a deep sandy soil. Larger fine and small root biomass was determined in the younger stand (151.4 g/m^2) than in the older one (118.5 g/m^2). In the older stand, biomass of fine and small roots decreased linearly with a soil depth. Through the period from May 1998 to October 1999, the fine root production in the younger stand was twice as high production in the older stand. The positive effect of fertilization on the fine and small root as production was observed in the younger stand at the soil layer of 10–20 cm.

Keywords: *Pinus thunbergii*; root biomass; root production; vitalizing fertilization

Roots are important for a tree to anchor it, to absorb water and nutrients from the soil, they are the place to store reserves, and to synthesize growth hormones. Fine and small roots represent a small part of the tree root biomass; however, they are a substantial part of its length (ROBERTS 1976). Fine roots are defined as fractions of the root system with less than 0.2 cm in diameter (some authors consider diameter of less than 0.1 cm) and small roots are defined as fractions with 0.2–0.5 cm in a diameter (BÖHM 1979). They are physiologically the most active elements of the tree root system in the process of water and nutrient absorption from the soil (KOZLOWSKI, PALLARDY 1997).

VOGT et al. (1998) indicate that whilst the methods to research coarse roots are simple and uncontroversial, the studies of fine and small roots require more complex methods, and sometimes a combination of several methods is required. Complexity to research small and particularly fine roots is caused by high root growth dynamics, when the new roots are growing and simultaneously the old roots are dying. Some authors (e.g. KOZLOWSKI, PALLARDY 1997) characterize them as "short-lived roots", meaning the roots with a short life expectancy. Another problem in fine and small root research is a great variability of their biomass in time (especially in accordance with climatic conditions) and in space (soil conditions' dependence). PERSSON (1996) recommended three basic methods to research fine and small roots: a) soil-core sampling, b) in-growth bags, and c) video record in so-called minirhizotrone. According to VOGT et al. (1998), the soil-core sampling is the most appropriate to determine the fine and small root biomass, and its spatial distribution. In-growth bags held well when determining the root production, as well as when examining impacts of soil conditions (e.g. different concentrations of nutrients or toxins) on fine and small root growth.

Several factors affecting the production and spatial distribution of fine and small tree roots were studied. Some studies were concerned with an effect of forest management, mainly tending and fertilization (SANTANTONIO, SANTANTONIO 1987). KEYES and GRIER (1981) studied the influence of site conditions and PERSSON et al. (1995) impacts of changes in nutrient and water content in soil on the fine and small root biomass. Fine roots were used as a sensitive stress indicator in trees, specifically in the case of soil acidification (BAUCE, ALLEN 1992). Surprisingly little information is available about the changes in root biomass and its spatial distribution according to stand age. This problem can be solved for instance by parallel research of tree stands of a different age but of the same climatic and soil conditions. Another important, but rarely researched area is seasonal changes in root biomass. This type of research could be interesting mainly in spring, when after the dormancy the metabolic processes in tree organisms are reactivated and become intensive.

The Japanese black pine (*Pinus thunbergii* Parl.) is one of the most frequently found conifers in Japan. It grows in the whole country, except for its northernmost island – Hokkaido. After World War II to a large extent, it was planted mainly on sandy soils at the seaside where it protected the soil from wind erosion. The Japanese black pine is easy on nutrients and moisture. On sandy soils, it has typically well developed root systems, both vertical and horizontal. Therefore, it resists storms frequently coming from the seas.

The objective of this paper is to determine biomass, that means the dry weight of living fine and small roots of the Japanese black pine, and their vertical distribution in stands of different age. Monthly changes in fine and small root biomass in the first half of the vegetation season were studied, and the impact of vitalizing fertilization on root production was evaluated.

MATERIALS AND METHODS

The research was conducted in two Japanese black pine stands of different age, 40 and 17 years old (hereinafter the older and the younger stand, respectively). Both stands grew on a deep sandy soil, previously used for agricultural purposes. The same technological processes were used when establishing both these stands. Three-year-old seedlings were manually planted at a spacing 1.3 × 1.5 m (or about 5,100 plants per 1 hectare). Both stands were located next to each other, about 2 km from the Japan Sea, approximately 10 km from Tsuruoka town, in the north-western part of the Honshu Island in Japan (latitude 38°49′ N, longitude 139°45′ E, altitude 30 m a.s.l.) (Fig. 1). The average annual temperature in the last ten years was 12.6°C and the cumulative annual precipitation was 1,811 mm. The stands belonged to a protective forest category with their main function to protect soil from erosion caused by frequent winds coming from the Japan Sea. The stands were monocultures with only a rare incidence of deciduous trees (*Fagus* sp. and *Quercus* sp.). The basal area of the older stand was 34.5 m^2/ha containing 1,022 trees per ha, with mean diameter at breast height of 20.8 cm. The LFH (litter, fermentation, and humus) horizon was 4.4 cm thick. The basal area of the younger stand was 28.5 m^2/ha containing 3,565 trees per ha, with mean diameter at breast height of 10.1 cm. The LFH horizon was 3.9 cm thick. In both stands, the LFH horizon consisted mainly of undecomposed, or partially decomposed residues with a thin humus layer. The layer of mineral soil was vertically homogeneous, very thick, comprising sand without any skeleton.

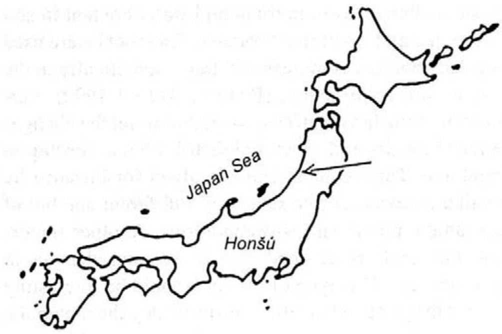

Fig. 1. The arrow on the map of Japan indicates approximate position of the study site

The field work was done in the years 1998 and 1999. Two methods: soil cores and in-growth bags were used to study the fine and small root biomass. An auger made of stainless steel of 4.2 cm in a diameter was used to obtain the soil core samples.

The in-growth bags were 20 cm high with 8.5 cm in diameter. They were made of a nylon net with mesh size of 0.55 cm. Soil-core sampling, as well as in-growth bags distribution was done randomly on a 50 × 50 m partial plot.

The first soil-core sampling was done in June 1998 to determine the fine and small root biomass and their vertical distribution. The samples were taken up to a depth of 50 cm of mineral soil. From the older stand 200 samples, and from the younger stand 90 samples were taken. Each soil core was separated into the LFH horizon and five sub-samples of mineral soil (depth of 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, and 40–50 cm). Until further processing, the samples were stored in plastic bags in a freezer at a –20°C temperature. The living fine and small roots measuring ≤ 0.5 cm in diameter were manually separated from the thawed samples. To differentiate the pine roots from other plant species, characteristics such as color, smell, morphology, existence of root hairs and the wood structure were employed. The roots considered to be alive (meaning living at the time of soil sample collection) were typical by their high resilience, flexibility, good adhesion between the cortex and the stele, and their characteristic color. All dead roots, as well as those roots from other plants were excluded from further studies. The living roots were sorted into two groups (fine roots < 0.2 cm in diameter, and small roots 0.2–0.5 cm) and rinsed in water. They were dried for constant weight in an oven at a 70°C temperature (the fine roots for 24 hours, and the small roots for 48 hours). The dried roots were weighed to the nearest 1 mg. Based on the surface of soil samples, the fine and small root biomass per m^2 by particular soil layers was calculated.

Subsequent samples of soil cores were taken in 1999, at the end of April, May, June and July, respectively. To study monthly changes in the fine and small root biomass, a layer of mineral soil (depth of 0–20 cm) was examined. Monthly, 128 samples were taken from the older stand and 100 samples from the younger stand. Each soil sample was separated into two sub-samples (depth of 0–10 cm and 10–20 cm), and subjected to the same examination as the samples taken in June 1998.

To study the impacts of vitalizing fertilization on root production, in-growth bags were utilized. Two substrates, a control and a fertilized soil were used. Soil from stu-

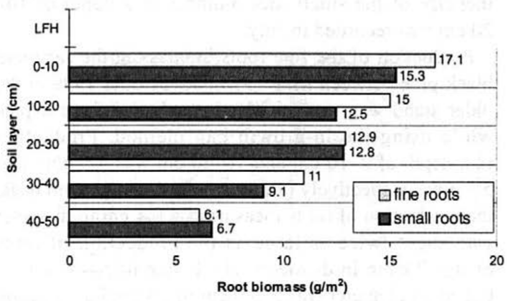

Fig. 2a. The vertical distribution of fine ands small root biomass in the 40-year-old stand of Japanese black pine

died stands cleaned of any roots, was used in this part of the study. 100 g of Hyponex® per 0.01m^3 of soil was used as a fertilizer, containing 6% N, 40% P, 6% K and 15% Mg. In the stands, the in-growth bags were put into holes 20 cm deep with 8.5 cm diameter, and filled with soil substrates. In both stands, 20 control and 20 fertilized in-growth bags were used so that their upper surface matched the border line between the LFH horizon and the mineral soil. An adequate layer of humus and litter was used to cover the in-growth bags. The in-growth bags were installed into soil at the end of May 1998 and were taken out at the end of October 1999. Each in-growth bag was separated into two sub-samples (depth of 0–10 cm, and 10–20 cm). The samples were stored and the roots subsequently separated in the same way as the soil cores. The only exception was that roots were divided into three categories according to their thickness: < 0.1cm, 0.1–0.2 cm, and 0.2–0.5 cm. In 0.1–0.2 cm, and 0.2–0.5 cm diameter classes, also the root length was measured. The roots were rinsed in water, and handled in the same way as for the soil-core samples. Roots biomass per 1 m^2 was calculated, and a linear correlation and Student's *t*-test were used for statistical analysis.

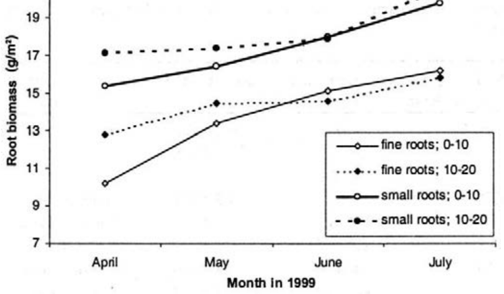

Fig. 3a. The development of fine and small root biomass in the 40-year-old stand of Japanese black pine in the soil layers of 0–10 cm and 10–20 cm

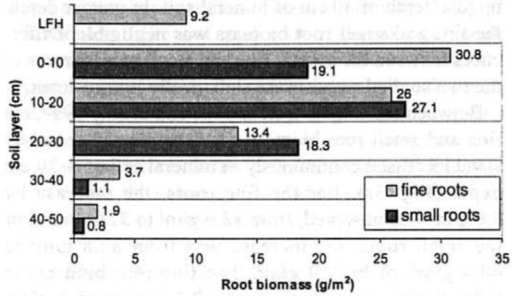

Fig. 2b. The vertical distribution of fine and small root biomass in the 17-year-old stand of Japanese black pine

RESULTS

In June 1998 in the old stand, 62.1 g/m^2 of fine root, and 56.4 g/m^2 of small root biomass of Japanese black pine were found. The largest part of fine and small root biomass was in mineral soil in a depth of 0–10 cm with 17.1 g/m^2 and 15.3 g/m^2, respectively (Fig. 2a). In the LFH horizon, no pine roots were found, but many roots of a variety of herbaceous plants were present. Root biomass decreased with the depth of mineral soil. This relationship can be expressed by linear correlation ($y = -0.26x + 18.90$, $r = 0.97$, $P < 0.01$ for fine roots, and $y = -0.19x + 15.95$, $r = 0.94$, $P < 0.05$ for small roots). Extrapolations from this linear model showed that root biomass in deeper mineral soil layers than 50 cm represented about 15% of an overall root biomass.

In the younger stand, 85.0 g/m^2 of fine roots and 66.4 g/m^2 of small roots were found. The largest portion of fine root biomass (30.8 g/m^2) was found in mineral soil in a depth of 0–10 cm (Fig. 2b). The largest portion of small roots (27.1 g/m^2) was found in a depth of 10–20 cm. Relatively few fine roots (9.2 g/m^2) and hardly any small roots were found in the LFH horizon. Further examination showed that the roots were well developed

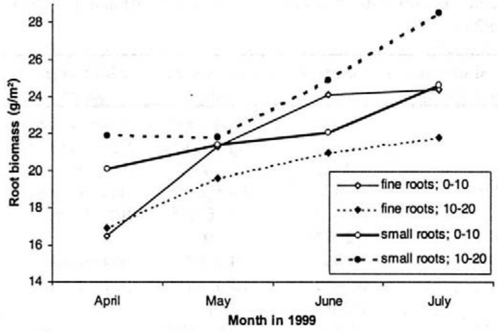

Fig. 3b. The development of fine and small root biomass in the 17-year-old stand of Japanese black pine in the soil layers of 0–10 cm and 10–20 cm

up to a depth of 30 cm of mineral soil. In greater depth, the fine and small root biomass was negligible. Differences between the overall fine and small root biomass of the two studied stands were statistically insignificant.

Between the end of April and the end of July 1999, the fine and small root biomass of black pine in the older stand increased continuously in mineral soil of 0–20 cm depth (Fig. 3a). For the fine roots, the increase by 9.0 g/m^2 was observed, from 23.0 g/m^2 to 32.0 g/m^2. For the small roots, the increase was from 32.5 g/m^2 to 40.4 g/m^2, or by 7.9 g/m^2. The fine root biomass in a depth of 0–10 cm grew from 10.2 g/m^2 to 16.2 g/m^2, and in a depth of 10–20 cm, it grew from 12.8 g/m^2 to 15.8 g/m^2. The small root biomass in a depth of 0–10 cm increased from 15.4 g/m^2 to 19.8 g/m^2, and in a depth of 10–20 cm from 17.1 g/m^2 to 20.6 g/m^2. Thus, a larger increase of the root biomass was detected in a depth of 0–10 cm compared to a depth of 10–20 cm.

In the younger stand, the root biomass grew continuously in a depth of 0–20 cm mineral soil through the observed season (Fig. 3b). The fine root increase was from 33.4 g/m^2 to 46.2 g/m^2, or by 12.8 g/m^2, while the small roots increased from 42.0 g/m^2 to 53.1 g/m^2, or by 11.1 g/m^2. The fine root biomass in a depth of 0–10 cm increased from 16.5 g/m^2 to 24.4 g/m^2, and from 16.9 g/m^2 to 21.8 g/m^2 in a depth of 10–20 cm. The small root biomass in a depth of 0–10 cm increased from 20.1 g/m^2 to 24.6 g/m^2, and from 21.9 g/m^2 to 28.5 g/m^2 in a depth of 10–20 cm. Thus also in the younger stand, increase of the fine root biomass in a depth of 0–10 cm was greater than that in a depth of 10–20 cm. The situation with small root biomass was opposite. Development of the root biomass in both stands had a similar trend. While the greatest increase of the fine root biomass in a depth of 0–10 cm was recorded in May, the greatest increase of the small root biomass in a depth of 10–20 cm was recorded in July.

Production of the fine roots biomass in the Japanese black pine between May 1998 and October 1999 in the older stand was very similar in both examined depths while using the in-growth bag method. Production in a depth of 0–10 cm and 10–20 cm was 4.6 g/m^2 and 5.3 g/m^2, respectively (Table 1a). In the in-growth bags, the production of roots measuring < 0.1 cm in diameter was about twice as large as the production of roots of 0.1–0.2 cm in diameter. The length of roots of 0.1–0.2 cm in diameter was 573.0 cm/m^2. A similar situation was in the in-growth bags with fertilized soil substrate. The results indicate that the fertilization did not affect the root production in the older stand, since the differences between biomasses in control and fertilized soils were not statistically significant.

The fine root production in the younger stand was almost identical in a depth of 0–10 cm and 10–20 cm, with values of 9.7 g/m^2 and 10.3 g/m^2, respectively (Table 1b). In the younger stand, about twice as much of the root biomass measuring < 0.1 cm in diameter was found as that of root biomass of 0.1–0.2 cm. The length of roots of 0.1–0.2 cm in diameter was 1,363.0 cm/m^2. Similar amount of the fine root biomass was in a depth of 0–10 cm in both control and fertilized substrate (9.7 g/m^2, and 10.1 g/m^2, respectively). The stimulating effect of fertilization was observed only in the layer of 10–20 cm, where the fine root biomass was twice larger than the control substrate (a statistically significant difference of $P < 0.01$). In addition to fine roots (20.2 g/m^2), in a layer of 10–20 cm also small roots appeared with biomass of 5.1 g/m^2, or 224.8 cm/m^2. The value of the small root biomass in a depth of 0–10 cm in the fertilized substrate represented only about a tenth of the value of the small root biomass in a 10–20 cm depth. Comparison of the results from these two stands showed that in the younger

Table 1a. The fine and small root production (average ± standard deviation) by diameter classes in the 40-year-old stand of Japanese black pine in the control soil substrate at depths of 0–10 cm (C10) and 10–20 cm (C20) cm, as well as in the fertilized soil substrate at depths of 0–10 cm (F10) and 10–20 cm (F20)

Soil substrate and soil depth	Diameter class (cm)	Root biomass (g/m^2)	Root length (cm/m^2)
C10	< 0.1	3.1 ± 1.8**	not measured
	0.1–0.2	1.5 ± 0.8*	275.9 ± 184.3**
	0.2–0.5	0	0
C20	< 0.1	3.4 ± 2.0**	not measured
	0.1–0.2	1.9 ± 1.1*	297.1 ± 206.8**
	0.2–0.5	0	0
F10	< 0.1	3.1 ± 2.0**	not measured
	0.1–0.2	1.8 ± 1.2**	320.0 ± 216.7*
	0.2–0.5	0	0
F20	< 0.1	3.3 ± 1.9***	not measured
	0.1–0.2	1.6 ± 0.9***	251.2 ± 168.3***
	0.2–0.5	0	0

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Table 1b. The fine and small root production (average ± standard deviation) by diameter classes in the 17-year-old stand of Japanese black pine in the control soil substrate at depths of 0–10 cm (C10) and 10–20 cm (C20) as well as in the fertilized soil substrate at depths of 0–10 cm (F10) and 10–20 cm (F20)

Soil substrate and soil depth	Diameter class (cm)	Root biomass (g/m^2)	Root length (cm/m^2)
C10	< 0.1	6.5 ± 4.0	not measured
	0.1–0.2	3.2 ± 1.8	663.8 ± 432.3
	0.2–0.5	0	0
C20	< 0.1	7.2 ± 4.1	not measured
	0.1–0.2	3.1 ± 1.6	699.2 ± 448.4
	0.2–0.5	0	0
F10	< 0.1	6.8 ± 3.6	not measured
	0.1–0.2	3.3 ± 1.7	651.5 ± 431.5
	0.2–0.5	0.5 ± 0.3	22.9 ± 13.1
F20	< 0.1	13.3 ± 7.3	not measured
	0.1–0.2	6.9 ± 3.7	1.234.2 ± 642.7
	0.2–0.5	5.1 ± 3.0	224.8 ± 132.4

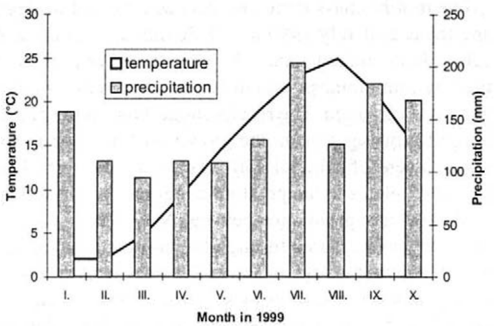

Fig. 4. The course of mean monthly temperatures and precipitation from January to October 1999 (source: Meteorological station at Sakata)

stand the fine root production in a control substrate was about a double of the production in the older one (a statistically significant difference, $P < 0.01$). In none of these stands, the dead roots were found in the ingrowth bags. The asterisks in Table 1a identify statistically significant differences in root biomass production in particular layers of soil between the two examined stands.

A relationship between climatic conditions and root growth was assumed. Fig. 4 describes values of the average monthly temperatures and precipitation between January and October 1999. Meteorological station at Sakata, positioned about 12 km from the examined stands, provided the data. The area is typical by its high amount of precipitation, with the highest incidence of precipitation in July during monsoons. In the second half of winter, there is a thick cover of snow in this area, which for instance in 1999, in studied stands lasted until the end of March. Temperatures between April and June 1999 increased every month by about 4.5°C.

For completeness it has to be mentioned that in framework of complex research, the whole root systems of five black pines were excavated (KONÔPKA et al. 2000). Results showed that the coarse roots (> 0.5 cm in diameter) were well developed in both vertical and horizontal directions. The horizontal roots were found almost explicitly in a depth of less than 50 cm. Typically, about three to four vertical tap roots grew and penetrated into a depth of maximally 2.3 m. Only minimal amount of fine and small roots was found on the vertical coarse roots.

DISCUSSION

More fine and small root biomass of the Japanese black pine was observed in the 17-year-old stand than in the 40-year-old stand. However, in the younger stand there were about three-and-half times more trees than in the older stand. Therefore, the value of average fine and small roots biomass per one tree was higher in the older stand. Specifically, in the older stand on average, there was 608 g of fine roots and 552 g of small roots per 1 tree in a soil depth of up to 50 cm. These values were 238 g of fine roots, and 186 g of small roots in the younger stand. Some authors (e.g. KARIZUMI 1968; VOGT et al. 1987) report the increment of the root biomass in conifers with age up to a certain developmental stage of the stand. The maximum root biomass frequently matches the timing of the canopy closure. In our case, the younger stand was shortly after the canopy closure stage. Therefore, it can be assumed that the fine and small root biomass was close to its maximum.

In the older stand, the fine and small root biomass gradually decreased with the depth of mineral soil, with up to 15% of roots being in a depth of 50 cm or deeper. The fine and small roots in the younger stand were well developed only up to a depth of 30 cm. Results suggest a linear model of vertical distribution of fine and small root biomass in adult stands of the Japanese black pine that grows on a deep sandy soil. ARES and PEINEMANN (1992) stated more homogeneous and deeper root distribution of conifers on sandy soils than on clay or loam. COILE (1937) found that up to 90% of roots of the red pine (*Pinus resinosa* Ait.) was in the upper 12.5 cm clayey soil. Several papers (e.g. PERSSON et al. 1995) pointed to a high proportion of tree fine roots in the LFH horizon of soil. In our case, the LFH horizon was only weakly developed and thickly overgrown with roots of herbaceous plants. As a result of different light conditions in the studied stands, denser grass and herb layer was in the older stand. In both stands, the roots of other plants typically expanded only up to a depth of about 3 cm of mineral soil. From the above, one could assume a strong competitive pressure among roots in the LFH horizon, especially in the older stand.

In both stands between April and July 1999, a gradual increase in the root biomass of the Japanese black pine in a depth of 0–20 cm of mineral soil was noticed. The results indicated a larger increase of the fine root biomass than the increase of the small root biomass through the month of May. This could suggest that at the beginning of vegetation season pines need first to reconstruct their system of fine roots, because a portion of fine roots likely dies in winter due to unfavorable climatic conditions. Sufficient amount of fine roots then ensures water and nutrient absorption, and thus creates conditions for the growth of other parts of the root system. In May, an increase of fine roots in mineral soil in a depth of 0–10 cm was significantly greater than that in a depth of 10–20 cm. This probably relates to different temperatures in these two depths. The average monthly temperature of air in May 1999 was 14.5°C, which was probably sufficient to warm up only the upper layer of soil, and therefore an increase in fine roots in a depth of 10–20 cm was smaller. In July, a larger biomass increase in small roots compared to fine roots was observed. It can be assumed that during this period of time, part of fine roots thickened and moved into a group of small roots. According to KOZLOWSKI and PALLARDY (1997), in majority of coniferous stands in the temperate zone, the root growth during the growing season begins earlier and finishes later than the growth of shoots. A similar situation was observed in our pine stands, where the fine root biomass significantly increased between the end of April and the end of May, while the first signs of shoot-flushing were observed in the last days of May. Research on the Japanese black pine in the period of April–July 1999 indicated a slightly higher growth of the fine root biomass as compared to a growth of the small root biomass. During this research period, a slightly higher increase in the fine and small root biomass was observed in the younger stand than in the older stand.

Results from the in-growth bags experiment showed about a double production of fine roots in mineral soil of 0–20 cm depth in the younger stand as compared to the older stand. This is probably related to the starting situation in root biomass at the beginning of this experiment, when in June 1998 in the above mentioned layer of soil (i.e. in the vicinity of in-growth bags) there were about twice as many fine roots in the younger stand as those in the older stand. ADAMS and HUTCHINSON (1992), when utilizing the method of in-growth bags, discovered a significant stimulating result of fertilizer with greater dominance of phosphorus in sugar maple production (*Acer saccharum* Marsh.). Controversial results are in regard to impacts of different concentrations of nitrogen on the fine root biomass. Sometimes addition of this element into the soil had a stimulating impact while in other cases the root biomass declined (HENDRICKS et al. 1993). In our study in the older stand, no impacts occurred within the researched period of time. This may have been related to the fact that roots in this stand grew inside the in-growth bags only recently, and the exposition time of fertilizer impact was too short. Vitalizing fertilization stimulated the root production in the younger stand in a depth of 10–20 cm only. The fine root biomass was here twice as large as biomass in the control soil, and significantly stimulated production of small roots. The important finding is that in the younger stand, the impact of fertilizer on root production in a depth of 0–10 cm was not observed as opposed to its impact on root production in a depth of 10–20 cm. Since the research was conducted in areas with deep sandy soils and abundance in precipitation, it is probable that a significant part of the fertilizer was leached from an upper soil layer into a lower one, and therefore no positive impact of the fertilizer in the upper layer (0–10 cm) was recorded.

CONCLUSIONS

The research on the Japanese black pine on a deep sandy soil provided conclusions that more fine and small root biomass of this tree species was found in the 17-year-old stand than in the 40-year-old stand. A linear decrease of root biomass with soil depth was identified, when up to 15% of roots were in a depth of 50 cm and deeper. In the younger stand, the fine and small roots were well developed only up to a depth of 30 cm.

The root biomass increased between the end of April and the end of July 1999 in a 0–20 cm layer of mineral soil in both studied stands. In May, a higher growth of the fine root biomass, and in July of the small root biomass was observed. The results suggest that at the beginning of growing season, the growth of fine roots in the upper layers of mineral soil was most intensive. This probably relates to temperature conditions in the soil.

The fine root production between May 1998 and October 1999, as measured through the in-growth bag method in a depth of 0–20 cm, was in the younger stand twice as big as the production in the older stand. It was assumed that this difference was caused by different amounts of the fine root biomass in the vicinity of in-growth bags at the beginning of this experiment. Vitalizing fertilization resulted in increased root production only in the younger stand in the soil layer of 10–20 cm depth. From the results of this experiment a conclusion can be drawn that fast dissolving fertilizers are not suitable for the above mentioned type of soil in areas that are abundant in precipitation because of probable leaching of the fertilizer from the upper layers of soil.

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Produkcia a vertikálna distribúcia jemných a tenkých korienkov japonskej borovice čiernej na piesčitej pôde

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ABSTRAKT: Biomasa jemných a tenkých korienkov, ich vertikálna distribúcia a produkcia sa skúmala v dvoch porastoch japonskej borovice čiernej (*Pinus thunbergii* Parl.) rôzneho veku, rastúcich na hlbokej piesčitej pôde. Viac biomasy jemných a tenkých korienkov sa zistilo v mladšom poraste (151,4 g/m^2) než v poraste staršom (118,5 g/m^2). V staršom poraste množstvo biomasy jemných a tenkých korienkov klesalo lineárne s hĺbkou pôdy. Počas obdobia máj 1998 až október 1999 produkcia jemných korienkov v mladšom poraste bola dvakrát väčšia než ich produkcia v staršom poraste. Pozitívny vplyv hnojenia na produkciu jemných a tenkých korienkov sa zaznamenal v mladšom poraste, a to v hĺbke pôdy 10–20 cm.

Kľúčové slová: *Pinus thunbergii*; biomasa korienkov; produkcia korienkov; vitalizačné hnojenie

Výskum sa sústredil na dva porasty japonskej borovice čiernej (*Pinus thunbergii* Parl.) s vekom 40 a 17 rokov (ďalej sa uvádzajú ako starší a mladší porast). Obidva porasty rástli na hlbokej piesčitej pôde (asi 2 km od pobrežia Japonského mora) v severozápadnej časti ostrova Honšú v Japonsku. Použili sa dve výskumné metódy, a to pôdne vývrty a vrastavé valce. Pôdne vývrty sa odoberali kovovým vrtákom s vnútorným priemerom 4,2 cm. Vrastavé valce boli valcovitého tvaru s výškou 20 cm a priemerom 8,5 cm, pričom sa vyrobili z nylonovej sieťoviny s veľkosťou oka 5,5 mm.

Odber pôdnych vývrtov v júni 1998 sa vykonal za účelom odvodenia biomasy žijúcich jemných a tenkých korienkov, ako aj ich vertikálnej distribúcie. Pritom sa sledoval LFH horizont (organogénny nadložný horizont) a minerálna pôda do hĺbky 50 cm. Zo staršieho porastu sa odobralo 200 vývrtov a z mladšieho porastu 90 pôdnych vývrtov. Každý pôdny vývrt sa rozdelil na LFH horizont a päť podvzoriek minerálnej pôdy (hĺbky 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm). Žijúce jemné a tenké korienky borovice čiernej sa vyseparovali z pôdnych vzoriek. Jemné korienky sa definovali maximálnou hrúbkou 0,2 cm a tenké korienky hrúbkou 0,2–0,5 cm. Korienky sa vysušili na konštantnú hmotnosť a odvážili. Následne sa vyjadrila ich biomasa v g/m^2.

Odber pôdnych vývrtov v roku 1999 sa uskutočnil opakovane štyrikrát – koncom mesiacov apríl, máj, jún a júl. Do sledovania mesačných zmien biomasy korienkov sa zahrnula minerálna pôda s hĺbkou 0–20 cm. Každý mesiac sa odobralo 128 pôdnych vývrtov zo staršieho a 100 z mladšieho porastu. Každý pôdny vývrt sa rozdelil na dve podvzorky (hĺbky 0–10 cm a 10–20 cm) a podrobil sa rovnakému skúmaniu ako pri vzorkách z júna 1998.

Pre sledovanie produkcie korienkov s ohľadom na vitalizačné hnojenie sa využila metóda vrastavých valcov. Použili sa dva druhy pôdneho média, a to kontrolné a prihnojené. Vitalizačné hnojenie sa uskutočnilo primiešaním 100 g hnojiva Hyponex® do 0,01 m^3 pôdy. Hnojivo obsahovalo 6 % N, 40 % P, 6 % K a 15 % Mg. V polovici mája 1998 sa v každom poraste nainštalovalo do pôdy 20 kontrolných a 20 prihnojených vrastavých valcov. Vrastavé valce sa z pôdy vybrali v októbri 1999. Korienky sa vyseparovali z pôdneho média a zmerala sa dĺžka korienkov hrúbkovej triedy 0,1–0,2 cm a 0,2–0,5 cm. Následne sa odvodila biomasa jemných a tenkých korienkov, ktorá sa vyjadrila v g/m^2.

Zistilo sa 62,1 g/m^2 jemných korienkov a 56,4 g/m^2 tenkých korienkov borovice čiernej v staršom poraste. Veľká časť jemných a tenkých korienkov sa nachádzala v hĺbke minerálnej pôdy 0–10 cm (konkrétne to bolo 17,1 g/m^2 a 15,3 g/m^2). Vertikálna distribúcia jemných ako aj tenkých korienkov sa dala vyjadriť negatívnou lineárnou koreláciou (t.j. biomasa korienkov postupne klesala s hĺbkou minerálnej pôdy). Možno predpokladať, že tento lineárny model vertikálnej distribúcie korienkov je typický pre porasty borovice čiernej vyšších vekových stupňov, rastúcich na hlbokých piesčitých pôdach. V mladšom poraste sa zistilo 85,0 g/m^2 jemných korienkov a 66,4 g/m^2 tenkých korienkov. Veľká časť jemných korienkov (30,8 g/m^2) rástla v hĺbke minerálnej pôdy 0–10 cm. Najviac tenkých korienkov (27,1 g/m^2) sa zistilo v hĺbke minerálnej pôdy 10–20 cm. Biomasa jemných a tenkých korienkov v hlbších vrstvách minerálnej pôdy než 30 cm bola zanedbateľná.

Počas sledovaného obdobia (apríl–júl 1999) biomasa jemných a tenkých korienkov postupne narastala v obidvoch porastoch borovice čiernej. V staršom poraste biomasa jemných korienkov vzrástla z 23,0 g/m^2 na 32,0 g/m^2 a biomasa tenkých korienkov z 32,5 g/m^2 na 40,4 g/m^2. V mladšom poraste biomasa jemných korienkov vzrástla z hodnoty 33,4 g/m^2 na 46,2 g/m^2 a biomasa tenkých korienkov z 42,0 g/m^2 na 53,1 g/.m^2. Výsledky naznačili väčšiu rastovú aktivitu jemných korienkov v porovnaní s tenkými korienkami na začiatku vegetačného obdobia. Opačná situácia bola v júli, kedy sa zistil väčší prírastok biomasy tenkých korienkov než jemných korienkov. V máji a júni jemné korienky v hĺbke minerálnej pôdy 0–10 cm rástli rýchlejšie než v hĺbke 10–20 cm. V júli sa zistil väčší prírastok na biomase tenkých korienkov v hĺbke minerálnej pôdy 10–20 cm než v hĺbke 0–10 cm. Za sledované obdobie sa zaznamenal väčší prírastok biomasy jemných a tenkých korienkov v mladšom poraste než v poraste staršom.

V staršom poraste bola produkcia jemných korienkov (ich biomasa nachádzajúca sa vo vnútri vrastavých valcov) za obdobie máj 1998–október 1999 veľmi podobná v kontrolnom aj prihnojenom pôdnom médiu (9,9 g/m^2 a 9,8 g/m^2). Korienky s hrúbkou 0,1–0,2 cm predstavovali dĺžku 573,0 cm/m^2 v kontrolnom pôdnom médiu a 571,2 cm/m^2 v prihnojenom pôdnom médiu. V staršom poraste neboli žiadne tenké korienky vo vrastavých valcoch. Zistilo sa, že hnojenie nemalo na biomasu korienkov v sledovanom období žiadne pozitívne účinky v staršom poraste. Mohlo tomu tak byť v dôsledku toho, že korienky prerastali do vrastavých valcov len v ostatnom krátkom období, takže expozičný čas účinku hnojiva na ne nebol dostatočný na stimuláciu ich rastu. Nezistili sa štatisticky významné rozdiely v produkcii biomasy jemných korienkov medzi vrstvami minerálnej pôdy 0–10 a 10–20 cm v staršom poraste. V mladšom poraste produkcia jemných korienkov počas obdobia máj 1998–október 1999 bola 20,0 g/m^2 v kontrolnej pôde a 30,3 g/m^2 v prihnojenej pôde. Korienky s priemerom 0,1–0,2 cm mali dĺžku 1 363,0 cm/m^2 v kontrolnom médiu a 1 885,7 cm/m^2 v prihnojenom médiu. Produkcia biomasy jemných korienkov v hĺbke minerálnej pôdy 0–10 cm bola podobná v kontrolnom aj v prihnojenom médiu (9,7 g/m^2 a 10,1 g/m^2). Pozitívny vplyv vitalizačného hnojenia na produkciu korienkov sa zaznamenal v hĺbke minerálnej pôdy 10–20 cm v mladšom poraste. Kým v prihnojenej pôde v hĺbke 10–20 cm bolo 20,2 g/m^2 jemných korienkov a 5,1 g/m^2 tenkých korienkov, v tej istej hĺbke kontrolnej pôdy bolo len 10,3 g/m^2 jemných korienkov a žiadne tenké korienky. Vzhľadom na to, že sledované územie je bohaté na zrážky (hlavne počas monzúnového obdobia v prvej polovici leta), pravdepodobne došlo k vymytiu podstatnej časti hnojiva z najvrchnejšej vrstvy minerálnej pôdy.

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