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# Production potential and ecological stability of mixed forest stands in uplands – IV. A mixed spruce/pine stand in the forest type group 2S (fresh, nutrient-medium beech-oak stand)

**P. Jelínek, P. Kantor**

*Mendel University of Agriculture and Forestry, Faculty of Forestry and Wood Technology, Brno, Czech Republic*

**ABSTRACT**: The paper assesses growth, development production and stability of a 76-year-old Norway spruce (*Picea abies*) monoculture with other species from natural seeding. The stand is situated at an altitude of 410 m. Since 1958, the stand has been left to its spontaneous development without intentional thinning measures. At that time, the stand was characterized as a 33-year-old single tree mixture, in view of diameter and height markedly differentiated spruce pole-stage stand with admixed Scots pine (*Pinus sylvestris*), interspersed European larch (*Larix decidua*) and broadleaved species – oak (*Quercus petraea*), hornbeam (*Carpinus betulus*), aspen (*Populus tremula*) and birch (*Betula verrucosa*). Under conditions of an extreme decline of spruce, this allochthonous forest ecosystem did not completely disintegrated only because the role of the main species was taken over by originally interspersed and later on admixed Scots pine from natural regeneration. The improving position of interspersed species, viz larch, oak and subdominant hornbeam, was also significant. It was demonstrated again that the initial insignificant proportion of single admixed and interspersed tree species can ensure not only the existence but also the production and stability of forest ecosystems even after a dramatic decline of the originally dominant species, Norway spruce in this case.

**Keywords**: Norway spruce; mixed stands; monoculture; natural development; ecological stability

The paper is the 4th communication presenting results of the project *Ecological stability and production potential of mixed forest stands in anthropically changed conditions of uplands as a basis for the proposal of a target species composition*. It refers to one of the principal research projects solved at the Department of Forest Establishment and Silviculture (DFES), Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry, Brno. The project has been in progress since the beginning of the nineties.

The content and main objectives of the project are already evident from its title. It was presented to the forestry and scientific community by an introductory paper in the journal Lesnictví-Forestry, Vol. *43*, No. 5 (KANTOR 1997).

Thematically, the project is based on the evaluation of a series of precisely established (in 1958–1963) and regularly measured permanent research plots in mixed stands of the 2nd and 3rd forest vegetation zones. These are traditional long-term thinning research plots where thinning from below and crown thinning are compared with control plots. In total 10 (or 11) research areas of the type are available to the scientists from DFES, particularly in the Křtiny Training Forest Enterprise, from simple beech/larch mixed stands to mixed stands with a rich palette of ten tree species. Specification of the stands is given in the above mentioned paper in Lesnictví-Forestry, 1997, No. 5.

The first, and in our opinion the extraordinarily valuable stage of evaluation of research studies is based on the analysis of time series of *control plots* that are (since the establishment of the experiments and virtually since the origin of the stands) completely left to their spontaneous development without any intentional thinning measures and only dead trees are removed.

The long-time series of monitoring (40–45 years) and the extent and precision of plot establishment make it possible to evaluate changes in species composition by

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natural development, to construct scales of mortality and vitality of particular species, to assess competition relations of trees, production potentials of various mixtures and their ecological stability. These data will then serve as a basis for the proposal of target species composition in actual site conditions of upland regions.

Production potential and stability of all 10 experimental stands will be gradually analysed in the Journal of Forest Science. The first three communications were published in Vol. *44* (KANTOR, PAŘÍK 1998), Vol. *46* (KNOTT, KANTOR 2000) and Vol. *47* (KANTOR et al. 2001).

Thus, the paper is the fourth scientific communication presenting the results of further natural development of a stand (without intentional thinning measures) in the Vranov Forest District (Křtiny Training Forest Enterprise), registration No. 469C7. The stand originated as an unmixed monoculture by artificial regeneration of Norway spruce in a clear-cut area in 1925. At the same time, natural spontaneous regeneration by border seeding of pine and larch occurred. Similarly, interspersed broadleaved species also come from natural regeneration.

The proportion of the most important and widespread tree species in the Czech Republic, i.e. Norway spruce, is to be reduced from the present 55% to less than 40% in the course of the next 100 years. With respect to an anthropic stress and uncertainty associated with the development of climate a significant reduction in the proportion of allochthonous spruce is expected particularly in forest ecosystems of upland regions (2nd to 4th forest vegetation zones). The findings of this project can also serve as a basis for the objective evaluation of the production potential and ecological stability of spruce at these allochthonous sites.

## METHODS OF FIELD MEASUREMENTS

Stand 469C7 is situated on a gentle slope of max. 5° towards north. The stand ranks among the fresh, nutrient-medium Beech-Oak forest type (2S2). The total area of the stand is 6.41 ha and as already mentioned it originated by artificial regeneration of spruce (*Picea abies*) on a clear-cut area in 1925. At the same time, natural spontaneous enrichment of the plantation occurred by border seeding of pine (*Pinus sylvestris)* and larch (*Larix decidua*). Similarly, interspersed broadleaved species also come from natural regeneration. In the year of establishing the research plots (1958) the stand was characterized as a 33-year-old single tree mixture, a pole-stage spruce stand differentiated from the aspect of diameter and height with interspersed larch and broadleaves – oak (*Quercus petraea*), hornbeam (*Carpinus betulus*), aspen (*Populus tremula*) and birch (*Betula verrucosa*).

The control plot of a total area 0.32 ha (8 plots 20 × 20 m each) evaluated in this paper has been left without any intentional felling measures for the whole period of investigation (42 years).

Methodology of assessing the growth and development of particular experimental stands is unified within the whole research project being already published in the journal Lesnictví-Forestry (KANTOR 1997; KANTOR, PAŘÍK 1998; KNOTT, KANTOR 2000; KANTOR et al. 2001) and, therefore, we give only basic facts here.

In regular 5-year intervals, height, diameter at breast height (d.b.h.), crown height, crown length and crown cover are measured in each of the trees. In a 42-year time series (from 1958 to 2000), the following parameters are evaluated separately in each of the species of the assessed mixture:

- total frequency and mortality of trees;
- frequency in height and diameter classes;
- average stand height;
- average d.b.h.;
- basal area;
- growing stock;
- stand density and species composition.

In the stand, particular species have been recorded and summarized already from the height class 1 m (b.h. 1.3 m) and d.b.h. 4 cm.

The following procedures were used to construct and assess the evaluation criteria:

- Mortality (expressed in % of dead trees) in five-year examination intervals is always related to the frequency of the previous measurement.
- Data on the top height of a stand are of preliminary character. The height was determined in each of the species at $n > 20$ as a mean of the 10 tallest trees, at $n < 20$ the height was calculated only from 5 trees.
- Growing stock and periodical volume increment derived from it are related only to the dominant stand, wood of dead trees is not included here.
- Stand density was calculated according to standard mensurational practices from the ratio of the actual basal area (b.a.) of particular species and table data.
- Based on the reduced areas species composition was determined. To determine table b.a. mensurational tables were used (ÚHÚL 1990).
- On the basis of the evaluation the importance and proportions of particular species were assessed with respect to the production potential and ecological stability of tree components of the assessed mixed stand. At the same time, data were obtained for the accomplishment of the project strategic goal, viz. specification and presentation of the proposal (proposal variants) of the target species composition in the most important management sets of stands of upland regions.

## RESULTS OF THE STUDY – ANALYSIS OF THE NATURAL DEVELOPMENT OF STAND 469C7

Basic characteristics of the control plot of Stand 469C7 between 1958 and 1995 has been already published (KANTOR et al. 1997, 2000). In 1958, the year of estab-

Table 1. Basic data on the stand in 1958–2000

| Species | Number of trees per hectare | *h* (m) | Mean tree d.b.h. (cm) | *v* (m³) | Growing stock (m³/ha) | Stand basal area (m²/ha) | Stand density | Species composition (%) |
|---|---|---|---|---|---|---|---|---|
| **1958** | | | | | | | | |
| Spruce | 1,659 | 11.8 | 10.8 | 0.067 | 111.2 | 16.901 | 0.59 | 53.8 |
| Pine | 478 | 15.3 | 17.8 | 0.192 | 92.0 | 12.714 | 0.38 | 34.9 |
| Larch | 94 | 13.9 | 12.9 | 0.097 | 9.1 | 1.306 | 0.05 | 4.3 |
| Oak | 28 | 12.6 | 10.3 | 0.050 | 1.4 | 0.251 | 0.01 | 1.0 |
| Hornbeam | 88 | 11.4 | 8.0 | 0.020 | 1.7 | 0.470 | 0.02 | 2.1 |
| Aspen | 41 | 13.6 | 13.1 | 0.086 | 3.5 | 0.559 | 0.04 | 3.8 |
| Birch | 3 | 10.0 | 5.5 | 0.009 | 0.0 | 0.007 | 0.00 | 0.0 |
| Total | 2,391 | | | | 218.9 | 32.209 | 1.09 | 100.0 |
| **1965** | | | | | | | | |
| Spruce | 1,184 | 14.7 | 12.8 | 0.116 | 136.8 | 16.543 | 0.53 | 49.6 |
| Pine | 428 | 18.2 | 20.5 | 0.293 | 125.2 | 14.925 | 0.41 | 38.4 |
| Larch | 84 | 16.7 | 14.3 | 0.152 | 12.8 | 1.454 | 0.05 | 4.6 |
| Oak | 28 | 14.6 | 11.1 | 0.072 | 2.0 | 0.291 | 0.01 | 1.2 |
| Hornbeam | 88 | 12.6 | 8.4 | 0.024 | 2.1 | 0.529 | 0.03 | 2.4 |
| Aspen | 41 | 15.0 | 13.6 | 0.103 | 4.2 | 0.598 | 0.04 | 3.8 |
| Total | 1,853 | | | | 283.2 | 34.341 | 1.07 | 100.0 |
| **1970** | | | | | | | | |
| Spruce | 1,016 | 16.0 | 14.0 | 0.152 | 154.8 | 17.104 | 0.52 | 47.2 |
| Pine | 428 | 19.2 | 22.1 | 0.357 | 152.9 | 17.332 | 0.46 | 42.4 |
| Larch | 69 | 18.4 | 16.1 | 0.206 | 14.2 | 1.473 | 0.05 | 4.2 |
| Oak | 25 | 15.6 | 11.7 | 0.088 | 2.2 | 0.288 | 0.01 | 1.1 |
| Hornbeam | 88 | 13.4 | 8.7 | 0.028 | 2.5 | 0.574 | 0.03 | 2.5 |
| Aspen | 28 | 15.8 | 13.9 | 0.111 | 3.1 | 0.428 | 0.03 | 2.6 |
| Total | 1,653 | | | | 329.7 | 37.198 | 1.09 | 100.0 |
| **1975** | | | | | | | | |
| Spruce | 925 | 17.2 | 14.8 | 0.183 | 169.4 | 17.338 | 0.51 | 46.0 |
| Pine | 419 | 20.6 | 23.3 | 0.426 | 178.4 | 18.927 | 0.49 | 44.5 |
| Larch | 66 | 19.6 | 17.0 | 0.253 | 16.6 | 1.582 | 0.05 | 4.4 |
| Oak | 22 | 16.8 | 12.9 | 0.109 | 2.4 | 0.299 | 0.01 | 1.1 |
| Hornbeam | 88 | 12.7 | 8.9 | 0.030 | 2.6 | 0.593 | 0.03 | 2.6 |
| Aspen | 16 | 17.2 | 14.6 | 0.131 | 2.0 | 0.262 | 0.02 | 1.5 |
| Total | 1,534 | | | | 371.5 | 39.000 | 1.10 | 100.0 |
| **1980** | | | | | | | | |
| Spruce | 672 | 20.0 | 16.8 | 0.267 | 179.2 | 16.151 | 0.44 | 42.0 |
| Pine | 378 | 23.3 | 25.8 | 0.569 | 215.1 | 20.605 | 0.50 | 48.0 |
| Larch | 66 | 21.7 | 18.1 | 0.327 | 21.4 | 1.806 | 0.05 | 5.0 |
| Oak | 22 | 18.0 | 13.9 | 0.142 | 3.1 | 0.351 | 0.01 | 1.3 |
| Hornbeam | 84 | 13.3 | 9.4 | 0.036 | 3.1 | 0.647 | 0.03 | 2.9 |
| Aspen | 6 | 19.3 | 15.5 | 0.162 | 1.0 | 0.117 | 0.01 | 0.6 |
| Total | 1,228 | | | | 422.9 | 39.677 | 1.04 | 100.0 |
| **1985** | | | | | | | | |
| Spruce | 381 | 21.8 | 19.9 | 0.381 | 145.4 | 12.496 | 0.31 | 33.3 |
| Pine | 359 | 24.0 | 27.4 | 0.656 | 235.6 | 22.100 | 0.53 | 56.0 |
| Larch | 53 | 22.9 | 20.6 | 0.426 | 22.6 | 1.863 | 0.05 | 5.4 |
| Oak | 19 | 18.8 | 15.1 | 0.178 | 3.3 | 0.356 | 0.01 | 1.5 |
| Hornbeam | 78 | 13.8 | 9.9 | 0.042 | 3.3 | 0.668 | 0.03 | 3.3 |
| Aspen | 3 | 19.5 | 16.2 | 0.180 | 0.6 | 0.064 | 0.00 | 0.4 |
| Total | 894 | | | | 410.8 | 37.548 | 0.94 | 100.0 |

| Species | Number of trees per hectare | h (m) | Mean tree d.b.h. (cm) | v (m³) | Growing stock (m³/ha) | Stand basal area (m²/ha) | Stand density | Species composition (%) |
|---|---|---|---|---|---|---|---|---|
| **1990** | | | | | | | | |
| Spruce | 366 | 22.7 | 21.2 | 0.454 | 166.0 | 13.709 | 0.34 | 33.8 |
| Pine | 341 | 25.3 | 29.3 | 0.785 | 267.4 | 23.901 | 0.55 | 55.6 |
| Larch | 53 | 23.8 | 22.3 | 0.516 | 27.4 | 2.194 | 0.06 | 5.8 |
| Oak | 16 | 20.3 | 16.9 | 0.237 | 3.7 | 0.369 | 0.01 | 1.4 |
| Hornbeam | 63 | 14.4 | 12.0 | 0.061 | 3.8 | 0.756 | 0.03 | 3.4 |
| Total | 838 | | | | 468.2 | 40.930 | 0.99 | 100.0 |
| **1995** | | | | | | | | |
| Spruce | 225 | 23.5 | 21.9 | 0.497 | 111.9 | 8.968 | 0.22 | 24.7 |
| Pine | 319 | 26.4 | 30.5 | 0.888 | 283.2 | 24.203 | 0.55 | 62.6 |
| Larch | 53 | 25.6 | 23.0 | 0.604 | 32.1 | 2.354 | 0.06 | 7.0 |
| Oak | 16 | 20.9 | 17.7 | 0.268 | 4.2 | 0.405 | 0.01 | 1.7 |
| Hornbeam | 53 | 14.4 | 13.2 | 0.073 | 3.9 | 0.786 | 0.03 | 4.0 |
| Total | 666 | | | | 435.2 | 36.717 | 0.87 | 100.0 |
| **2000** | | | | | | | | |
| Spruce | 197 | 24.1 | 23.7 | 0.594 | 116.9 | 9.233 | 0.21 | 23.4 |
| Pine | 297 | 27.5 | 32.3 | 1.042 | 309.4 | 25.293 | 0.57 | 62.6 |
| Larch | 50 | 26.7 | 24.5 | 0.705 | 35.3 | 2.515 | 0.06 | 6.9 |
| Oak | 16 | 22.3 | 19.1 | 0.339 | 5.3 | 0.482 | 0.02 | 1.8 |
| Hornbeam | 56 | 15.8 | 15.9 | 0.116 | 6.5 | 1.172 | 0.05 | 5.3 |
| Total | 616 | | | | 473.4 | 38.695 | 0.91 | 100.0 |

lishment (age 33 years), it was a Norway spruce pole-stage stand (1,659 trees/ha) with admixed Scots pine (478 trees/ha) and other interspersed species. The stand was characterized as fully stocked (1.1) with b.a. of 32.2 m²/ha and standing volume of 218.9 m³/ha.

## STAND DENSITY DEVELOPMENT AND MORTALITY

In the course of 42 years (1958–2000) when regular measurements were carried out stand density decreased due to spontaneous development from the initial 2,391 trees/ha to 616 trees/ha (Tables 1 and 2). Thus, total mortality amounted to 74%.

Particularly spruce mortality is extremely high amounting to 88%; out of the original number of 1,659 trees/ha 1,463 trees died. Dieback of spruce is high not only in the initial years of measurements but also in the last years. In the periods 1980–1985 and 1990–1995, it was 43.3% and nearly 40%, respectively. Of interest is a hypothesis on the potential effect of the climate, particularly precipitation, on this species, allochthonous in uplands. In the period 1985–1990, rich in precipitation in the growing season and particularly in May–August (Table 3), only 15 spruce trees/ha (4%) died whereas in a 5-year period before and after the humid period spruce mortality was considerably high.

On the other hand, admixed pine and interspersed species showed relatively low total mortality, their dieback not being so closely connected with extreme precipitation. The second most important species of the stand, Scots pine, showed total mortality less than 40% and similar results were obtained in other species of the mixture, viz larch, hornbeam and oak. Fig. 1 indicates the gradual conversion of spruce monoculture to a mixed stand with dominant position of pine. The rich broadleaved component of intermediate trees indicates further development of the stand towards the natural broadleaved mixture of hornbeam/oak stand.

## SPECIES FREQUENCY IN HEIGHT AND DIAMETER CLASSES

From the tables of frequency in height and diameter classes (Tables 4a–f) we can observe the development of particular species in the studied period and distribution of dead trees in particular height and diameter classes. The development of frequency distribution in spruce representing initially a dominant component of the examined mixture is of particular interest. In the first years of measurements, mortality of spruce concentrated especially on subdominant, intermediate and suppressed trees of small dimensions. However, already at an age of 50 years (measurement in 1975) mortality of spruce involves all height classes and fifteen years later even all diameter classes. It is interesting that just spruce showed the highest ability to survive even as a subdominant or intermediate tree, which is demonstrated by a broad spectrum of height classes where the species occurs for the whole time.

The frequency of another important species, Scots pine, proved its heliophilous character. It is documented by the narrow spectrum of heights and also by the fact that pine died almost exclusively as a subdominant species and in

Table 2. The development of stand density (trees/ha) and *mortality* (%)

| Species | 1958 | 1965 | (%) | 1970 | (%) | 1975 | (%) | 1980 | (%) | 1985 | (%) | 1990 | (%) | 1995 | (%) | 2000 | (%) | Total mortality to 1958 N | Total mortality to 1958 (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Spruce | 1,659 | 1,184 | *28.63* | 1,016 | *14.25* | 925 | *8.92* | 672 | *27.36* | 381 | *43.26* | 366 | *4.10* | 225 | *38.46* | 197 | 12.50 | 1,463 | 88.14 |
| Pine | 478 | 428 | *10.46* | 428 | *0.00* | 419 | *2.19* | 378 | *9.70* | 359 | *4.96* | 341 | *5.22* | 319 | *6.42* | 297 | 6.86 | 181 | 37.91 |
| Larch | 94 | 84 | *10.00* | 69 | *18.52* | 66 | *4.55* | 66 | *0.00* | 53 | *19.05* | 53 | *0.00* | 53 | *0.00* | 50 | 5.88 | 44 | 46.67 |
| Oak | 28 | 28 | *0.00* | 25 | *11.11* | 22 | *12.50* | 22 | *0.00* | 19 | *14.29* | 16 | *16.67* | 16 | *0.00* | 16 | 0.00 | 13 | 44.44 |
| Hornbeam | 88 | 88 | *0.00* | 88 | *0.00* | 88 | *0.00* | 84 | *3.57* | 78 | *7.41* | 63 | *20.00* | 53 | *15.00* | 56 | –5.88 | 31 | 35.71 |
| Aspen | 41 | 41 | *0.00* | 28 | *30.77* | 16 | *44.44* | 6 | *60.00* | 3 | *50.00* | | | | | | | 41 | 100.00 |
| Birch | 3 | | *100.00* | | | | | | | | | | | | | | | 3 | 100.00 |
| Total | 2,391 | 1,853 | *22* | 1,653 | *11* | 1,534 | *7* | 1,228 | *20* | 894 | *27* | 838 | *6* | 666 | *21* | 616 | 8 | 1,775 | 74 |

Table 3. Monthly precipitation (in mm) at the Olomučany meteorological station in the period 1975–1996 (in KNOTT 1999)

| | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | Mean rf. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| January | 32.5 | 63.2 | **102.7** | 24.1 | 61.0 | 16.9 | 53.6 | 43.0 | 17.6 | 50.8 | 29.8 | 42.9 | 20.1 | 39.9 | 17.8 | 12.1 | 9.6 | 4.9 | 35.1 | 24.8 | 44.5 | 20.5 | 34.9 |
| February | 15.5 | 19.9 | **76.7** | 34.9 | **90.8** | 34.4 | 32.3 | 0.5 | 54.0 | **80.4** | 19.8 | 43.8 | 24.1 | 36.6 | 22.4 | 46.9 | 36.3 | 20.3 | 14.8 | 15.0 | 37.3 | 37.0 | 36.1 |
| March | 41.2 | 14.7 | 20.6 | 12.0 | **73.8** | 60.8 | 56.5 | 31.3 | 32.0 | 2.2 | 58.1 | 25.8 | 34.8 | 43.4 | 18.3 | 29.4 | 12.9 | **82.8** | 41.4 | 31.3 | 55.0 | 47.0 | 37.5 |
| April | 24.6 | 21.1 | 57.6 | 37.7 | 62.1 | **79.0** | 19.3 | 14.5 | 53.2 | **77.5** | 37.1 | 28.8 | 15.6 | 23.8 | **75.8** | **82.8** | 32.2 | 29.9 | 2.9 | 61.0 | 33.0 | 56.0 | 42.1 |
| May | **92.0** | **80.6** | 64.8 | 92.6 | 28.0 | 44.7 | **83.4** | 65.5 | 54.0 | **128.0** | **102.9** | **80.4** | **93.8** | 56.4 | 38.0 | 59.0 | **75.5** | 33.5 | 28.2 | 59.3 | 61.8 | 43.0 | 66.6 |
| June | 29.6 | 25.5 | 40.4 | 82.6 | **126.1** | **114.9** | 55.7 | 69.2 | **73.6** | 37.5 | **89.4** | **127.1** | **101.5** | **88.1** | 61.7 | **77.1** | **90.5** | 67.5 | 65.4 | 22.8 | 12.5 | **76.0** | 69.8 |
| July | 37.3 | 26.4 | **78.5** | 72.6 | 37.3 | **78.3** | **85.9** | **75.3** | 14.6 | 58.9 | **86.1** | **92.8** | **75.0** | 53.7 | 23.9 | 62.5 | 64.4 | 3.6 | 63.6 | 59.0 | 41.5 | **71.5** | 57.4 |
| August | 25.2 | **78.6** | **121.6** | 43.4 | **73.5** | 36.8 | 16.8 | **93.4** | 2.6 | 21.3 | **113.0** | **99.4** | 46.4 | **130.5** | 43.4 | 27.0 | 46.1 | 57.3 | 67.5 | **120.5** | 60.8 | 59.5 | 62.9 |
| September | 37.8 | 50.6 | 46.4 | 23.8 | 66.7 | 46.8 | **80.0** | 27.5 | 23.0 | 65.6 | 20.0 | 23.1 | **102.6** | 66.6 | **75.0** | **82.1** | 28.3 | 20.4 | 50.6 | 53.3 | **85.6** | 57.5 | 51.5 |
| October | 68.4 | 53.8 | 20.6 | 32.2 | 16.9 | 57.9 | **113.6** | 16.8 | 12.3 | 69.3 | 4.6 | 32.6 | 45.0 | 31.6 | 17.1 | 44.4 | 40.6 | **75.4** | 46.9 | 17.6 | 28.0 | 52.0 | 40.8 |
| November | 41.7 | **76.7** | 33.7 | 45.5 | **92.6** | 24.8 | 41.5 | 6.3 | 30.5 | 61.5 | **77.1** | 43.4 | 31.9 | 26.0 | 40.3 | 55.0 | 67.5 | 44.8 | 15.8 | 19.6 | 27.8 | 36.0 | 42.7 |
| December | 17.0 | 32.5 | 32.0 | 9.7 | 64.7 | 34.0 | 101.5 | 53.8 | 29.3 | 59.8 | 46.1 | 17.5 | 35.6 | 57.6 | 17.1 | 58.5 | 54.3 | 40.5 | 58.5 | 36.0 | 34.0 | 42.0 | 42.4 |
| Annual rainfall | 462.8 | 543.6 | 695.6 | 511.1 | 793.5 | 629.3 | 740.0 | 497.1 | 396.7 | 712.8 | 684.0 | 657.6 | 626.4 | 654.2 | 450.8 | 636.8 | 557.9 | 480.7 | 490.6 | 520.0 | 521.8 | 598.0 | 584.6 |

Table 4a. The development of spruce frequency in height classes (m) and *mortality* on the control plot (0.32 ha)

| Height class (m) | 1958 | *1959–1965* | 1965 | *1966–1970* | 1970 | *1971–1975* | 1975 | *1976–1980* | 1980 | *1981–1985* | 1985 | *1986–1990* | 1990 | *1991–1995* | 1995 | *1996–2000* | 2000 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | | | | | | | | | | | | | | | | | |
| 3 | 4 | *4* | | | | | | | | | | | | | | | |
| 4 | 4 | *4* | | | | | | | | | | | | | | | |
| 5 | 11 | *9* | 2 | *2* | | | | | | | | | | | | | |
| 6 | 16 | *12* | 2 | *1* | 1 | | 1 | *1* | | | | | | | | | |
| 7 | 25 | *20* | 6 | *3* | 1 | *1* | | | | | | | | | | | |
| 8 | 38 | *20* | 11 | *3* | 10 | *2* | 7 | *6* | 1 | *1* | | | | | | | |
| 9 | 43 | *22* | 11 | *5* | 4 | *1* | 3 | *1* | 2 | *2* | | | | | | | |
| 10 | 52 | *26* | 30 | *12* | 16 | *6* | 10 | *8* | 1 | *1* | | | | | | | |
| 11 | 49 | *14* | 27 | *6* | 18 | *5* | 6 | *4* | 1 | | 1 | | 1 | *1* | | | |
| 12 | 49 | *12* | 25 | *6* | 17 | *3* | 21 | *13* | 5 | *5* | | | | | | | |
| 13 | 51 | *6* | 23 | *6* | 19 | | 13 | *8* | 5 | *4* | 1 | | | | | | |
| 14 | 67 | *2* | 27 | *4* | 16 | *3* | 16 | *6* | 7 | *7* | | | 1 | | 1 | | 1 |
| 15 | 72 | *1* | 36 | *5* | 27 | *1* | 20 | *12* | 9 | *7* | 2 | | 2 | | 1 | | 1 |
| 16 | 31 | | 43 | | 25 | *4* | 18 | *3* | 8 | *5* | 3 | *1* | | | 1 | | |
| 17 | 15 | | 47 | | 35 | | 15 | *3* | 14 | *9* | 4 | *1* | 3 | *1* | 2 | | 3 |
| 18 | 3 | | 39 | *1* | 52 | *2* | 38 | *7* | 14 | *7* | 6 | | 7 | *4* | 3 | *1* | 1 |
| 19 | 1 | | 29 | | 34 | *1* | 31 | *2* | 14 | *6* | 6 | *1* | 6 | *3* | 2 | | 2 |
| 20 | | | 13 | | 26 | | 33 | *1* | 21 | *13* | 12 | *1* | 7 | *2* | 3 | *1* | 1 |
| 21 | | | 7 | | 17 | | 30 | | 24 | *5* | 8 | | 8 | *3* | 3 | | 3 |
| 22 | | | | | 5 | | 18 | *4* | 34 | *12* | 25 | | 16 | *5* | 8 | *2* | 7 |
| 23 | | | 1 | | 2 | | 11 | *1* | 32 | *5* | 24 | *1* | 15 | *7* | 7 | *2* | 4 |
| 24 | | | | | | | 4 | *1* | 15 | *2* | 19 | | 24 | *12* | 9 | *1* | 8 |
| 25 | | | | | | | 1 | | 6 | *2* | 8 | | 12 | *2* | 12 | *1* | 7 |
| 26 | | | | | | | | | 2 | | 2 | | 8 | *1* | 13 | *1* | 14 |
| 27 | | | | | | | | | | | 1 | | 4 | *2* | 4 | | 7 |
| 28 | | | | | | | | | | | | | 2 | *1* | 3 | | 2 |
| 29 | | | | | | | | | | | | | 1 | *1* | | | 2 |
| 30 | | | | | | | | | | | | | | | | | |
| Total (0.32 ha) | 531 | *152* | 379 | *54* | 325 | *29* | 296 | *81* | 215 | *93* | 122 | *5* | 117 | *45* | 72 | *9* | 63 |
| Per hectare | 1,659.4 | *475* | 1,184.4 | *168.75* | 1,015.6 | *90.625* | 925 | *253.13* | 671.88 | *290.63* | 381.25 | *15.625* | 365.63 | *140.63* | 225 | *28.125* | 196.88 |
| Mean height | 11.8 | | 14.7 | | 16 | | 17.2 | | 20 | | 21.8 | | 22.7 | | 23.5 | | 24.1 |

Table 4b. The development of pine frequency in height classes (m) and *mortality* on the control plot (0.32 ha)

| Height class (m) | 1958 | *1959 –1965* | 1965 | *1966 –1970* | 1970 | *1971 –1975* | 1975 | *1976 –1980* | 1980 | *1981 –1985* | 1985 | *1986 –1990* | 1990 | *1991 –1995* | 1995 | *1996 –2000* | 2000 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 6 | | | | | | | | | | | | | | | | | |
| 7 | 1 | *1* | | | | | | | | | | | | | | | |
| 8 | 1 | *1* | | | | | | | | | | | | | | | |
| 9 | | | | | | | | | | | | | | | | | |
| 10 | 3 | *3* | | | | | | | | | | | | | | | |
| 11 | 2 | *2* | | | | | | | | | | | | | | | |
| 12 | 1 | *1* | | | | | | | | | | | | | | | |
| 13 | 9 | *4* | | | | | | | | | | | | | | | |
| 14 | 23 | *2* | 3 | | 1 | | 1 | | 1 | *1* | | | | | | | |
| 15 | 40 | *3* | 7 | | 2 | *2* | | | | | | | | | | | |
| 16 | 47 | | 12 | | 8 | | 3 | *3* | | | | | | | | | |
| 17 | 16 | | 22 | | 14 | *1* | 11 | *6* | | | | | | | | | |
| 18 | 9 | | 32 | | 18 | | 6 | *2* | 1 | *1* | | | | | | | |
| 19 | 1 | | 33 | | 34 | | 17 | *2* | 3 | | 3 | *1* | 1 | | | | |
| 20 | 1 | | 15 | | 35 | | 22 | | 5 | *3* | 1 | | 1 | | 1 | | |
| 21 | | | 9 | | 12 | | 30 | | 9 | | 7 | *2* | 3 | | 2 | *1* | |
| 22 | | | 2 | | 11 | | 24 | | 20 | | 10 | | 8 | *2* | 4 | | 4 |
| 23 | | | 1 | | 1 | | 14 | | 27 | | 28 | *1* | 11 | *1* | 4 | *3* | 2 |
| 24 | | | | | 1 | | 4 | | 27 | *1* | 27 | *1* | 13 | *3* | 10 | *3* | 2 |
| 25 | | | | | | | 1 | | 18 | | 23 | *1* | 24 | | 8 | | 1 |
| 26 | | | | | | | 1 | | 7 | | 12 | | 21 | *1* | 24 | | 18 |
| 27 | | | | | | | | | 2 | | 2 | | 15 | | 18 | | 23 |
| 28 | | | | | | | | | 1 | | 2 | | 11 | | 21 | | 20 |
| 29 | | | | | | | | | | | | | 1 | | 5 | | 14 |
| 30 | | | | | | | | | | | | | | | 4 | | 7 |
| 31 | | | | | | | | | | | | | | | 1 | | 4 |
| 32 | | | | | | | | | | | | | | | | | |
| Total (0.32 ha) | 154 | *17* | 137 | *0* | 137 | *3* | 134 | *13* | 121 | *6* | 115 | *6* | 109 | *7* | 102 | *7* | 95 |
| Per hectare | 481.3 | *53.1* | 428.1 | *0* | 428.1 | *9.38* | 418.8 | *40.6* | 378.1 | *18.8* | 359.4 | *18.8* | 340.6 | *21.9* | 318.8 | *21.9* | 296.9 |
| Mean height | 15.3 | | 18.2 | | 19.2 | | 20.6 | | 23.3 | | 24 | | 25.3 | | 26.4 | | 27.5 |

Table 4c. The development of larch frequency in height classes (m) and *mortality* on the control plot (0.32 ha)

| Height class (m) | 1958 | *1959 –1965* | 1965 | *1966 –1970* | 1970 | *1971 –1975* | 1975 | *1976 –1980* | 1980 | *1981 –1985* | 1985 | *1986 –1990* | 1990 | *1991 –1995* | 1995 | *1996 –2000* | 2000 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 9 | | | | | | | | | | | | | | | | | |
| 10 | 1 | | | | | | | | | | | | | | | | |
| 11 | 1 | *1* | 1 | *1* | | | | | | | | | | | | | |
| 12 | 3 | *1* | 1 | *1* | | | | | | | | | | | | | |
| 13 | 5 | | | *1* | | | | | | | | | | | | | |
| 14 | 11 | *1* | 2 | *1* | | | | | | | | | | | | | |
| 15 | 6 | | 2 | | 1 | | | | | | | | | | | | |
| 16 | 3 | | 5 | *1* | 1 | *1* | 2 | | | | | | | | | | |
| 17 | | | 5 | | 5 | | | | 1 | *1* | | | | | | | |
| 18 | | | 5 | | 4 | | 5 | | 2 | *1* | 1 | | | | | | |
| 19 | | | 4 | | 6 | | 4 | | 2 | *1* | 1 | | | | | | |
| 20 | | | 2 | | 5 | | 3 | | 2 | | 1 | | 2 | | | | |
| 21 | | | | | | | 2 | | 1 | | 1 | | 1 | | 1 | | |
| 22 | | | | | | | 3 | | 5 | *1* | 1 | | 1 | | | | 1 |
| 23 | | | | | | | 2 | | 4 | | 6 | | 5 | | 3 | *1* | 2 |
| 24 | | | | | | | | | 3 | | 3 | | 2 | | 2 | | 1 |
| 25 | | | | | | | | | 1 | | 2 | | 3 | | 2 | | |
| 26 | | | | | | | | | | | 1 | | 1 | | 4 | | 4 |
| 27 | | | | | | | | | | | | | 1 | | 1 | | 3 |
| 28 | | | | | | | | | | | | | 1 | | 3 | | 1 |
| 29 | | | | | | | | | | | | | | | 1 | | 3 |
| 30 | | | | | | | | | | | | | | | | | 1 |
| 31 | | | | | | | | | | | | | | | | | |
| Total (0.32 ha) | 30 | *3* | 27 | *5* | 22 | *1* | 21 | *0* | 21 | *4* | 17 | *0* | 17 | *0* | 17 | *1* | 16 |
| Per hectare | 93.75 | *9.375* | 84.38 | *15.63* | 68.75 | *3.125* | 65.63 | *0* | 65.63 | *12.5* | 53.13 | *0* | 53.13 | *0* | 53.13 | *3.125* | 50 |
| Mean height | 13.9 | | 16.7 | | 18.4 | | 19.6 | | 21.7 | | 22.9 | | 23.8 | | 25.6 | | 26.7 |

Table 4d. The development of spruce frequency in diameter classes (cm) and *mortality* on the control plot (0.32 ha)

| Diameter class (cm) | 1958 | *1959 –1965* | 1965 | *1966 –1970* | 1970 | *1971 –1975* | 1975 | *1976 –1980* | 1980 | *1981 –1985* | 1985 | *1986 –1990* | 1990 | *1991 –1995* | 1995 | *1996 –2000* | 2000 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | | | | | | | | | | | | | | | | | |
| 2 | 1 | *1* | | | | | | | | | | | | | | | |
| 4 | 14 | *12* | 1 | *1* | | | | | | | | | | | | | |
| 6 | 65 | *49* | 13 | *5* | 7 | *1* | 6 | *6* | | | | | | | | | |
| 8 | 112 | *51* | 63 | *24* | 39 | *14* | 23 | *16* | 7 | *7* | | | | | | | |
| 10 | 101 | *27* | 62 | *12* | 47 | *7* | 42 | *23* | 15 | *14* | 1 | | 1 | *1* | | | |
| 12 | 91 | *7* | 64 | *8* | 51 | *1* | 48 | *13* | 30 | *21* | 9 | *2* | 6 | *3* | 3 | | 2 |
| 14 | 77 | *4* | 68 | *2* | 49 | *3* | 42 | *9* | 27 | *21* | 5 | | 5 | *1* | 4 | | 4 |
| 16 | 44 | *1* | 57 | *1* | 57 | *2* | 43 | *5* | 36 | *13* | 18 | | 17 | *6* | 10 | *2* | 5 |
| 18 | 18 | | 30 | | 36 | | 43 | *4* | 39 | *8* | 20 | *2* | 14 | *7* | 7 | *3* | 7 |
| 20 | 6 | | 13 | *1* | 21 | | 24 | *3* | 23 | *5* | 24 | | 14 | *5* | 7 | *2* | 5 |
| 22 | 2 | | 6 | | 10 | *1* | 13 | *2* | 18 | *2* | 20 | | 23 | *11* | 9 | | 5 |
| 24 | | | 1 | | 5 | | 6 | | 8 | | 10 | | 17 | *4* | 13 | *2* | 7 |
| 26 | | | 1 | | 2 | | 2 | | 5 | *1* | 6 | *1* | 8 | *1* | 7 | | 6 |
| 28 | | | | | 1 | | 3 | | 3 | | 3 | | 3 | *2* | 7 | | 11 |
| 30 | | | | | | | 1 | | 3 | *1* | 2 | | 2 | *1* | 1 | | 6 |
| 32 | | | | | | | | | 1 | | 2 | | 2 | | 2 | | 1 |
| 34 | | | | | | | | | | | 2 | | 3 | *1* | 2 | | 1 |
| 36 | | | | | | | | | | | | | 1 | *1* | | | 2 |
| 38 | | | | | | | | | | | | | 1 | *1* | | | 1 |
| 40 | | | | | | | | | | | | | | | | | |
| Total (0.32 ha) | 531 | *152* | 379 | *54* | 325 | *29* | 296 | *81* | 215 | *93* | 122 | *5* | 117 | *45* | 72 | *9* | 63 |
| Per hectare | 1,659 | *475* | 1,184 | *169* | 1,016 | *90.6* | 925 | *253* | 671.9 | *291* | 381.3 | *15.6* | 365.6 | *141* | 225 | *28.1* | 196.9 |
| Mean d.b.h. | 10.8 | | 12.9 | | 14 | | 14.8 | | 16.8 | | 19.9 | | 21.2 | | 21.9 | | 23.7 |

Table 4e. The development of pine frequency in diameter classes (cm) and *mortality* on the control plot (0.32 ha)

| Diameter class (cm) | 1958 | *1959 –1965* | 1965 | *1966 –1970* | 1970 | *1971 –1975* | 1975 | *1976 –1980* | 1980 | *1981 –1985* | 1985 | *1986 –1990* | 1990 | *1991 –1995* | 1995 | *1996 –2000* | 2000 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 6 | | | | | | | | | | | | | | | | | |
| 8 | 6 | *5* | | | | | | | | | | | | | | | |
| 10 | 8 | *4* | | | | | | | | | | | | | | | |
| 12 | 16 | *5* | 10 | | 6 | *1* | 4 | *4* | | | | | | | | | |
| 14 | 15 | *1* | 10 | | 9 | *1* | 8 | *4* | 3 | *1* | 1 | | | | | | |
| 16 | 25 | *1* | 12 | | 11 | *1* | 10 | *2* | 4 | *1* | 3 | *2* | 2 | *1* | 1 | | |
| 18 | 19 | | 18 | | 9 | | 7 | *2* | 6 | *2* | 2 | | 1 | | 1 | *1* | 1 |
| 20 | 26 | | 23 | | 24 | | 17 | *1* | 12 | | 8 | *1* | 5 | | 3 | | 2 |
| 22 | 20 | *1* | 23 | | 16 | | 18 | | 14 | *1* | 9 | *1* | 10 | *1* | 10 | *2* | 8 |
| 24 | 8 | | 20 | | 24 | | 18 | | 14 | | 17 | *1* | 10 | *3* | 4 | *1* | 3 |
| 26 | 6 | | 9 | | 15 | | 17 | | 17 | | 17 | | 9 | *1* | 10 | *2* | 4 |
| 28 | 3 | | 7 | | 12 | | 18 | | 17 | | 15 | | 18 | | 14 | | 11 |
| 30 | 1 | | 2 | | 5 | | 7 | | 18 | *1* | 14 | | 13 | | 15 | *1* | 12 |
| 32 | 1 | | 2 | | 2 | | 3 | | 8 | | 14 | *1* | 15 | *1* | 15 | | 14 |
| 34 | | | 1 | | 2 | | 4 | | 1 | | 5 | | 7 | | 6 | | 14 |
| 36 | | | | | 2 | | 1 | | 5 | | 3 | | 10 | | 10 | | 7 |
| 38 | | | | | | | | | | | 4 | | 2 | | 4 | | 5 |
| 40 | | | | | | | 2 | | | | 1 | | 4 | | 3 | | 5 |
| 42 | | | | | | | | | 2 | | | | 1 | | 3 | | 4 |
| 44 | | | | | | | | | | | 1 | | | | 1 | | 2 |
| 46 | | | | | | | | | | | 1 | | 1 | | | | 1 |
| 48 | | | | | | | | | | | | | 1 | | 1 | | |
| 50 | | | | | | | | | | | | | | | 1 | | 1 |
| 52 | | | | | | | | | | | | | | | | | |
| 54 | | | | | | | | | | | | | | | | | 1 |
| Total (0.32 ha) | 154 | *17* | 137 | *0* | 137 | *3* | 134 | *13* | 121 | *6* | 115 | *6* | 109 | *7* | 102 | *7* | 95 |
| Per hectare | 481.25 | *53.13* | 428.13 | *0* | 428.13 | *9.375* | 418.75 | *40.625* | 378.13 | *18.75* | 359.38 | *18.75* | 340.63 | *21.88* | 318.75 | *21.88* | 296.88 |
| Mean d.b.h. | 17.8 | | 20.5 | | 22.1 | | 23.3 | | 25.8 | | 27.4 | | 29.3 | | 30.5 | | 32.3 |

Table 4f. The development of larch frequency in diameter classes (cm) and *mortality* on the control plot (0.32 ha)

| Diameter class (cm) | 1958 | *1959 –1965* | 1965 | *1966 –1970* | 1970 | *1971 –1975* | 1975 | *1976 –1980* | 1980 | *1981 –1985* | 1985 | *1986 –1990* | 1990 | *1991 –1995* | 1995 | *1996 –2000* | 2000 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 4 | | | | | | | | | | | | | | | | | |
| 6 | 1 | *1* | | | | | | | | | | | | | | | |
| 8 | 2 | *1* | 1 | *1* | | | | | | | | | | | | | |
| 10 | 10 | *1* | 4 | *2* | 2 | *1* | 1 | | | | | | | | | | |
| 12 | 2 | | 6 | *2* | 4 | | 3 | | 4 | *3* | | | | | | | |
| 14 | 10 | | 4 | | 3 | | 3 | | 1 | | 1 | | 1 | | 1 | | 1 |
| 16 | | | 7 | | 8 | | 4 | | 4 | *1* | 3 | | 2 | | 1 | *1* | |
| 18 | 2 | | 1 | | 1 | | 6 | | 6 | | 4 | | 3 | | 3 | | 3 |
| 20 | 2 | | 1 | | 1 | | | | 2 | | 4 | | 3 | | 2 | | 1 |
| 22 | 1 | | 3 | | 1 | | 1 | | 1 | | | | 3 | | 4 | | 4 |
| 24 | | | | | 2 | | 2 | | | | 1 | | | | 1 | | 1 |
| 26 | | | | | | | 1 | | 2 | | 1 | | | | | | 1 |
| 28 | | | | | | | | | 1 | | 2 | | 2 | | | | |
| 30 | | | | | | | | | | | 1 | | 2 | | 2 | | 1 |
| 32 | | | | | | | | | | | | | 1 | | 2 | | 1 |
| 34 | | | | | | | | | | | | | | | 1 | | 2 |
| 36 | | | | | | | | | | | | | | | | | 1 |
| 38 | | | | | | | | | | | | | | | | | |
| Total (0.32 ha) | 30 | *3* | 27 | *5* | 22 | *1* | 21 | *0* | 21 | *4* | 17 | *0* | 17 | *0* | 17 | *1* | 16 |
| Per hectare | 93.8 | *9.38* | 84.4 | *15.6* | 68.8 | *3.13* | 65.63 | *0* | 65.6 | *12.5* | 53.1 | *0* | 53.1 | *0* | 53.1 | *3.13* | 50 |
| Mean d.b.h. | 12.9 | | 14.3 | | 16.1 | | 17 | | 18.1 | | 20.6 | | 22.3 | | 23 | | 24.5 |

Table 5. The development of mean height and *dead tree height* (all in m)

| Species | 1958 | *1959–1965* | 1965 | *1966–1970* | 1970 | *1971–1975* | 1975 | *1976–1980* | 1980 | *1981–1985* | 1985 | *1986–1990* | 1990 | *1991–1995* | 1995 | *1996–2000* | 2000 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Spruce | 11.8 | *8.8* | 14.7 | *10.9* | 16.0 | *12.4* | 17.2 | *14.0* | 20.0 | *18.4* | 21.8 | *19.1* | 22.7 | *22.6* | 23.5 | *22.8* | 24.1 |
| Pine | 15.3 | *12.1* | 18.2 | – | 19.2 | *15.7* | 20.6 | *17.3* | 23.3 | *19.5* | 24.0 | *22.3* | 25.3 | *23.7* | 26.4 | *23.4* | 27.5 |
| Larch | 13.9 | *12.4* | 16.7 | *13.1* | 18.4 | *16.5* | 19.6 | – | 21.7 | *19.3* | 22.9 | – | 23.8 | – | 25.6 | *23.0* | 26.7 |
| Oak | 12.6 | – | 14.6 | *13.9* | 15.6 | *11.0* | 16.8 | – | 18.0 | *15.0* | 18.8 | *15.5* | 20.3 | – | 20.9 | – | 22.3 |
| Hornbeam | 11.4 | – | 12.6 | – | 13.4 | – | 12.7 | *12.9* | 13.3 | *11.1* | 13.8 | *11.9* | 14.4 | *14.7* | 14.4 | – | 15.8 |
| Aspen | 13.6 | – | 15.0 | *15.4* | 15.8 | *14.9* | 17.2 | *17.1* | 19.3 | *19.0* | 19.5 | *19.5* | – | *0.0* | – | *0.0* | – |
| Birch | 10.0 | *10.0* | – | *0.0* | – | *0.0* | – | *0.0* | – | *0.0* | – | *0.0* | – | *0.0* | – | *0.0* | – |
| Total | 12.6 | *9.2* | 14.4 | *11.3* | 15.9 | *13.1* | 18.0 | *14.5* | 20.6 | *18.1* | 22.0 | *18.0* | 23.1 | *22.3* | 24.3 | *23.1* | 25.1 |

lower diameter classes. Of interest is considerable diameter differentiation in the last years when there are trees of both 16 cm and 54 cm in diameter in the stand.

As for the other admixed species, only larch and in the initial period also aspen reach the general level of the upper canopy; hornbeam and oak are interspersed only as subdominant species.

While the largest d.b.h. of spruce and larch did not exceed 36 cm during the last inventory in 2000, as for pine, 14 trees exceeded d.b.h. 40 cm and two pine trees showed d.b.h. even in excess of 50 cm.

## MEAN AND TOP HEIGHTS

It is evident from the development of mean heights (Table 5) that the stand is markedly height-differentiated. Conifers (spruce, pine and larch) occur as dominant and co-dominant trees whereas the broadleaved admixture (hornbeam and oak) occurs as subdominant and intermediate trees.

Mean heights of larch and pine are taller than mean heights of spruce for the whole period, which is caused to a certain extent by the high proportion of subdominant trees of spruce. Thus, top heights (Table 6) exhibit higher information values. It is obvious that pine and larch exceeded originally dominant spruce, today showing 2 m taller top heights than spruce.

The tallest pine and larch trees were 31 m (or 30 m) high, the tallest spruce trees 29 m.

## MEAN DIAMETER AT BREAST HEIGHT

The development of mean d.b.h. corresponds with its height distribution. Conifers show dynamic increments for the whole period of measurement (Table 7). However, from the beginning of the measurement, pine has been markedly differentiated and its mean d.b.h. has exceeded the mean d.b.h. of spruce and larch by almost 10 cm. On the other hand, broadleaved species have lagged behind and their low mean d.b.h. corresponds with their subdominant position in the stand.

## STAND BASAL AREA

To a certain extent, the characteristic informs about the production potential of particular species in the mixed stand which develops without intentional human measures. The basal area (b.a.) development in particular species and in the whole stand can bee seen in Table 8.

This table shows stagnation and even decrease in b.a. in some 5-year periods. It is evidently caused by the extraordinarily high mortality of spruce, originally a dominant species in the stand. Spruce decreased its b.a. by 45% during the period of measurements (1958–2000). The largest fluctuations occurred in the last years of the measurement (1985–2000). In the already mentioned more humid period 1985–1990, b.a. of spruce increased by 10% while in drier periods 1980–1985 and 1990–1995 it decreased by more than 20 or even 35%.

Table 6. The development of top height (m)

| Species | 1958 | 1965 | 1970 | 1975 | 1980 | 1985 | 1990 | 1995 | 2000 |
|---|---|---|---|---|---|---|---|---|---|
| Spruce | 17.38 | 20.52 | 21.405 | 23.16 | 24.725 | 25.025 | 26.5 | 26.675 | 27.13 |
| Pine | 17.82 | 20.83 | 21.855 | 23.545 | 25.85 | 26.35 | 27.875 | 29 | 29.925 |
| Larch | 14.725 | 17.74 | 18.605 | 19.805 | 21.975 | 24.9 | 26.2 | 28.4 | 29.2 |
| Oak | 13.7 | 16.22 | 17 | 17.54 | 19.1 | 19.4 | 20.3 | 20.9 | 22.3 |
| Hornbeam | 12.585 | 13.78 | 14.8 | 14.62 | 15 | 15.15 | 14.425 | 18.6 | 20.4 |
| Aspen | 14.44 | 16.44 | 16.76 | 17.24 | 19.25 | 19.5 | – | – | – |

On the other hand, b.a. of other species and particularly of pine regularly increased so that the value of b.a. for the whole stand increased although insignificantly from 32.2 in 1958 to 38.7 m²/ha in 2000.

## MAIN STAND GROWING STOCK

The total growing stock of the stand increased from the original value of 218.9 m³/ha in 1958 to 473.4 m³/ha in 2000. Table 9 shows that the increase in growing stock was irregular in two five-year periods (1980–1985 and 1990–1995), when even total decrease in the standing volume was recorded. In consequence of disintegration of the spruce component of the stand, the growing stock of the originally dominant species did not virtually increase in the course of 42 years (increase from 111.2 m³/ha at the first measurement to 116.9 m³/ha at the last measurement). Thus, volume production in the stand is based on pine increment. Its original standing volume (92.0 m³/ha in 1958) increased more than three times in the studied period (to 309.4 m³/ha). Although all other interspersed species show a relatively high growing stock increase, the figures appear not to be significant in absolute units due to the small proportion of the species (e.g. increase in larch, oak and hornbeam growing stock by 26.1, 3.9 and 4.8 m³/ha, respectively).

## STAND DENSITY AND SPECIES COMPOSITION

In spite of the spruce component disintegration the stand density ranged from 0.87 to 1.1 in the course of 42 years (minimum in 1995, maximum in 1975). From the silvicultural and production point of view, however, comparison of the development of partial stocking of particular species is more important (Table 10). We can find a noticeable decrease in stocking in spruce from 0.59 in 1958 to 0.21 in the last year of measurement and a considerable increase in the partial stocking of pine (from 0.38 to 0.57) which gradually replaces the declining spruce occupying the void together with other admixed species.

Table 11 is of similar importance as the previous table demonstrating the development of species composition in the stand. It shows the decline of spruce (its proportion decreased from 54% in 1958 to 23% in 2000). Today, pine with 63% is a prevailing species and the proportions of the other previously interspersed species increase.

## CONCLUSIONS

The results of a 42-year study of spontaneous development of a spruce monoculture in Stand 469C7, Křtiny Training Forest Enterprise, show its gradual disintegration and conversion to a mixed stand where the stand-forming function is fulfilled by admixed and interspersed species, in our case particularly by pine, but also this species is gradually replaced by broadleaved species in conformation to site conditions (more in JELÍNEK 2000).

In consequence of natural processes the dieback of spruce (88%) in the stand was extremely high during 42 years of measurements. Spruce dies even as a dominant and co-dominant tree already at an age of 50 years. The fact is very probably related to extreme climatic conditions, particularly precipitation deficit. On the other hand, the mortality of other originally admixed species

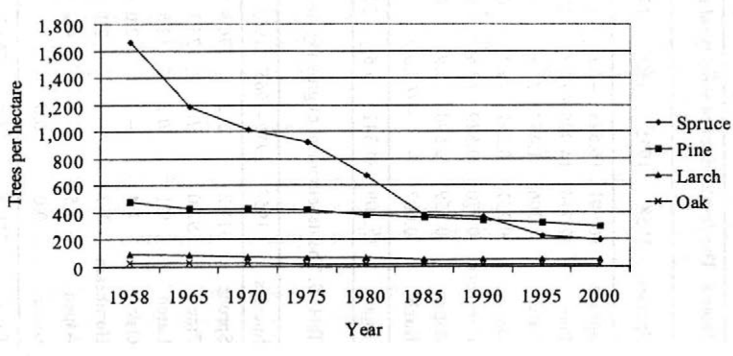


Fig. 1. Development of the number of spruce, pine, larch and oak trees (individuals per ha)

Table 7. The development of mean diameter (d.b.h.) and *dead tree diameter* (all in cm)

| Species | 1958 | *1959–1965* | 1965 | *1966–1970* | 1970 | *1971–1975* | 1975 | *1976–1980* | 1980 | *1981–1985* | 1985 | *1986–1990* | 1990 | *1991–1995* | 1995 | *1996–2000* | 2000 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Spruce | 10.8 | 7.7 | 12.8 | 9.4 | 14.0 | 10.2 | 14.8 | 11.6 | 16.8 | 13.9 | 19.9 | 17.0 | 21.2 | 21.1 | 21.9 | 19.6 | 23.7 |
| Pine | 17.8 | 11.5 | 20.5 | – | 22.1 | 14.0 | 23.3 | 14.6 | 25.8 | 19.0 | 27.4 | 21.5 | 29.3 | 24.1 | 30.5 | 24.2 | 32.3 |
| Larch | 12.9 | 8.4 | 14.3 | 9.8 | 16.1 | 11.1 | 17.0 | – | 18.1 | 12.7 | 20.6 | – | 22.3 | – | 23.0 | 16.3 | 24.5 |
| Oak | 10.3 | – | 11.1 | 10.8 | 11.7 | 6.5 | 12.9 | – | 13.9 | 10.7 | 15.1 | 10.4 | 16.9 | – | 17.7 | – | 19.1 |
| Hornbeam | 8.0 | – | 8.4 | – | 8.7 | – | 8.9 | 7.6 | 9.4 | 7.9 | 9.9 | 6.3 | 12.0 | 11.0 | 13.2 | – | 15.9 |
| Aspen | 13.1 | – | 13.6 | 13.7 | 13.9 | 13.1 | 14.6 | 14.2 | 15.5 | 14.9 | 16.2 | 16.2 | – | – | – | – | – |
| Birch | 5.5 | 5.5 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Total | 12.2 | 8.1 | 14.4 | 9.4 | 15.9 | 10.8 | 16.8 | 12.0 | 19.1 | 14.0 | 22.0 | 15.1 | 23.8 | 20.9 | 25.3 | 21.3 | 27.0 |

Table 8. The development of stand basal area ($m^2$/ha) and *its increase in per cent*

| Species | 1958 | 1965 | (%) | 1970 | (%) | 1975 | (%) | 1980 | (%) | 1985 | (%) | 1990 | (%) | 1995 | (%) | 2000 | (%) | Total increase to 1958 | (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Spruce | 16.901 | 16.543 | –2.1 | 17.104 | 3.4 | 17.338 | 1.4 | 16.151 | –6.8 | 12.496 | –22.6 | 13.709 | 9.7 | 8.968 | –34.6 | 9.233 | 3.0 | –7.668 | –45.37 |
| Pine | 12.714 | 14.925 | 17.4 | 17.332 | 16.1 | 18.927 | 9.2 | 20.605 | 8.9 | 22.100 | 7.3 | 23.901 | 8.1 | 24.203 | 1.3 | 25.293 | 4.5 | 12.578 | 98.93 |
| Larch | 1.306 | 1.454 | 11.3 | 1.473 | 1.3 | 1.582 | 7.4 | 1.806 | 14.2 | 1.863 | 3.2 | 2.194 | 17.8 | 2.354 | 7.3 | 2.515 | 6.8 | 1.209 | 92.52 |
| Oak | 0.251 | 0.291 | 16.1 | 0.288 | –1.2 | 0.299 | 3.9 | 0.351 | 17.3 | 0.356 | 1.6 | 0.369 | 3.7 | 0.405 | 9.8 | 0.482 | 18.9 | 0.232 | 92.34 |
| Hornbeam | 0.470 | 0.529 | 12.6 | 0.574 | 8.5 | 0.593 | 3.3 | 0.647 | 9.2 | 0.668 | 3.2 | 0.756 | 13.2 | 0.786 | 4.0 | 1.172 | 49.2 | 0.703 | 149.67 |
| Aspen | 0.559 | 0.598 | 6.9 | 0.428 | –28.5 | 0.262 | –38.7 | 0.117 | –55.2 | 0.064 | –45.1 | – | –100.0 | – | – | – | – | –0.559 | –100.00 |
| Birch | 0.007 | – | –100.0 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | –0.007 | –100.00 |
| Total | 32.209 | 34.341 | 6.6 | 37.198 | 8.3 | 39.000 | 4.8 | 39.677 | 1.7 | 37.548 | –5.4 | 40.930 | 9.0 | 36.717 | –10.3 | 38.695 | 5.4 | 6.5 | 20.1 |

Table 9. The development of growing stock and *standing volume of dead trees* (all in $m^3$/ha)

| Species | 1958 | *1959–1965* | 1965 | *1966–1970* | 1970 | *1971–1975* | 1975 | *1976–1980* | 1980 | *1981–1985* | 1985 | *1986–1990* | 1990 | *1991–1995* | 1995 | *1996–2000* | 2000 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Spruce | 111.2 | 3.2 | 136.8 | 2.2 | 154.8 | 1.8 | 169.4 | 7.7 | 179.2 | 15.4 | 145.4 | 1.3 | 166.0 | 20.5 | 111.9 | 3.4 | 116.9 |
| Pine | 92.0 | 1.1 | 125.2 | – | 152.9 | 0.3 | 178.4 | 1.7 | 215.1 | 1.7 | 235.6 | 2.3 | 267.4 | 3.5 | 283.2 | 3.4 | 309.4 |
| Larch | 9.1 | 0.1 | 12.8 | 0.2 | 14.2 | 0.2 | 16.6 | – | 21.4 | 0.5 | 22.6 | – | 27.4 | – | 32.1 | 0.3 | 35.3 |
| Oak | 1.4 | – | 2.0 | 0.1 | 2.2 | 0.0 | 2.4 | – | 3.1 | 0.1 | 3.3 | 0.1 | 3.7 | – | 4.2 | – | 5.3 |
| Hornbeam | 1.7 | – | 2.1 | – | 2.5 | – | 2.6 | 0.0 | 3.1 | 0.0 | 3.3 | 0.1 | 3.8 | 0.1 | 3.9 | – | 6.5 |
| Aspen | 3.5 | – | 4.2 | 0.3 | 3.1 | 0.5 | 2.0 | 0.4 | 1.0 | 0.1 | 0.6 | 0.2 | 0.0 | – | 0.0 | – | 0.0 |
| Birch | 0.0 | 0.0 | – | – | 0.0 | – | 0.0 | – | 0.0 | – | 0.0 | – | 0.0 | – | 0.0 | – | 0.0 |
| Total | 218.9 | 4.4 | 283.2 | 2.8 | 329.7 | 2.8 | 371.5 | 9.9 | 422.9 | 17.9 | 410.8 | 3.9 | 468.2 | 24.1 | 435.2 | 7.0 | 473.4 |

Table 10. The development of stand density

| Species | 1958 | 1965 | 1970 | 1975 | 1980 | 1985 | 1990 | 1995 | 2000 |
|---|---|---|---|---|---|---|---|---|---|
| Spruce | 0.59 | 0.53 | 0.52 | 0.51 | 0.44 | 0.31 | 0.34 | 0.22 | 0.21 |
| Pine | 0.38 | 0.41 | 0.46 | 0.49 | 0.50 | 0.53 | 0.55 | 0.55 | 0.57 |
| Larch | 0.05 | 0.05 | 0.05 | 0.05 | 0.05 | 0.05 | 0.06 | 0.06 | 0.06 |
| Oak | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.02 |
| Hornbeam | 0.02 | 0.03 | 0.03 | 0.03 | 0.03 | 0.03 | 0.03 | 0.03 | 0.05 |
| Aspen | 0.04 | 0.04 | 0.03 | 0.02 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 |
| Birch | 0.00 | – | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Total | 1.09 | 1.07 | 1.09 | 1.10 | 1.04 | 0.94 | 0.99 | 0.87 | 0.91 |

Table 11. The development of species composition (in %)

| Species | 1958 | 1965 | 1970 | 1975 | 1980 | 1985 | 1990 | 1995 | 2000 |
|---|---|---|---|---|---|---|---|---|---|
| Spruce | 53.8 | 49.6 | 47.2 | 46.0 | 42.0 | 33.3 | 33.8 | 24.7 | 23.4 |
| Pine | 34.9 | 38.4 | 42.4 | 44.5 | 48.0 | 56.0 | 55.6 | 62.6 | 62.6 |
| Larch | 4.3 | 4.6 | 4.2 | 4.4 | 5.0 | 5.4 | 5.8 | 7.0 | 6.9 |
| Oak | 1.0 | 1.2 | 1.1 | 1.1 | 1.3 | 1.5 | 1.4 | 1.7 | 1.8 |
| Hornbeam | 2.1 | 2.4 | 2.5 | 2.6 | 2.9 | 3.3 | 3.4 | 4.0 | 5.3 |
| Aspen | 3.8 | 3.8 | 2.6 | 1.5 | 0.6 | 0.4 | 0.0 | 0.0 | 0.0 |
| Birch | 0.0 | – | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Total | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |

was substantially lower and they were gradually replacing spruce in the stand. Conifers occur as dominant and co-dominant species whereas broadleaves occur as subdominant and intermediate species.

In the period 1958–2000, stand basal area increased only insignificantly (from 32.2 to 38.7 $m^2$/ha) due to high mortality of spruce. Standing volume, however, irregularly but significantly increased from 219 to 417 $m^3$/ha particularly with respect to the dynamic increase in the volume of pine.

Spruce monocultures at allochthonous sites of uplands are so unstable that they are not capable to fulfil their functions. In these warm regions with critical precipitation deficit, not only monocultures but also stands with the dominant position of spruce very probably disintegrate before they achieve rotation age, not accomplishing their wood-producing or non-wood-producing roles. Uncertain development of the climate in the next 100 years still emphasizes the absolute unsuitability of establishing these allochthonous stands.

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# Produkční potenciál a ekologická stabilita smíšených lesních porostů v pahorkatinách – IV. Smíšený porost smrku s borovicí v souboru lesních typů 2S

P. JELÍNEK, P. KANTOR

*Mendelova zemědělská a lesnická univerzita, Lesnická a dřevařská fakulta, Brno, Česká republika*

**ABSTRAKT**: Ve studii je posuzován růst, vývoj, produkce a stabilita smrkové monokultury s dalšími nalétlými dřevinami, založené před 76 lety. Porost leží v nadmořské výšce 410 m a je od roku 1958 ponechán samovolnému vývoji bez úmyslných probírkových zásahů. V té době byl porost charakterizován jako 33letá jednotlivě smíšená, tloušťkově i výškově výrazně rozrůzněná smrková tyčovina s přimíšenou borovicí, s vtroušeným modřínem a listnáči (dub, habr, osika, bříza). Tento nepůvodní lesní ekosystém se zcela nerozpadl pouze proto, že úlohu nosné hlavní dřeviny zde převzala při extrémním ústupu smrku původně jednotlivě vtroušená, později přimíšená borovice z přirozené obnovy. Nezanedbatelné bylo ve svém součtu i zlepšující se postavení vtroušených dřevin – modřínu, dubu a podúrovňového habru. Znovu tak bylo potvrzeno, že zpočátku nevýznamný podíl jednotlivě přimíšených a vtroušených dřevin může zajistit existenci, popř. i produkci a stabilitu lesních ekosystémů i po dramatickém úhynu původně dominantní dřeviny, v našem případě smrku.

**Klíčová slova**: smrk; smíšené porosty; produkce; monokultura; přirozený vývoj; ekologická stabilita

Studie je v pořadí čtvrtým sdělením v rámci širokého výzkumného projektu *Produkce a ekologická stabilita smíšených lesních porostů v antropicky se měnících podmínkách jako podklad pro návrh cílové druhové skladby dřevin* (KANTOR 1997; KANTOR, PAŘÍK 1998; KNOTT, KANTOR 2000; KANTOR et al. 2001), který se řeší na Lesnické a dřevařské fakultě Mendelovy zemědělské a lesnické univerzity v Brně.

Porost 469C7 leží na Školním lesním podniku Křtiny v souboru lesních typů 2S v nadmořské výšce 410 m. Jeho dendrometrické charakteristiky od doby založení experimentu (1958) až do posledního měření v roce 2000 ukazuje tab. 1. Výsledky ze 42letého sledování samovolného vývoje smrkové monokultury v porostu ukazují její postupný rozpad a přeměnu ve smíšený porost, v němž porostotvornou funkci přebírají přimíšené a vtroušené dřeviny, v našem případě zejména borovice. I ta je postupně podrůstána stanovištně původními listnáči. V porostu došlo vlivem přirozených procesů během 42 let měření k extrémnímu hynutí smrku (88% – tab. 2 a obr. 1). Již ve věku 50 let smrk hyne dokonce i v úrovni (tab. 4a). To je s vysokou pravděpodobností způsobeno extrémními klimatickými podmínkami, zejména pak nedostatkem srážek. Měsíční úhrny srážek v klimatické stanici Olomučany ukazuje tab. 3 (zvýrazněny jsou měsíce se srážkami přesahujícími 70 mm). Naproti tomu další – původně vtroušené – dřeviny vykazovaly úmrtnost podstatně nižší, a tak postupně nahradily smrk v porostu. Jehličnaté dřeviny obsadily úroveň a nadúroveň, zatímco listnaté dřeviny podúroveň (tab. 4b–e).

Ve sledovaném období 1958–2000 se zvýšila kruhová výčetní základna porostu (tab. 8) jen nepatrně (ze 32.2 $m^2$/ha na 38.7 $m^2$/ha), a to v důsledku vysoké mortality smrku. Zásoba porostu (tab. 9) naproti tomu nepravidelně, ale významně vzrůstá z 219 $m^3$/ha na 417 $m^3$/ha, což je způsobeno zejména dynamickým nárůstem objemu borovic.

Smrkové monokultury jsou na nepůvodních stanovištích pahorkatin prokazatelně natolik nestabilní, že nejsou schopny plnit své produkční ani mimoprodukční funkce. Nejen monokultury, ale i porosty s dominantním postavením smrku se v těchto teplých oblastech s kritickým nedostatkem srážek s vysokou pravděpodobností rozpadnou ještě před dosažením mýtního věku, aniž by splnily své produkční či mimoprodukční poslání. Nejistota vývoje klimatu v příštích 100 letech nesprávnost zakládání těchto alochtonních porostů ještě umocňuje.

*Corresponding author:*

Ing. PETR JELÍNEK, PhD., Mendelova zemědělská a lesnická univerzita, Lesnická a dřevařská fakulta, Lesnická 37, 613 00 Brno, Česká republika
tel.: + 420 5 45 13 41 24, fax: + 420 5 45 21 14 22, e-mail: jelen@mendelu.cz

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# Effect of increased nitrogen depositions and drought stress on the development of Scots pine (*Pinus sylvestris* L.) – I. Response of above-ground parts

**E. PALÁTOVÁ**

*Mendel University of Agriculture and Forestry, Faculty of Forestry and Wood Technology, Brno, Czech Republic*

**ABSTRACT**: Effect of drought stress, stress by increased nitrogen depositions and combined effect of the two stress factors on the growth of Scots pine (*Pinus sylvestris* L.) were studied in two experimental series in the period 1994–1997. The drought stress was induced by reduction of atmospheric precipitation by 60%, the increased nitrogen depositions were simulated by repeated applications of ammonium sulphate at a dose corresponding to 100 kg N/ha per year. All stress factors under study affected the height increment of above-ground parts, length and colour of needles, number of buds in the terminal rosette, content of free amino acids and the ratio of elements in dry matter of assimilatory tissue. Drought acted as a stress factor stronger than the nitrogen depositions themselves. The strongest impact was recorded in the simultaneous influence of the stress factors.

**Keywords:** *Pinus sylvestris* L.; nitrogen; drought; height increment; habit; defoliation; content of free amino acids

Nitrogen inputs represent an important site factor in the forests of Central and Northern Europe. Only several years ago nitrogen used to be an element that considerably limited the growth and production of tree species. Since approximately the 1960s the production of spruce and pine stands in particular has been increasing, which is ascribed to the increasing nitrogen depositions (KENNEL 1994; KREUTZER 1994; ROTHE 1994). However, despite the positive effect of nitrogen depositions on the production, a number of authors point out the potentially unfavourable consequences of continuing inputs of nitrogen into forest ecosystems such as imbalance of nutrients, soil acidification, qualitative and quantitative changes of humus, eutrophication of waters, etc. (KÖLLING 1991; EICHHORN, PAAR 1992), and also some adverse responses of tree species such as impaired frost resistance (DUECK et al. 1991), changes in the shoot to root ratio (HOLOPAINEN, HEINONEN-TANSKI 1993), or impaired mechanical stability and wind resistance due to the increased size of crowns (KREUTZER 1994).

Nitrogen depositions on sites with the naturally low N-supply manifest in a markedly elevated increment. Some experiments indicated that there is a correlation between growth and N-content in needles. For example a mathematical model by HOFMANN et al. (1990) claims that pine stands achieve their maximum increment with needle N-content ranging between 1.8% and 2.3%; the authors assume that the culmination of increment occurs at the content of 2.1% N. According to BERGMANN (1983), the N-content in 1-year pine needles ranging between 1.4% and 1.7% signals a sufficient element supply. However, recent analyses found the N-contents > 2% in some localities, which are considered to be toxic, inducing needle browning and dieback (HUNGER 1989; HEINSDORF 1991). Further increase of nitrogen in the plant leads to decreasing increment and results in stand opening. The increased uptake of nitrogen and imbalance in the contents of other nutrients induce deviations in the plant metabolism and usually relate to the high content of organic detergent soluble N in the form of free amino acids whose composition is species-specific and might differ also according to the impacting stress (RABE 1990; NÄSHOLM, ERICSSON 1990).

Another problem recently subjected to a massive discussion is global climate changes due to the glasshouse effect. Some models worked out by various laboratories

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predict a possible prolongation of intervals between precipitation events in central latitudes, especially in the spring and summer seasons, which would mean exposure of plants to drought stress.

Contemplating about the effect of drought on tree species we can make use of information obtained in the extremely dry years 1906, 1911, 1921, 1947, 1949 and 1976 (WOLZ, RICKLI 1987). Summarizing the published data the authors arrived at a conclusion that the impact of drought showed regional variations and was site-dependent, drought primarily affected plantings, young crops and advance growths with mature stands showing less damage, and damage occurred particularly as a result of dry spring and autumn periods. However, the analysis of data from previous years does not make it possible to draw unambiguous conclusions because the health condition of trees has worsened due to anthropogenic air-pollution, which reflects in a much higher susceptibility of tree species to stress and any other change of conditions.

HSIAO et al. (1976 in MENGEL, KIRKBY 1978) claim that the stress induced by water deficit affects physiological processes adversely influencing the growth and elongation of cells, building of cell walls, protein synthesis, and inducing an enzyme-pool decrease, which particularly holds for nitrate reductase. By means of turgor water stress inhibits the opening of stomata and hence transpiration and $CO_2$ assimilation. The low water potentials may also decrease respiration and translocation of photosynthates. The water deficit also affects plant-growth regulators, namely abscisic acid, the concentration of which would grow conspicuously. Drought stress is accompanied by the accumulation of free amino acids, proline in particular, which is generally considered to be one of the drought stress indicators (GUSTKE, LÜTTSCHWAGER 1990).

The complex of the above-mentioned drought-induced physiological changes is usually reflected in reduced growth. The growth of above-ground parts may also be reduced by restricted formation of buds from which new shoots are to grow next year (KOZLOWSKI 1971) as well as by later flushing (KATTNER 1992). Reduced growth of plants due to drought is also attributed to reduced uptake of nutrients from dry soil (MENGEL, KIRKBY 1982 in LEHTO 1992). The reduction of height increment in experimental conditions under the influence of simulated drought was documented mainly in spruce (BEIER et al. 1995; NILSSON, WIKLUND 1992; MAUER, PALÁTOVÁ 1996) but it was also found in pine as a consequence of climatically dry years (KRAUSS 1965). DILS

Table 1. Scheme of trial establishment

| Experimental series | Pot Trial | Stand *in situ* |
|---|---|---|
| Period | 1994–1997 | 1996–1997 |
| Method | Pine seedlings 2 + 0 were planted into 10l plastic pots filled with earth from a mixed stand. The pots were placed in shelters designed to eliminate penetration of atmospheric precipitation but to allow for air flow; they did not affect the hydrothermal regime in the above-ground part space. | Stand 336A1, age 12 years, primary management group HS 223, forest type 2S3, SW exposure. Reduction of precipitation in drought variants was ensured by structures with frames covered with transparent backed foil which was installed 120–20 cm above the soil surface. Precipitation water was drained off. |
| Variants | | |
| Control | Current irrigation 2× a week, total amount of supplied water 500 mm/year. Irrigation was made with fountain water complying with the standard for tap water. | Natural amount of precipitation: (1996 – 637 mm; 1997 – 713 mm).* In 1996 and 1997, wet deposition of $NO_3$-N was 0.25–0.50 g/m$^3$/year and wet deposition of $NH_4$-N was 0.25–0.50 g/m$^3$/year.** |
| Drought | Current irrigation 1× in 2 weeks, total amount of supplied water corresponded to 40% of the Control. | Reduction of precipitation to 40% of the Control. |
| Nitrogen | Irrigation identical as in the Control + 100 kg N/ha/year as $(NH_4)_2SO_4$. Application in 3 partial doses at all times in the 1st half of the growing period. | Natural amount of precipitation + 100 kg N/ha/year as $(NH_4)_2SO_4$. Application in 3 partial doses at all times in the 1st half of the growing season. |
| Drought + N | Irrigation identical as in var. Drought + 100 kg N/ha/year as $(NH_4)_2SO_4$. Application in 3 partial doses at all times at the beginning of the growing season. | Reduction of precipitation to 40% of the Control + 100 kg N/ha/year as $(NH_4)_2SO_4$. Application in 3 partial doses at all times at the beginning of the growing season. |

*Source: Czech Hydrometeorological Institute, Brno

**Source: Air pollution in the Czech Republic in 1996, 1997 (published by the Czech Hydrometeorological Institute, Air Quality Protection Department) and DAY (1952 in LYR et al. 1967) found out that even several-week summer periods of drought may have a significant effect on height increment that can be reduced by 30–70%. According to LYR et al. (1967) critical is a sequence of several dry years. Susceptible tree species may respond by suppressed growth for several years with their recovery proceeding very slowly.

It is obvious from the above survey that the issues of increased N-depositions and drought and their effect on forest ecosystems and tree species as their edificators are paid great attention at present. Norway spruce has been the main object of interest until now – e.g. Skogaby Project in Sweden (NILSSON, WIKLUND 1992), Klosterhede in Denmark (GUNDERSEN et al. 1995) or MAUER and PALÁTOVÁ (1996) in the Czech Republic. The response of Scots pine to increased N-depositions and drought stress has not been subjected to a complex research so far either abroad or in the conditions of the Czech Republic. Taking into account the specific site requirements of the species, the knowledge from research on other tree species cannot be unambiguously applied to pine, which led us to establish experiments whose goal was to contribute to the exact knowledge of Scots pine and its response to the above stress factors.

## MATERIAL AND METHODS

### MATERIAL AND GENERAL SCHEME OF TRIAL ESTABLISHMENT

The effect of increased nitrogen depositions and drought stress on Scots pine (*Pinus sylvestris* L.) was studied in two experimental series: in a Pot Trial to study responses of plants immediately after planting, and in a Stand *in situ* to study responses of a 12-year pine stand. Detailed data on the establishment of the two experimental series are presented in Table 1.

### METHODOLOGICAL PROCEDURES OF PARTIAL ANALYSES

#### Biometrical characteristics of above-ground parts

Parameters measured in all plants and in all variants of the two experimental series at the end of each growing season in the course of the study were total height and above-ground part increment.

#### Tree habit

Stem form was assessed in the Pot Trial from the second year of measurements in order to find out the incidence of trees with straight and crooked stems in the respective variants. Trees with crooked stems were further classified by the reason of stem crook (substitution of terminal shoot and without apparent reason). Numbers of trees with form variations were expressed as per cent of the total number of plants in the variant. From the second year of study all plants in the respective variants of Pot Trial were measured for the number of branches in the last whorl and for the number of buds in the terminal rosette at the end of each growing season.

#### Needle length, defoliation

Length of the last generation needles was measured in all variants of both experimental series at the end of the growing season. Needles were sampled from the upper third of the crown. Each variant included measurements of 500 needles. Final assessment in the Pot Trial was an assessment of the degree of defoliation in all plants in three needle years. Individual needle years were visually assessed to estimate the percentage of present needles (100% = complete needle year). The measured values were used to calculate mean defoliation of the given needle year and to express in per cent the number of trees affected by defoliation.

#### Losses

Losses in the respective variants of both experimental series were assessed every year; the number of dead trees was expressed as per cent of the total number of trees in the variant.

#### Analysis of needle dry matter and element ratios

Samples for the chemical analysis of needles were collected at the end of each growing season, simultaneously with sampling the last needle year for length measurements. Dry matter of the needles was measured in three replications for N, P, K, Ca, Mg, total S and total Al contents. In the last year of study the measurements were extended to detect boron content in both experimental series. The measured values served for the calculation of element ratios.

#### Needle content of free amino acids

Contents of free amino acids were determined according to methodological procedures described by NGUYEN and PAQUIN (1971) and KRISHCHENKO (1978) on the liquid chromatograph Mikrotechna Type AAA 344 with ion-ex column of 20 cm and with the packing Ostion LG FA manufactured by Spolchemia Ústí nad Labem; the used method was jump elution with lithium citrate buffers and ninhydrin detection with the photometer of 520nm wave length. Quantitative assessment was made by the programme Amik regularly supplied with AAA 344. The needle samples were collected from the upper part of the crown towards the end of the growing season. The content of free amino acids was measured only in 1996.

#### Mathematical and statistical assessment

Results of the measurements were processed by common statistical methods. Significance of results was determined by *t*-test on the level of significance 95% (signs in Tables: + significant variation; – insignificant variation).

## RESULTS

Pines responded to the effects of simulated stress factors by a number of changes on their above-ground parts

Table 2. Responses of some parameters of above-ground parts to the impact of stress factors in the experimental series Pot Trial and Stand

| Experimental series | Pot Trial | | | | Stand | |
|---|---|---|---|---|---|---|
| Year | 1994 | 1995 | 1996 | 1997 | 1996 | 1997 |
| | Height increment (cm) | | | | | |
| Control | 19.4 ± 4.5 | 26.6 ± 7.4 | 36.3 ± 4.9 | 32.3 ± 5.1 | 58.9 ± 18.4 | 66.9 ± 11.3 |
| Drought | 17.4 ± 4.2+ | 19.5 ± 6.7+ | 15.5 ± 4.9+ | 12.1 ± 4.4+ | 61.7 ± 17.5– | 40.4 ± 8.6+ |
| Nitrogen | 19.1 ± 4.7– | 26.8 ± 6.6– | 26.8 ± 6.0+ | 25.7 ± 6.3+ | 55.5 ± 13.8– | 57.3 ± 7.9+ |
| Drought + N | 17.1 ± 6.0+ | 18.2 ± 6.3+ | 12.8 ± 4.9+ | 4.5 ± 1.9+ | 58.9 ± 12.8– | 49.1 ± 9.1+ |
| | Needle length (mm) | | | | | |
| Control | 50.0 ± 8.2 | 42.3 ± 6.4 | 32.8 ± 7.3 | 31.2 ± 6.1 | 47.2 ± 9.0 | 58.6 ± 8.8 |
| Drought | 38.2 ± 7.8+ | 34.9 ± 5.3+ | 27.8 ± 4.4+ | 26.5 ± 6.2+ | 41.6 ± 9.5+ | 53.6 ± 10.9+ |
| Nitrogen | 52.6 ± 6.3+ | 53.8 ± 9.6+ | 48.7 ± 13.0+ | 44.9 ± 9.2+ | 53.3 ± 11.1+ | 79.6 ± 10.3+ |
| Drought + N | 41.3 ± 7.6+ | 34.5 ± 6.4+ | 36.8 ± 6.8+ | 20.7 ± 5.1+ | 55.2 ± 9.4+ | 61.0 ± 11.3+ |
| | Losses (%) | | | | | |
| Control | 0 | 0 | 0 | 0 | 0 | 0 |
| Drought | 0 | 2 | 2 | 4 | 0 | 0 |
| Nitrogen | 0 | 0 | 0 | 7 | 0 | 0 |
| Drought + N | 0 | 2 | 2 | 75 | 0 | 0 |

with the trend of responses in both experimental series being identical in the absolute majority of cases and differing only in the intensity of manifestation.

**Height of above-ground parts:** Height increment was adversely affected by all induced stresses in both experimental series with drought being a stronger stress factor than N-depositions (Table 2). While a significant reduction in the Pot Trial was discernible immediately in the first year of research and was increasing with the time of exposure, in the experimental series Stand it appeared with a year's delay. N-depositions did not initially affect the height increment significantly but their negative effect was observed from the third year in the Pot Trial and from the second year in the Stand. The strongest and fastest response of pines in both experimental series was exhibited to the simultaneous combination of stress factors (var. Nitrogen + Drought).

**Plant habit:** Anomalies in the habit of trees were found only in the experimental series Pot Trial in the course of the study (Table 3). The variant Drought showed a decreasing number of branches in the whorl from the second year of exposure. In this variant, the number of buds in the terminal rosette gradually decreased from the second year of exposure to 47% of the Control in the last year of research. The combined stress exhibited the strongest impact and decreased the number of branches in the whorl after 4 years of exposure to 35% and the number of buds in the terminal rosette to mere 23% of the Control. In the variant Nitrogen the number of buds did not show any change; the buds were however apparently larger than those in the Control. Apart from the abovementioned morphological abnormalities there were also some deviations from the normal stem form in the Pot Trial (not presented in Tables). A considerable percent-

Table 3. Number of branches in the last whorl, number of buds in the terminal rosette – experimental series Pot Trial

| Year | 1994 | 1995 | 1996 | 1997 |
|---|---|---|---|---|
| | Number of branches in the last whorl | | | |
| Control | not measured | 5.4 ± 1.7 | 5.3 ± 0.9 | 5.2 ± 0.9 |
| Drought | not measured | 5.1 ± 2.1– | 3.7 ± 0.9+ | 2.7 ± 0.9+ |
| Nitrogen | not measured | 6.3 ± 1.5+ | 5.4 ± 0.8– | 4.5 ± 0.9+ |
| Drought + N | not measured | 5.2 ± 1.9– | 3.6 ± 1.0+ | 1.8 ± 1.1+ |
| | Number of buds in the terminal rosette | | | |
| Control | not measured | 5.1 ± 1.2 | 5.5 ± 0.6 | 5.3 ± 0.7 |
| Drought | not measured | 4.1 ± 1.3+ | 2.8 ± 1.1– | 2.5 ± 0.9+ |
| Nitrogen | not measured | 5.1 ± 1.6– | 5.2 ± 0.9– | 5.2 ± 0.9– |
| Drought + N | not measured | 4.1 ± 1.5+ | 2.4 ± 0.9+ | 1.2 ± 0.8+ |

Table 4. Needle loss at the end of the growing season (1997) – experimental series Pot Trial

| Variant | Needle loss | | | | | |
|---|---|---|---|---|---|---|
| | Needle-year class 1 | | Needle-year class 2 | | Needle-year class 3 | |
| | Occurrence in % of trees | Defoliation (%) | Occurrence in % of trees | Defoliation (%) | Occurrence in % of trees | Defoliation (%) |
| Control | 0 | 0 | 0 | 0 | 0 | 0 |
| Drought | 0 | 0 | 46 | 30.9 ± 18.2 | 87 | 60.7 ± 32.0 |
| Nitrogen | 0 | 0 | 2 | 31.0 ± 1.4 | 72 | 48.8 ± 29.6 |
| Drought + N | 0 | 0 | 78 | 68.6 ± 28.5 | 100 | 92.5 ± 15.4 |

age of trees showed crooked stems with the crook being evoked either by the substitution of the terminal shoot or without any apparent reason. The first crooked stems appeared in the variant Drought from the second year of the experiment. There were 96% of crooked stems at the end of the study: 18% of cases were terminal substitutions and the crooked stems in the remaining plants were not explained by any apparent reason. The variant Nitrogen + Drought had only 9% of straight stems at the end of the study. The variant Nitrogen showed negative variations as late as in Year 4 of the combined effect of stress factors with 89% of plants showing the crooked stems without any apparent reason.

**Assimilatory tissues:** Length and colour of needles were also changing under the influence of stress factors. Plants in the variants with induced drought exhibited shorter needles just from the first year of exposure in both experimental series (Table 2). N-depositions permanently stimulated the length of needles in both experimental series. The two series showed different responses to the simultaneous stress, though. While the combined stress adversely affected the length of needles in the Pot Trial, plants in this variant of the Stand showed significantly longer needles than the Control. Needles from the variant Nitrogen had a deep green colour in both experimental series while needles from the variants with drought (var. Drought and var. Nitrogen + Drought) exhibited a lighter shade than those in the control plants. Variants with simulated drought in the Pot Trial showed a gradual fall of needle year classes 3 and 2 while the control plants had three complete needle year classes (Table 4).

**Contents of amino acids:** Free amino acids accumulated in the needles under the influence of stress factors (Table 5). All variants of the two experimental series showed the presence of γ-aminobutyric acid and alanine. In addition, the Pot Trial exhibited arginine in all variants with induced stresses plus ornithine in variants with the simulated N-deposition (var. Nitrogen, var. Nitrogen + Drought). In the experimental series Stand arginine appeared only in the variant Nitrogen + Drought.

**Leaf analysis:** In the course of the experiment, some changes were recorded in the content of essential biogenic elements in dry matter of the last-year needles. The nitrogen content was gradually increasing in the Pot Trial and reached 1.98% in the variant Nitrogen and 2.19% in the variant Nitrogen + Drought at the end of the study. A similar trend was also recorded in the experimental series Stand, where both variants with additional nitro-

Table 5. Contents of free amino acids in needle DM at the end of the study (1997) – experimental series Pot Trial and Stand

| Experimental series | | Pot Trial | Stand |
|---|---|---|---|
| | Free amino acids | | |
| | Name | Content (g/kg DM) | |
| Control | not found | – | – |
| Drought | arginine | 6.66 | – |
| | γ-aminobutyric acid | 1.43 | 5.87 |
| | alanine | 1.08 | 4.02 |
| Nitrogen | arginine | 3.69 | – |
| | ornithine | 1.31 | – |
| | γ-aminobutyric acid | 1.68 | 5.87 |
| | alanine | 1.60 | 8.50 |
| Drought + Nitrogen | arginine | 6.62 | 6.15 |
| | ornithine | 2.05 | – |
| | γ-aminobutyric acid | 1.29 | 6.41 |
| | alanine | 1.19 | 6.82 |

gen exhibited an increased N-content in needles although the increase was not so conspicuous (1.45% and 1.58%, resp., in comparison with the Control at 1.21% N). The increased content of nitrogen in needle DM was also reflected in the changed element ratios (Table 6). Pronounced changes occurred particularly in the Pot Trial where the B/N ratio dropped to a third and to a fourth of the Control value in the variant Nitrogen and Nitrogen + Drought, respectively. The B/N ratio in the Stand experimental series also showed a certain decrease in the above-mentioned variants but the drop was not so pronounced.

**Losses:** The first losses in the Pot Trial were recorded after the second year of simulated stresses in the variants with induced drought where 2% of plants died in the var. Drought (Table 2). The losses were quite low even in the following years, and the total number of plants that died in this variant before the end of the trial was 8%. The Nitrogen var. exhibited losses as late as in the last year of research – 7%. The variant Nitrogen + Drought showed at first losses identical to those recorded in the variant with drought itself but a sudden dieback of 75% plants occurred in this variant at the turn of Year 3 and Year 4 of the study. The experimental series Stand did not show any losses in any of its variants until the end of the trial.

## DISCUSSION

Two experimental series – Pot Trial and Stand – were established to acquire information about the response of Scots pine to increased nitrogen depositions, drought stress and a simultaneous exposure to the two stresses. The method of simulated stresses was to reveal how the stress factors affect both the young crops immediately after planting and the young Scots pine stands.

The increased N-depositions were simulated by adding ammonium sulphate in split doses so that the total nitrogen amount was 100 kg N per hectare/year. The dose was higher than the annual N-depositions per hectare found in Central Europe, where current values are e.g. 40–80 kg N in the Netherlands (KUYPER 1990), 19 kg N in Austria (Northern Tyrol) (SMIDT, HERMAN 1997), 18–29 kg N in Saxony (RABEN et al. 1996) although there were also extreme depositions of 200–300 kg N found locally (BREEMEN, DIJK 1988 in KUYPER 1990). The dose higher than the above-mentioned present load was chosen not only with regard to the time limitation of the project but also because the Stand experimental series was established in a locality which ranks – based on the results of leaf analyses – to localities with a lower N supply of soil. Comparable doses are used in similar experiments established recently, i.e. 100 kg N (NILSSON, WIKLUND 1992, 1994). The reason why we chose ammonium sulphate for the simulation of nitrogen depositions was that according to some authors (SARJALA 1993; AARNES et al. 1995) the conifers prefer the reduced (ammonium) form of nitrogen. Supplementary nitrogen in the ammonium form also increases the probability of earlier "saturation" of the plant with nitrogen, that means possible responses can be anticipated to occur earlier.

In order to induce drought in the experimental series Stand we used special constructions covered with transparent foil that captured and drained atmospheric precipitation so that their amount could be reduced by 60% as compared with the Control. It was only vertical precipitation that was taken into account for the calculation. A similar method of drought stress induction by means of "roofs" was also described in the literature (NILSSON, WIKLUND 1994; GUNDERSEN et al. 1995). In comparison with the Pot Trial where the amount of watering could be maintained constant and with no fluctuations, the level of stress in the Stand experimental series depended on total precipitation in the given year. The rate of reduction (by 60%) appears comparable with e.g. the Skogaby experiment in which precipitation in the spruce stand was reduced by 2/3, i.e. by 67% (NILSSON, WIKLUND 1992).

The results mentioned in this paper were obtained during four years of simulating the stress factors in the Pot Trial and during 2-year simulation in the experimental series Stand. The difference in research time resulted from the fact that Stand 335 D1 which was originally selected for the establishment of the Stand experimental series experienced a sudden fire that destroyed the constructions to restrict rainfall penetration as well as the stock of trees. The experimental measurements were made only in the years 1996 and 1997 in a newly established experimental series Stand (in Stand 336 A1). This is why the comparison of the dynamics of changes could not be completed as originally planned and the hitherto results obtained from the experimental series Stand can only suggest the trends of plants responses. Although the effects of the studied stress factors can be expected to increase, it is impossible to eliminate a priori another dynamics of tree responses.

Plants in the two experimental series responded to the induced stresses by growth and metabolic changes detectable on their above-ground parts.

Height increment of the plants was influenced in both experimental series by all induced stresses with drought acting as a stronger stress factor than N-depositions (Table 2). The level of responses was different too. While in the Pot Trial a significant increment reduction started to show in the variants with drought immediately after the first growing season, it was recorded in the experimental series Stand after a year's delay; the reason for the time delay was apparently a higher level of stress in the Pot Trial from the first year of exposure. The variance could also result from the fact that the 12-year old Stand is a more stable ecosystem while the pine plants freshly planted out usually suffer a transplanting shock and can respond more sensitively.

The height increment reduction under the influence of drought was described not only in experimental conditions with artificially induced drought e.g. in spruce (BEIER et al. 1995; NILSSON, WIKLUND 1992; MAUER, PALÁTOVÁ 1996), but it was also detected in pine as a consequence of climatically dry years (KRAUSS 1965). DILS and DAY (1952 in LYR et al. 1967) found out that even several-week summer periods of drought can result in a significant impact on height increment that can be reduced by 30–70%. LYR et al. (1967) consider several successive dry years as critical (analogy to our experiment). The variants with increased N-depositions did not initially show any significant responses in height increment; however, the indifferent effect of the factor gradually changed into negative both in the Pot Trial and in the experimental series Stand. A number of papers reported that in general the input of nitrogen into ecosystems insufficiently supplied with nitrogen leads to improved growth. It was confirmed for pine for example by HOFMANN et al. (1990).

Experiments with nitrogen fertilization (particularly in localities with this element being limited) also demonstrated the increased growth of young pine plantations (KRAUSS 1965; HOFMANN, VELDMAN 1965, and other). The response was not immediate, however. For example, neither FIEDLER and HÖHNE (1965) nor KRAUSS (1965) found any significant effect on the height increment in pine in the first years of trials with N-fertilization a reason being most probably the fact that height increment depends on the nutrition and on the level of nutrient supply produced and stored in the preceding year, and this is why the height growth differences are not displayed immediately after fertilization (KRAUSS 1965). FIEDLER and HÖHNE (1965) described the relation between height increment and needle N-content on the basis of their own experiments. They claim that growth is optimal at the needle N-content ranging between 1.8–1.9%. HOFMANN et al. (1990) corroborated that there is a correlation between needle N-content and height increment. The authors consider the values 1.8–2.0% N in pine needles to be the manifestation of starting N-deposition and at the same time a threshold value for the culmination of height increment since further increase of N-content in the plant results in height increment retardation. Pine needle N-contents ranging from 1.7% to 2.19% detected in the variants with N-deposition in the Pot Trial correspond with the quoted references and bring evidence to the time sequence. In the same growing season when the N-contents in 1-year needles reached a critical level we also recorded a significant reduction in height increment. The correlation does not hold for the experimental series Stand where considerably lower needle N-contents were found in the variant Nitrogen and in the variant Nitrogen + Drought (1.45% and 1.57%, respectively) which ranged between 1.4% and 1.7%, i.e. the level which is considered to be a sufficient supply with this element by BERGMANN (1983), and yet the increment was reduced. The phenomenon could have been related to the infestation of young pine plantations with pine needle-cast fungus (*Lophodermium pinastri* [Schrad.] Chev.) which appeared in the whole region in 1996 and was also found on the experimental plot. The reduction or loss of needles in older needle-year classes could have been a good reason for varying responses of trees in this experimental series. The simultaneous exposure to both studied stress factors showed a much more unfavourable effect on the height increment than the exposure to either of these factors separately, particularly in the Pot Trial. A similar response was described by NILSEN (1995) in spruce although in his experiment the two stresses were not applied simultaneously but the stress by increased N-depositions preceded the exposure to drought. On the other hand, MAUER and PALÁTOVÁ (1996) found out that nitrogen partly eliminated the negative influence of drought during the simultaneous stress applied onto spruce.

The length of needles in both experimental series was adversely affected primarily by the exposure to drought only (Table 2). The plants in the two experimental series responded differently to a simultaneous stress. While the combined stress (var. Nitrogen + Drought) induced a significant reduction in needle length in the Pot Trial from the first year of exposure, in this variant the experimental series Stand exhibited needles significantly longer than those in the Control (but shorter than with the additional nitrogen). The variation could have resulted both from a higher level of stress in the Pot Trial but at the same time also from a lower supply of nitrogen in the experimental series Stand, which can be documented by different contents of this element in the last needle-year class of both experimental series. Similarly, FIEDLER and HÖHNE (1965) found out in a fertilization trial that additional nitrogen was reflected in longer needles. Although the needle lengths under the influence of N-depositions were significantly higher in both experimental series than in the Control, no occurrence of hypertrophic needles with abnormal growth was observed, whose development at the higher nitrogen content was described by FOCKE (1991a).

Apart from changes in the biometrical characteristics of above-ground parts the experimental variants of the Pot Trial exhibited changes in the plant habit that resembled ill-formed pines occurring in the commercial crops in some regions of the Czech Republic. FOCKE (1991b) described branching abnormalities in pine induced by high nitrogen depositions that – according to the author – were caused by damage to meristems due to high N concentrations. The author assumes that the gradual loss of vitality of terminal meristems results in reduced apical dominance and subsequent variations in the tree habit. Nevertheless, the shape changes we could see in the Pot Trial differed from the described manifestation. Buds in the terminal rosette were considerably larger in the var. Nitrogen, but we could observe neither the increased number of whorl buds nor the development of proleptic shoots. Young stems exhibited sinuate to procumbent growth which was not induced by the reduction of apical dominance but could have been attributed to the changed character of cells and insufficient representation of reinforcing tissues in the stem. Drought induced a significant reduction of buds in the terminal rosette, which was

Table 6. Element ratios in needle DM after 4 years of exposure to stress factors in the experimental series Pot Trial and after 2 years in the experimental series Stand

| Experimental series | Pot Trial | | | | | Stand | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Needle DM element ratios | | | | | | | | | |
| | P/N | K/N | Ca/N | Mg/N | B/N | P/N | K/N | Ca/N | Mg/N | B/N |
| Control | 14.7 | 69.6 | 22.9 | 18.0 | 165.5 | 11.5 | 57.8 | 25.6 | 9.1 | 94.8 |
| Drought | 10.6 | 38.8 | 19.4 | 12.9 | 90.6 | 10.9 | 52.1 | 26.9 | 9.2 | 94.7 |
| Nitrogen | 7.6 | 33.3 | 20.2 | 12.1 | 56.5 | 10.3 | 49.0 | 20.7 | 6.9 | 76.7 |
| Drought + Nitrogen | 6.3 | 32.9 | 24.7 | 8.2 | 42.8 | 8.9 | 45.8 | 18.5 | 6.4 | 77.2 |

subsequently manifested also in the reduced number of branches in the whorl in the following year (Table 3). The findings correspond with those of KOZLOWSKI (1971). However, there were also observed crooked stems in addition to the reduced number of buds in the terminal rosette with the crook having been induced by the dieback of terminal bud and substitution of terminal shoot by one of the branches in a lower proportion of plants. In the majority of plants the visual reason could not be found, though.

Nutrient supply is an important criterion for the good health condition of trees since stands at a sound level of nutrition can resist stress better than less vital trees. Parameters used to characterize the level of nutrition are those of element contents in 1-year needle class. The contents of elements gradually varied under the influence of simulated stress factors. Drought as a single stress factor did not affect N-content in needles with the only exception being Year 3 and Year 4 in this variant of the Pot Trial where the needle N-content somewhat increased. Data on the effect of drought on the pine needle N-content are sporadic while in spruce it was repeatedly evidenced that neither short-time summer drought (BEIER et al. 1995) nor long-term exposure of plants to drought (NILSSON, WIKLUND 1994) affected the amount of nitrogen in needles. In our experiments, the drought did not influence the uptake of other nutrients (P, K) either, which is in good agreement with conclusions drawn by NILSSON and WIKLUND (1994) or BEIER et al. (1995) in spruce. The increased supply of nitrogen after additional ammonium sulphate was reflected in both experimental series by a significant increase in N-content in 1-year needle classes. The increase was relatively slow at the beginning, which corresponds with findings of HOFMANN et al. (1990), who recorded only a negligible increase in N-content in needles (from 1.40% to 1.50%) in Year 1 irrespective of the supplied dose, and only in Year 3 an increase up to 2.00% N. According to these authors, the needle N-contents exhibited a linear increase from Year 3 in dependence on the dose so that for example at the annual dose of 100 kg N the needles contained 2.24% N in Year 5. Similar dynamics of gradually increasing needle N-content was also described by KRAUSS (1965) and FIEDLER and HÖHNE (1965).

In addition to the absolute contents of elements in assimilatory tissues, other important parameters to determine the level of tree nutrition are ratios of individual elements. We can speak about the optimum nutrition if the element contents are sufficient and at mutually well-balanced ratios. Nitrogen depositions affect the growth of plants particularly on nutrient-poor soils where sufficient amounts of K, Mg, Ca and Mn are not available to the plants and where a disequilibrium of ions rapidly develops (OLSTHOORN et al. 1991). Deviations from the reference values of harmonic element ratios may suggest a disharmonic supply of elements in the rhizosphere and are considered for example by NILSSON and WIKLUND (1995) to be more sensitive indicators of nitrogen load than the absolute needle contents of elements. The ratios P/N, K/N and Mg/N decreased both in the Pot Trial and in the experimental series Stand, particularly in the variants with the simulated nitrogen stress (Table 6). Similar results for spruce after an application of ammonium sulphate were published by ROSENGREN-BRINCK and NIHLGARD (1995). The drought in our experiments did not exhibit such a pronounced effect since it did not result in the increased N-content in the Pot Trial with the exception of the last two years. The Pot Trial deserves attention for its B/N ratio which under the influence of N-depositions dropped to a third or even a fourth of the value found in the Control.

With an undisturbed metabolism, optimum nutrition and water supply, the content of free amino acids in needles is very low. This was confirmed in the control variants of both experimental series, where no free amino acids were detected. It is a well-known fact that plants respond to stress by accumulating free amino acids with the composition of these amino acids being species-specific and varying even according to individual types of stress (RABE 1990), which was partly corroborated in both experimental series. As compared with the control variants, the variants with the simulated N-depositions in both experimental series exhibited higher contents of free amino acids. Their composition was however different (Table 5). The dominating free amino acid in the Pot Trial was arginine, which – according to KÄTZEL and LÖFLER (1995), HUHN and SCHULZ (1996) and others – represents an amino acid that usually occurs in conifers saturated with nitrogen. In the experimental series Stand arginine was detected only in the variant with the combined stress; arginine was not detected in the variant with the nitrogen stress only. An explanation can be seen in the needle N-content still not reaching a high level and ranging within the values of normal nutrition with the element (BERGMANN 1983).

Although some authors (HUHN, SCHULZ 1996; NÄSHOLM, ERICSSON 1990) described a manifold increase in arginine content in needles of plants exposed to excessive nitrogen, our experiments showed an increase which was lower by an order. It can be due to the fact that arginine is primarily accumulated in roots and stems and to a lesser extent in needles as described by AARNES et al. (1995). Alanine which occurred in our experiments in the variants with additional nitrogen was also found for example in spruce needles growing under the influence of nitrogen (AARNES et al. 1995).

Similarly like in our experiments, NÄSHOLM and ERICSSON (1990) found an increased content of γ-aminobutyric acid in pine needles in response to the increased nitrogen supply. The authors claim that the content of this amino acid is subjected to considerable fluctuations during the year, reaching its maxima in the spring and in the autumn. This could be a good explanation both for its higher representation in our material because the samples for analyses were collected in the autumn, and for the fact that it is not usually mentioned by other authors in connection with the increased N-uptake. Our variants with additional nitrogen in the Pot Trial also exhibited the increased contents of ornithine, which is in good agreement with observations of HUHN and SCHULZ (1996), who analyzed pine needles from regions loaded with N-depositions and found a correlation between the ornithine content and the high needle N-content. According to the literary data (TESCHE 1987; GUSTKE, LÜTTSCHWAGER 1990), we anticipated an increased content of proline in the variants with the simulated drought, which is generally considered to be one of the drought stress indicators. However, our analyses did not reveal any proline, which might be related to the autumn sampling because – as claimed by NÄSHOLM and ERICSSON (1990) – this amino acid exhibits similar seasonal fluctuations with its content decreasing during summer and autumn. Another explanation might also be the increased content of proline in other tissues, e.g. in the phloem, as described by GUSTKE and LÜTTSCHWAGER (1990) at the disturbed water regime of pine.

## CONCLUSIONS

Effects of drought stress, stress by increased nitrogen depositions, and combined simultaneous exposure to both stress factors on the growth of Scots pine (*Pinus sylvestris* L.) were studied in two experimental series in the period 1994–1997. The experimental series represented different age classes of the experimental material, i.e. plants immediately after planting (Pot Trial) and a 12-year old stand (Stand). The drought stress was induced by a reduction of atmospheric precipitation by 60%; the increased nitrogen depositions were simulated by repeatedly added ammonium sulphate at a dose which corresponded to 100 kg/ha per year.

Results of the 4-year Pot Trial and 2-year research made in the experimental series Stand can be summarized into the following conclusions:

- Drought affected height increment, reduced needle length, induced defoliation, colour change and accumulation of free amino acids in needles. Plants in the Pot Trial responded to the drought also by reducing the number of buds in the terminal rosette, by reducing the number of branches in the whorl, and by changes in the essential biogenic elements in the dry matter of needles.
- Nitrogen depositions reduced height increment, induced the increased length of needles and their deep green colour, accumulation of free amino acids and changes in the ratios of essential biogenic elements in the dry matter of needles. Plants in the Pot Trial also showed abnormal shapes (procumbent growth).
- Combined stress caused a reduction of height increment, reduction of needle length in the Pot Trial and increased needle length in the experimental series Stand, changes in the ratios of the essential biogenic elements and accumulation of free amino acids in the dry matter of needles. Furthermore, the plants in the Pot Trial responded to the combined stress also by reducing the number of buds in the terminal rosette, number of branches in the whorl and ill-formed stems.
- In the period of study and in both experimental series the drought showed to be a stronger stress factor than the nitrogen depositions.
- The combined impact of stress factors was strongest in the Pot Trial where it resulted in a sudden and mass dieback of 75% plants after three years of exposure.
- The negative effect of the stresses under study does not always have an increasing trend with the increasing time of exposure. Partial analyses revealed that the adverse effect is followed by certain regeneration which may last for a short time only.

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# Vliv zvýšených depozic dusíku a stresu suchem na vývoj borovice lesní *(Pinus sylvestris* L.) – I. Reakce nadzemní části

E. PALÁTOVÁ

*Mendelova zemědělská a lesnická univerzita, Lesnická a dřevařská fakulta, Brno, Česká republika*

**ABSTRAKT**: V letech 1994–1997 byl sledován ve dvou experimentálních řadách vliv stresu suchem, stresu zvýšenými depozicemi dusíku a vliv souběžného působení obou stresových faktorů na růst borovice lesní (*Pinus sylvestris* L). Stres suchem byl vyvolán redukcí atmosférických srážek o 60 %, zvýšené depozice dusíku byly simulovány opakovaným dodáváním síranu amonného v dávce odpovídající 100 kg N/ha za rok. Všechny sledované stresové faktory ovlivnily výškový přírůst nadzemní části, délku a barvu jehlic, počet pupenů v terminální rozetě, obsah volných aminokyselin a poměr prvků v sušině asimilačního aparátu. Sucho působilo jako silnější stresový faktor než samotné depozice dusíku. Souběžné působení stresových faktorů mělo nejsilnější vliv.

**Klíčová slova**: *Pinus sylvestris* L.; dusík; sucho; výškový přírůst; habitus; defoliace; obsah volných aminokyselin

V letech 1994–1997 byl ve dvou experimentálních řadách sledován vliv stresu suchem, stresu zvýšenými depozicemi dusíku a souběžného působení obou stresových faktorů na růst borovice lesní (*Pinus sylvestris* L.). Experimentální řady prezentovaly různé stáří pokusného materiálu, a to rostliny bezprostředně po výsadbě (Nádobový pokus) a dvanáctiletý porost *in situ* (Porost). Stres suchem byl vyvolán redukcí atmosférických srážek o 60 %. V Nádobovém pokusu byly semenáčky borovice 2+0, vysazené do desetilitrových plastových nádob, umístěny v přístřešcích eliminujících průnik atmosférických srážek. Kontrolní rostliny byly průběžně zavlažovány tak, aby množství dodané vody odpovídalo 500 mm za rok, ve variantách s navozeným suchem byla závlahová dávka redukována na 40 % Kontroly. V experimentální řadě Porost byla redukce srážek ve variantách se suchem zajištěna pomocí konstrukcí, potažených kašírovanou fólií, které redukovaly srážky na 40 % Kontroly (přirozené množství srážek). Zvýšené depozice dusíku byly simulovány opakovaným dodáváním síranu amonného v dávce odpovídající 100 kg N/ha za rok aplikované ve třech dílčích dávkách vždy na počátku vegetačního období. V obou experimentálních řadách byly založeny varianty: Kontrola, Sucho, Dusík, Dusík + Sucho (tab. 1). Nádobový pokus byl hodnocen v letech 1994–1997, Porost 1996–1997. Na nadzemní části rostliny byly hodnoceny: výškový přírůst, habitus stromů, délka a barva jehlic, defoliace, obsah základních biogenních prvků a volných aminokyselin v jednoletých jehlicích.

Na stresy, simulované čtyři roky v Nádobovém pokusu a dva roky v experimentální řadě Porost, reagovaly rostliny změnami na nadzemní části rostlin (tab. 2–6).

- Sucho snížilo výškový přírůst, redukovalo délku jehlic, vyvolalo defoliaci, změnu barvy a hromadění volných aminokyselin v jehlicích. Rostliny z Nádobového pokusu reagovaly na sucho i snížením počtu pupenů v terminální rozetě, snížením počtu větví v přeslenu a změnami poměrů základních biogenních prvků v sušině jehlic.

- Depozice dusíku redukovaly výškový přírůst, vyvolaly nárůst délky jehlic a jejich sytě zelené zbarvení, hromadění volných aminokyselin a změny poměrů základních biogenních prvků v sušině jehlic. Na rostlinách z Nádobového pokusu byly zjištěny i tvarové abnormity (poléhavý růst).
- Souběžný stres vyvolal snížení výškového přírůstu, redukci délky jehlic v Nádobovém pokusu a nárůst délky jehlic v experimentální řadě Porost, změny v poměrech základních biogenních prvků a hromadění volných aminokyselin v sušině jehlic. Rostliny z Nádobového pokusu reagovaly na souběžný stres i snížením počtu pupenů v terminální rozetě, počtu větví v přeslenu a abnormitami tvaru kmene.
- Ve sledovaném období a v obou experimentálních řadách působilo sucho jako silnější stresový faktor než samotné depozice dusíku.
- Souběžné působení stresových faktorů mělo nejsilnější vliv a po třech letech působení v Nádobovém pokusu vyvolalo náhlý a hromadný úhyn 75 % rostlin.

Negativní působení sledovaných stresů nemá vždy vzhledem k době jejich působení narůstající tendenci. V dílčích analýzách bylo zjištěno, že po negativním ovlivnění dochází k jisté regeneraci, která může mít krátkodobé trvání.

*Corresponding author:*

RNDr. Ing. EVA PALÁTOVÁ, PhD., Mendelova zemědělská a lesnická univerzita, Lesnická a dřevařská fakulta, Lesnická 37, 613 00 Brno, Česká republika
tel.: + 420 5 45 13 41 32, fax: + 420 5 45 21 14 22, e-mail: evapal@mendelu.cz

# Dynamics of changes in dead wood share in selected beech virgin forests in Slovakia within their development cycle

**M. SANIGA[1], J. P. SCHÜTZ[2]**

[1]*Technical University, Forestry Faculty, Zvolen, Slovak Republic*
[2]*University Zurich, Forestry Faculty, Zurich, Switzerland*

**ABSTRACT**: The paper deals with the dynamics of dead wood formation within the development cycle of beech virgin forests Rožok, Havešová and Kyjov, which have been observed for 20–30 years. In addition to absolute values, the ratio of dead wood volume to living wood volume also proved to be a good index. The most balanced values were found in the beech virgin forest Rožok, with the values of the mentioned indices at the optimum stage ranging from 1:18 to 1:25, at the grow-up stage from 1:2.5 to 1:7.5 and at the breakdown stage from 1:3 to 1:3.5. The highest variability of the mentioned ratio was found in the beech forest Havešová, with values at the optimum stage from 1:4.5 to 1:18, at the breakdown stage from 1:5.5 to 1:14 and at the grow-up stage from 1:3.5 to 1:5.5.

**Keywords**: beech; virgin forest; development cycle; dead wood

## PROBLEMS

Dead wood is the basic component of natural forests. During the phylogenetic evolution, natural forests have developed a specific rich and balanced spectrum of organisms dependent on each other and, at the same time, on the external and internal environment. The process of rise and extinction is significantly conditioned by the basic, determinant component of a virgin forest – tree species. The problems of dead dendromass (necromass) have become the object of attention in coherence of virgin forest research in the last decades. It is just necromass that is an important building element in the process of nutrient and energy cycling in a natural forest. Destructors and reductors, mainly fungi and insects, are associated with this element.

Nutrient cycling in natural forest forms a balanced, closed cycle linked up with narrow relationships between micro-organisms – fungi – higher plants – various animals, and with the properties of environment. Lack or entire absence of woody necromass can mean dying out of some species of low organisms important for the nutrient cycling, whose reactions to the change of environment are sensitive and immediate. The sets of edaphon organisms, litterfall and humus saprophytes, nematodofauna, communities of molluscs, lichens, mosses etc. react sensitively to the level and course of humification processes (LOŽEK 1980; STEFUREAC 1976). The activity and the species richness of soil organisms depend on the content of nutrients in lying-wood necromass and in the soil litterfall. Along with its reduction, biological activity decreases, which results in adverse effects on soil properties and, at the same time, on water regime. In this way, the carrying capacity of soil is reduced, tree species dispose of less nutrients, ecological conditions for soil organisms are deteriorating (KÖHLER 1990; OTTO 1994). According to SCHMID (1990), in Bavaria, approx. 25% of fungi associated with dead wood is endangered in relation to the absence of dead wood. GEISER (1989) presented even almost 60% of beetles associated with the forest ecosystems on the red list of menaced species. Generally, in European forests, about 20–30% of the endangered higher fungi live on dead wood (DETSCH et al. 1994; SCHALES 1992).

Virgin forest as a forest ecosystem is characterized by a dynamic balance between the growth of biomass and its decay (necromass). This relationship is based on a certain proportionality of living and dead components of forest ecosystem and life links created and stabilized between them.

The mentioned complex also comprises necromass in various stages of decay, together with organisms (fungi), for which dead wood represents their environment. The necromass as a transitional form of organic matter transformation in the matter and energy cycling within the life cycle of virgin forest represents its basic component. Dead wood contributes to the balance and stability of this developmental cycle of natural forest.

Within the research on the virgin forest reserves in several European countries, the volume and structure of dead wood were also scored. The most widely known virgin forests in the neighbouring countries are predominantly composed of three tree species (spruce, fir, beech), which also dominate in our country. Within the vegetation zonation, they correspond approximately to the communities of 5th and 6th altitudinal vegetation zone of our nomenclature. Among these reserves, natural forests of soft-wood broadleaves, natural ecosystems of beech and broadleaved communities with beech component are absent. Such objects, having been observed for a log time, are Boubín and the virgin forest Žofín in the Czech Republic (PRŮŠA 1985), Rotwald in Austria (MAYER et al. 1979), Čorkova Uvala in Croatia (PRPIČ et al. 1994), Perućica in Bosnia (PINTARIČ 1978), Rajnehavski Rog in Slovenia (BONČINA 1997) and others. Dead wood volume in these virgin forests is relatively high, ranging on average from 130 to 220 $m^3$ per hectare, which represents 19–32% of average volume of living trees. Among the measured research plots, the highest volume was found in Rajnehavski Rog, namely 474 $m^3$ per hectare (BONČINA 1997). In the mentioned objects, the lying dead wood predominated within total necromass.

These results represent a static assessment of necromass volume in individual virgin forests. The first results characterizing the change in the share of necromass within the development cycle of virgin forest during a longer period (40 years) are presented by SANIGA, SCHÜTZ (2001). In this study, results obtained in two virgin forests which have been observed for the longest time in Slovakia, and generally in Europe, Badín and Dobroč virgin forests, are analysed and evaluated.

The results of measurements for the mentioned period confirmed that the share of dead wood defined as the per cent of living dendromass varies in dependence on the development stage. At the grow-up stage, this ratio ranges from 1:2 (Badín virgin forest) to 1:2 or 1:3 as the case may be (Dobroč virgin forest). The largest difference between dead wood and living dendromass is at the optimum stage with the values in the range from 1:5 to 1:6. At the breakdown stage without distinction between phases, the ratio of necromass to living dendromass ranges from 1:2 to 1:2.5.

The course of decay and formation of dendromass in similar ecological conditions as expressed by the volume of wood with d.b.h. more than 7 cm is balanced, with signs of oscillation.

The highest absolute value of dead wood in the Badín virgin forest, 455.36 $m^3$ per hectare, was determined at the breakdown stage. In the Dobroč virgin forest, the highest value of 439.16 $m^3$ per hectare was also recorded at the breakdown stage.

In the Dobroč virgin forest, average values of the share of dead wood as % of total volume of wood with d.b.h. > 7 cm (living and dead wood) during the whole period of observation ranged from 21.41% to 29.24%. In the Badín virgin forest, this relative share of dead wood was significantly higher, and ranged from 27.02% to 37.38%. More balanced and lower shares of dead wood in the Dobroč virgin forest are due to the balance of production conditions and equilibrium in the tree species composition, where two predominant species (spruce, fir) survive approximately up to the same physical age, whereby they determine the development cycle of virgin forest. In the Badín virgin forest, the representation of both tree species, their productive capacity and physical age are more differentiated.

The aim of this paper is the analysis of dynamics of changes in dead wood share within the development cycle of a virgin forest in selected beech forests in the West Carpathians (National Nature Reserves Rožok, Havešová and Kyjov) during the last 20–30 years.

## RESEARCH OBJECTS AND METHODS

### BEECH VIRGIN FOREST NATIONAL NATURE RESERVE HAVEŠOVÁ

The reserve with the area of 171.32 ha is situated in the Bukovské Mts. at the altitude of 500–650 m a.s.l., in the zone of Krosno flysch zone within the Upper Eocene layer. The soil type is a brown forest mesotrophic soil, medium deep to deep, stony, slightly humic. According to the climate, it belongs to the moderately warm zone (B8) with moderate annual precipitation of 700–800 mm, precipitation during the vegetation period of 450–500 mm, and average annual temperature of 7°C.

Three forest type groups (phytosociological units) occur in the reserve: *Fagetum pauper* (*Dentaria bulbifera-Prenanthes purpurea-nudum* type), *Fagetum typicum* (*Carex pilosa-Asperula odorata-pauper, Dentaria bulbifera-Prenanthes purpurea* type) and *Fagetum tiliosum* (*Carex pilosa-Asperula odorata-Mercurialis perennis* type and *Asperula odorata-Mercurialis perennis-Dentaria enneaphylos* type) (KORPEĽ 1989).

In 1979, three permanent research plots (PRP) were established by the Department of Silviculture, each of them on 0.5 ha. PRP 1 is situated at the initial phase of grow-up stage, PRP 2 at the initial phase of optimum stage, and PRP 3 at the initial phase of breakdown stage.

### BEECH VIRGIN FOREST NATIONAL RESERVE ROŽOK

This primary beech virgin forest covering an area of 67.1 ha is situated in the Bukovské Mts., in the part of Kremenec mountain range, 500–790 m a.s.l., mainly on the north, partly west and north-west oriented slope with angle of 40–50%. The average annual temperature is 7°C, average annual precipitation 780 mm, the length of the vegetation period is 190 days. The parent rock is predominantly formed of sandstone with poor calcareous cement and crystallline grain, the smaller part of the area is formed of argillaceous shales. Predominant soil type is a mesotrophic brown forest soil. The soil in the upper layer is sandy and loamy, humic, in the lower layer loamy to clayey with gravel; unsaturated, acid to very acid, with a favourable moisture and nitrogen content, poor in potassium and phosphorus. The most frequent forest type group (around 85% of the virgin forest area) is the upper-zone type of *Fagetum pauper* with predominant community type *Dentaria bulbifera nudum,* i.e. the communities of 4th beech forest altitudinal vegetation zone. In a continuous strip in the uppermost part (approx. 15% of the preserve area) the forest type group *Fagetum typicum* is represented, with the community types: *Asperula odorata-Oxalis acetosella-Lamium galeobdolon-Mercurialis perennis, Carex pilosa-Asperula odorata-Dentaria bulbifera-Prenanthes purpurea,* i.e. communities of 5th fir-beech altitudinal vegetation zone (KORPEĽ 1989).

In 1979 three permanent research plots (PRP) were established by the Department of Silviculture, each of them on 0.5 ha. PRP 1 is situated at the advanced phase of grow-up stage, PRP 2 at the advanced phase of optimum stage, and PRP 3 at the advanced phase of breakdown stage.

## BEECH VIRGIN FOREST NATIONAL RESERVE KYJOV

This beech virgin forest reserve with the area of 53.4 ha is situated in the north-west part of the Vihorlat Mts. below the summit of the mountain Kyjov, 700–820 m a.s.l., facing north to north-west.

The average annual temperature is 6°C, the annual precipitation averages 750–800 mm, the vegetation period with an average temperature of 13.5°C lasts 190–200 days. The bedrock is formed of andesite. The soil is a sandy to loamy brown forest soil, rich in nutrients, deep, moderately deep in areas below the crest, slightly acidic.

The prevalent phytosociological class is *Fagetum pauper*, *Fraxineto-Aceretum* covers approximately 8% of the area in lateral guiches, and *Fageto-Aceretum* takes up to 12% in areas below the crests (KORPEĽ 1989).

In the virgin forest, four permanent research plots (hereinafter referred to as PRP) were established in 1963. PRP 1 represents the initial phase of breakdown stage, PRP 2 the phase of optimum stage, PRP 3 is situated in the initial phase of grow-up stage and PRP 4 is in the advanced phase of breakdown stage (KORPEĽ 1989).

## METHODS OF DEAD WOOD MEASUREMENT

On each PRP in virgin forests, dead wood was measured as either standing or lying. The volume of standing trees was estimated from d.b.h. and heights by means of the volumetric tables in the same way as in living trees. The volume of standing trees with broken stems was calculated in a similar way except that the remains were identified on the ground and added to the tree heights.

The volume of lying trees was calculated according to Huber's formula:

$$V = \frac{\pi \cdot d_{1/2}^2}{4} \cdot l$$

where: $d_{1/2}$ – tree diameter in the half of its length,
$l$ – tree length.

For both forms, the dead wood volume was classified according to the decay stage as follows:

a – trees fallen recently or dead standing trees having relatively healthy wood with bark,
b – rotten but still compact logs, bark peels off, species can be recognized,
c – advanced decay stage, wood loses its compactness and breaks down.

The necromass assessment was carried our repeatedly with other measurements in 10-year intervals on PRPs. Biometric indicators were recalculated per 1 ha.

## ANALYSIS OF RESULTS

### HAVEŠOVÁ BEECH VIRGIN FOREST

This virgin forest ranks among the best ones as for both production quality and quantity. In addition, during the whole research period no climatic extremities occurred that would considerably disturb the development cycle of this virgin forest. Information on the change in production conditions and necromass dynamics in individual stages of the development cycle over a 20-year period is given in Table 1.

The evaluation of average biomass and necromass volumes during the virgin forest development cycle shows just a small fluctuation in the range between 817.99 m³ and 858.73 m³/ha. Speaking of the necromass to total volume ratio, it can be stated that the fluctuations were even smaller, from 14.32% to 14.75% over the 20-year period. The volume of living trees represents on average 85% of the total volume of biomass and necromass during the observed period. The analysis of necromass in the respective stages within the development cycle indicates fluctuations but without significant signs of dependence on development stages of the virgin forest. An exception from this general pattern was recorded in 1979, when the necromass volume corresponded to the virgin forest development cycle i.e. in the initial phase of optimum stage it reached its lowest value – 40.0 m³/ha, accounting for only 5.26% of the total volume of biomass and necromass, whereas in the following period an increase to 157.46 m³ per ha in 1989 and 136.77 m³ per ha in 1999 was observed. This value was higher than the necromass volume in the initial phase of breakdown stage. This fact can be observed precisely at the onset of optimum stage when individual trees of the previous generation, whose volume was around 20–22 m³, were still surviving.

The volume of the standing dead wood in a beech virgin forest is also interesting. Its average value during the whole development cycle and measured in 10-year intervals ranged between 27.61% and 32.24%.

Table 1. The volume of living trees and dead wood according to categories in beech virgin forest Havešová in the period 1979–1999

| Year | FRP | Development stage | Volume of living trees and necromass (m³/ha) | Volume of living trees (m³/ha) | Volume of living trees (%) | Dead trees: Total volume (m³/ha) | Percentage out of total volume | Volume of lying trees (m³/ha) | Percentage of lying trees | Volume of standing trees (m³/ha) | Percentage of standing trees | Volume of 3rd grade of decomposition (m³/ha) | Percentage of 3rd grade of decomposition |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1979 | I | The initial phase of grow-up stage | 915.36 | 714.18 | 78.02 | 201.18 | 21.98 | 146.62 | 72.88 | 54.56 | 27.12 | 134.30 | 66.76 |
| | II | The initial phase of optimum stage | 759.94 | 719.94 | 94.74 | 40.00 | 5.26 | 26.94 | 67.35 | 13.06 | 32.65 | 13.46 | 33.65 |
| | III | The initial phase of breakdown stage | 778.66 | 657.84 | 84.48 | 120.82 | 15.52 | 64.50 | 53.39 | 56.32 | 46.61 | 62.90 | 52.06 |
| | | Average of the development cycle | 817.99 | 697.32 | 85.25 | 120.66 | 14.75 | 79.35 | 65.76 | 41.31 | 34.24 | 70.22 | 58.20 |
| 1989 | I | The initial phase of grow-up stage | 773.14 | 654.66 | 84.68 | 118.48 | 15.32 | 60.94 | 51.43 | 57.54 | 48.57 | 43.44 | 36.66 |
| | II | The initial phase of optimum stage | 844.03 | 686.57 | 81.34 | 157.46 | 18.66 | 118.82 | 75.46 | 38.64 | 24.54 | 22.66 | 14.39 |
| | III | The initial phase of breakdown stage | 853.53 | 772.79 | 90.54 | 80.74 | 9.46 | 78.46 | 97.18 | 2.28 | 2.82 | 34.48 | 42.70 |
| | | Average of the development cycle | 823.56 | 704.67 | 85.56 | 118.89 | 14.44 | 86.07 | 72.39 | 32.82 | 27.61 | 33.53 | 28.20 |
| 1999 | I | The initial phase of grow-up stage | 841.95 | 668.47 | 79.40 | 173.48 | 20.60 | 110.01 | 63.41 | 63.47 | 36.59 | 46.87 | 27.02 |
| | II | The initial phase of optimum stage | 812.35 | 675.58 | 83.16 | 136.77 | 16.84 | 87.15 | 63.72 | 49.62 | 36.28 | 38.87 | 28.42 |
| | III | The initial phase of breakdown stage | 921.90 | 863.14 | 93.63 | 58.76 | 6.37 | 55.74 | 94.86 | 3.02 | 5.14 | 24.46 | 41.63 |
| | | Average of the development cycle | 858.73 | 735.73 | 85.68 | 123.00 | 14.32 | 84.30 | 68.54 | 38.70 | 31.46 | 36.73 | 29.86 |

The amount of dead wood in the 3rd stage of decay was more variable mainly in 1979, when its average value for all stages of the virgin forest development cycle was 58.20%. In the following periods of observation this value decreased and ranged from 28.20 to 29.86%. Considering the temporally regular dying of trees and the length of their decomposition, which is approx. 25–30 years in beech, the latter values are congruent with this process. The values recorded in 1979 indicate relatively favourable climatic conditions over a period of at least 10 years preceding the time of the respective measurements that slowed down the mortality process in overmature, dying beech trees and thereby increased the relative share of necromass, which reached the 3rd stage of decay.

As for the dead wood formation dynamics within the whole development cycle of the Havešová beech virgin forest, it manifests a continuous character without any significant excesses, proving its high ecological and production stability.

## ROŽOK BEECH VIRGIN FOREST

The information on production and necromass structure from this beech virgin forest is given in Table 2.

At the beginning, it must be stated that the overall biomass and necromass production in this virgin forest is higher than in Havešová although both stands grow on similar sites close to each other. This relates to the advanced phase of grow-up and optimum stages, where the biomass production exceeded 1,000 $m^3$ per ha. This virgin forest may serve as an excellent "textbook" illustration of the necromass dynamics within the virgin forest development cycle. The minimum (3.85–5.16%) is reached at the optimum stage, namely in the advanced phase, when trees of the preceding virgin forest generation died away long before and their decomposition was completed whereas the currently largest trees are still vital. In the case of a normal course of climatic processes (wind and snow) they are not damaged and consequently do not die away. In the other stages of the development cycle, the total proportion of necromass ranges from 1/4 and 1/5 of the total volume of living and dead trees. When assessing the average necromass amount within all stages of the virgin forest development cycle, its share in the total volume of biomass and necromass is similar like in the Havešová virgin forest, and ranges between 13.14% and 19.60% (Table 2).

The analysis of the lying necromass volume has shown that its share is higher than in the Havešová virgin forest. The volume of lying trees ranged from 77.5 to 82.58% in the observed period.

The beech necromass being at the 3rd stage of decay exhibits a similar course, and considering the proximity of the two virgin forests, the same explanation as for Havešová is applicable for Rožok (Table 2).

Generally, we can state that the structure of the Rožok beech virgin forest, its spatial texture of development stages provides conditions for a high ecological stability and development independence. The necromass formation dynamics within the energy flows in the virgin forest is continuous and shows general patterns similar to those of the Havešová virgin forest.

## KYJOV BEECH VIRGIN FOREST

The longest research has been carried out in the Kyjov beech virgin forest. Information on the structure of necromass and biomass from a 30-year research period is presented in Table 3.

The highest necromass volume was recorded in 1993 at the initial phase of grow-up stage (247.81 $m^3$/ha). The share of dead wood in the whole biomass + necromass volume shows a similar course like in the Rožok beech virgin forest. At the initial phase of optimum stage, in 1963 and 1973, the share of necromass was lowest; expressed in relative values it makes 7.89% and 6.84%, respectively. In the following period, when the remaining trees of the previous generation aborted, its share increased to 131.48 $m^3$/ha (22.37%) in 1983, and to 164.40 $m^3$/ha (26.98%) in 1993.

Average necromass volume within the development cycle of virgin forest expressed as per cent of the total standing volume of living trees and dead wood ranges from 15.57% in 1963 to 29.4% in 1993 (Table 3). Particularly, the last two measurements show a higher variability and an increase in dead wood share, mainly if expressed in per cent. Absolute values in this beech virgin forest fall within the variation range of both previously mentioned virgin forests. Higher percentage of necromass is associated with a substantially lower standing stock of living trees, which results from worse climatic and soil conditions in the Kyjov beech virgin forest. The analysis of standing volume and dead wood structure indicates a different character of values as compared with both previously mentioned virgin forests. Average share of standing dead wood within the entire development cycle of virgin forest expressed as per cent ranges from 28.82% to 62.18%, in absolute values, it ranges from 55.90 $m^3$/ha to 80.52 $m^3$/ha. It can be stated that in this virgin forest, significantly more beech trees die back standing than

Table 2. The volume of living trees and dead wood according to categories in beech virgin forest Rožok in the period 1979–1999

| Year | FRP | Development stage | Volume of living trees and necromass ($m^3$/ha) | Volume of living trees ($m^3$/ha) | Volume of living trees (%) | Dead trees: Total volume ($m^3$/ha) | Percentage out of total volume | Volume of lying trees ($m^3$/ha) | Percentage of lying trees | Volume of standing trees ($m^3$/ha) | Percentage of standing trees | Volume of 3rd grade of decomposition ($m^3$/ha) | Percentage of 3rd grade of decomposition |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1979 | I | The advanced phase of grow-up stage | 878.81 | 776.13 | 88.32 | 102.68 | 11.68 | 75.26 | 73.29 | 27.42 | 26.71 | 51.82 | 50.47 |
| | II | The advanced phase of optimum stage | 826.01 | 794.22 | 96.15 | 31.79 | 3.85 | 29.30 | 92.17 | 2.49 | 7.83 | 23.92 | 75.24 |
| | III | The adv. phase of breakdown stage | 767.28 | 576.98 | 75.20 | 190.30 | 24.80 | 147.12 | 77.30 | 43.18 | 22.70 | 116.71 | 61.33 |
| | | Average of the development cycle | 824.03 | 715.78 | 86.86 | 108.25 | 13.14 | 83.89 | 77.50 | 24.36 | 22.50 | 64.15 | 59.26 |
| 1989 | I | The advanced phase of grow-up stage | 1,006.92 | 709.85 | 70.50 | 297.07 | 29.50 | 250.71 | 84.39 | 46.36 | 15.61 | 35.28 | 11.85 |
| | II | The advanced phase of optimum stage | 964.65 | 914.88 | 94.84 | 49.77 | 5.16 | 40.43 | 81.23 | 9.34 | 18.77 | 18.39 | 38.95 |
| | III | The adv. phase of breakdown stage | 931.79 | 709.50 | 76.14 | 222.29 | 23.86 | 178.91 | 80.48 | 43.38 | 19.52 | 89.22 | 40.14 |
| | | Average of the development cycle | 967.79 | 778.08 | 80.40 | 189.71 | 19.60 | 156.68 | 82.58 | 33.03 | 17.42 | 47.63 | 25.11 |
| 1999 | I | The advanced phase of grow-up stage | 968.68 | 764.36 | 78.91 | 204.32 | 21.09 | 182.38 | 89.26 | 21.94 | 10.74 | 42.65 | 20.87 |
| | II | The advanced phase of optimum stage | 1,077.54 | 1,029.42 | 95.53 | 48.12 | 4.47 | 24.96 | 51.87 | 23.16 | 48.13 | 20.75 | 43.12 |
| | III | The adv. phase of breakdown stage | 844.19 | 653.15 | 77.37 | 191.04 | 22.63 | 137.48 | 71.96 | 53.56 | 28.04 | 62.50 | 32.72 |
| | | Average of the development cycle | 963.47 | 815.64 | 84.66 | 147.83 | 15.34 | 114.94 | 77.75 | 32.89 | 22.25 | 41.97 | 28.39 |

Table 3. The volume of living trees and dead wood according to categories in beech virgin forest Kyjov in the period 1963–1993

| Year | FRP | Development stage | Volume of living trees and necromass ($m^3$/ha) | Volume of living trees ($m^3$/ha) | Volume of living trees (%) | Dead trees: Total volume ($m^3$/ha) | Dead trees: Percentage out of total volume | Dead trees: Volume of lying trees ($m^3$/ha) | Dead trees: Percentage of lying trees | Dead trees: Volume of standing trees ($m^3$/ha) | Dead trees: Percentage of standing trees | Dead trees: Volume of 3rd grade of decomposition ($m^3$/ha) | Dead trees: Percentage of 3rd grade of decomposition |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1963 | I | The initial phase of breakdown stage | 472.84 | 406.34 | 85.94 | 66.50 | 14.06 | 47.30 | 71.13 | 19.20 | 28.87 | 35.33 | 53.13 |
| | II | The initial phase of optimum stage | 485.60 | 447.28 | 92.11 | 38.32 | 7.89 | 24.31 | 63.44 | 14.01 | 36.56 | 19.99 | 52.17 |
| | III | The initial phase of grow-up stage | 622.06 | 477.80 | 76.81 | 144.26 | 23.19 | 99.16 | 68.74 | 45.10 | 31.26 | 85.13 | 59.01 |
| | IV | The advanced phase of breakdown stage | 618.49 | 525.24 | 84.92 | 93.25 | 15.08 | 38.10 | 40.86 | 55.15 | 59.14 | 22.05 | 23.65 |
| | | Average of the development cycle | 549.76 | 464.17 | 84.43 | 85.59 | 15.57 | 52.22 | 61.01 | 33.37 | 38.99 | 40.63 | 47.47 |
| 1973 | I | The initial phase of breakdown stage | 572.98 | 497.40 | 86.81 | 75.58 | 13.19 | 52.72 | 69.75 | 22.86 | 30.25 | 46.32 | 61.29 |
| | II | The initial phase of optimum stage | 569.30 | 530.38 | 93.16 | 38.92 | 6.84 | 25.84 | 66.39 | 13.08 | 33.61 | 23.94 | 61.51 |
| | III | The initial phase of grow-up stage | 678.92 | 493.84 | 72.74 | 185.08 | 27.26 | 126.96 | 68.60 | 58.12 | 31.40 | 94.68 | 51.16 |
| | IV | The advanced phase of breakdown stage | 701.36 | 595.08 | 84.85 | 106.28 | 15.15 | 40.50 | 38.11 | 65.78 | 61.89 | 21.04 | 19.80 |
| | | Average of the development cycle | 630.65 | 529.18 | 83.91 | 101.47 | 16.09 | 61.51 | 60.62 | 39.96 | 39.38 | 46.50 | 45.83 |
| 1983 | I | The initial phase of breakdown stage | 582.50 | 454.68 | 78.06 | 127.82 | 21.94 | 51.50 | 40.29 | 76.32 | 59.71 | 43.06 | 33.69 |
| | II | The initial phase of optimum stage | 587.88 | 456.40 | 77.63 | 131.48 | 22.37 | 45.00 | 34.23 | 86.48 | 65.77 | 23.00 | 17.49 |
| | III | The initial phase of grow-up stage | 638.70 | 512.32 | 80.21 | 126.38 | 19.79 | 54.42 | 43.06 | 71.96 | 56.94 | 24.80 | 19.62 |
| | IV | The advanced phase of breakdown stage | 678.06 | 545.76 | 80.49 | 132.30 | 19.51 | 44.98 | 34.00 | 87.32 | 66.00 | 32.10 | 24.26 |
| | | Average of the development cycle | 621.79 | 492.29 | 79.17 | 129.50 | 20.83 | 48.98 | 37.82 | 80.52 | 62.18 | 30.74 | 23.74 |
| 1993 | I | The initial phase of breakdown stage | 549.52 | 429.38 | 66.11 | 220.14 | 33.89 | 175.69 | 79.81 | 44.45 | 20.19 | 52.38 | 23.79 |
| | II | The initial phase of optimum stage | 623.30 | 458.90 | 73.62 | 164.40 | 26.38 | 93.33 | 56.77 | 71.07 | 43.23 | 18.18 | 11.06 |
| | III | The initial phase of grow-up stage | 650.30 | 402.49 | 61.89 | 247.81 | 38.11 | 188.07 | 75.89 | 59.74 | 24.11 | 65.41 | 26.40 |
| | IV | The advanced phase of breakdown stage | 714.48 | 571.09 | 79.93 | 143.39 | 20.07 | 95.04 | 66.28 | 48.35 | 33.72 | 12.64 | 8.82 |
| | | Average of the development cycle | 659.40 | 465.47 | 70.59 | 193.93 | 29.41 | 138.03 | 71.18 | 55.90 | 28.82 | 37.15 | 19.16 |

in Havešová and Rožok virgin forests (Tables 1–2).

Dynamics of the complete decomposition of beech wood proceeds in the same pace as in both previously mentioned virgin forests (Tables 1–3).

Generally, it can be stated that the ecological stability of the Kyjov beech virgin forest is high, which allows a fluent dynamics of necromass formation and decomposition.

## DISCUSSION

No long-term observations of the dynamics of dead wood formation in virgin forests within their development cycle have been done. There is a lack of data in this field in Europe. The first work describing this process within a time period of 40–50 years is the study published by SANIGA, SCHÜTZ (2001), dealing with research carried out in Dobroč and Badín virgin forests. The ratio of dead wood to biomass in both virgin forests, as mentioned in the introduction, varies in dependence on the development stages of virgin forest from 1:5 to 1:6 at the optimum stage to 1:2–1:3 at the grow-up or decomposition stages. This ratio in beech virgin forests of Slovakia is very differentiated. In Rožok beech virgin forest, where the permanent research plot is characterized as the advanced phase of optimum stage, the ratio of dead wood to volume of living trees ranges from 1:25 to 1:18. This ratio is significantly lower than that in the investigated virgin forests (SANIGA, SCHÜTZ 2001). It is caused by a different tree species composition. In beech virgin forests, the whole process is influenced by the physical age and ageing process of one tree species; the process is "more homogeneous". The optimum stage lasts here only 40 years; therefore, at its advanced stage, all beech trees of the previous generation are decomposed and, considering a high stability, the new generation in its development cycle has not yet reached a physical age that could result in dying off of at least a part of individuals and thus in an increase of the dead wood volume. In case that virgin forests consist of more tree species and their physical age and share in the tree species composition vary significantly, the dieback of tree species is different. If the life (development) cycle length is determined by the tree species with the longest physical age, which is silver fir surviving up to 400 years, this tree species together with Norway spruce participate by more than 65–70% in the volume and tree census of the Dobroč virgin forest and thus it also determines the length of its development cycle. As a result, beech at the physical age of 220–230 years may die off just at the initial phase of optimum stage. Thus, the share of dead wood increases at this stage and the biomass to necromass ratio assumes the previously mentioned values. A different situation occurs in beech virgin forests at the initial phase of optimum stage, where a mass dieback of individuals of the previous generation occurs at the final phase of grow-up stage. The aborted individuals remain present in the forest, so that the necromass to biomass ratio is 1:2 to 1:4 and 1:2.5 to 1:7 in the Kyjov and Rožok virgin forests, respectively. In the case of the Havešová beech virgin forest, this ratio at the grow-up stage ranges from 1:3.5 to 1:6. Similar ranges of dead/living wood ratios were observed in all virgin forests at the breakdown stage.

In conclusion, it can be stated that the richer the tree species composition of virgin forests and the larger the difference in their length of physical age, the higher and more balanced is the volume of dead wood within the life cycle of virgin forests as compared with monospecific ones. If we compare the absolute volume of dead wood between the virgin forests, in some cases this value is twice as high in the Badín and Dobroč virgin forests than in beech virgin forests. The presented knowledge is given by the total standing stock of these virgin forests that is significantly higher as compared with beech virgin forests, and also by a partial synchronization of dieback of several tree species within the development cycle of the Badín and Dobroč virgin forests.

## CONCLUSIONS

The results of investigations into dead wood in beech virgin forests of Slovakia can be summarized as follows:

In the Havešová beech virgin forest, the volume of dead wood in the development stage of optimum ranged from 40.0 $m^3$/ha to 157.46 $m^3$/ha, accounting for 5.26% and 18.66%, respectively, of the total volume of living trees and necromass. In the breakdown stage, the volume of necromass ranged from 58.86 $m^3$/ha to 120.82 $m^3$/ha during the observation period. At the stage of growing up, the volume of necromass is highest, ranging from 118.48 $m^3$/ha to 201.18 $m^3$/ha. The average share of dead wood amounts to 14–15% of the total volume of living trees and necromass in the whole observation period and the entire development cycle.

The necromass volumes in the optimum stage of the Rožok beech virgin forest are different from those in the Havešová virgin forest. The volume of dead wood was lowest at this stage and ranged from 31.79 $m^3$/ha to 49.77 $m^3$/ha, which accounts for 3.85% and 5.16%, respectively, of the total volume of living trees and necromass. This is due to the fact that the research plot has developed to the advanced phase of optimum stage, when the trees of the previous beech generation are not present and the trees of the current development cycle culminate in their production. In this phase, lasting approximately 20 years in beech virgin forests, tree mortality is very low.

At other stages of the development cycles, absolute volumes of necromass are similar to those in the Havešová beech virgin forest. At the stage of growing up, the dead wood volume ranged from 102.68 $m^3$/ha to 297.07 $m^3$/ha. At the breakdown stage, it was between 191.30 $m^3$/ha and 222.29 $m^3$/ha.

Average share of dead wood within the whole development cycle of virgin forest ranged from 13.14% to 19.6% of the total volume of living and dead trees.

The Kyjov beech virgin forest, which was observed for the longest time (30 years), has similar characteristics of the dead wood volume like the Havešová beech virgin forest. The absolute volume of dead wood at the optimum stage ranged from 38.32 $m^3$/ha to 164.40 $m^3$/ha, which accounts for 7.89% and 26.38%, respectively, of the total volume of living and dead trees. In this virgin forest, the permanent research plot TVP 2 has reached the initial phase of optimum stage, when trees of the previous generation die off, which results in an increase in the necromass volume. At the stage of breakdown, the absolute values of necromass were between 66.5 $m^3$/ha and 220.14 $m^3$/ha. At the stage of growing up, these values were higher, and ranged from 126.38 $m^3$/ha to 247.81 $m^3$/ha.

The average share of necromass, calculated from the total volume of living and dead trees within the entire development cycle of the beech virgin forest ranged from 15.57% to 29.41%.

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# Dynamika zmeny podielu mŕtveho dreva vo vybraných bukových pralesoch Slovenska v rámci ich vývojového cyklu


M. SANIGA[1], J. P. SCHÜTZ[2]

[1]*Technická univerzita, Lesnícka fakulta, Zvolen, Slovenská republika*

[2]*ETH, Lesnícka fakulta, Zürich, Švajčiarsko*



**ABSTRAKT**: Práca pojednáva o dynamike tvorby mŕtveho dreva v rámci vývojového cyklu bukových pralesov Rožok, Havešová a Kyjov, ktoré boli sledované 20–30 rokov. Okrem absolútnych hodnôt je dobrým ukazovateľom pomer medzi objemom nekromasy a objemom živých stromov. Najvyrovnanejšie hodnoty boli zistené v bukovom pralese Rožok, kde pomer medzi uvedenými ukazovateľmi bol v štádiu optima v rozpätí od 1 : 18 do 1 : 25, v štádiu dorastania od 1 : 2;5 do 1 : 7,5 a v štádiu rozpadu od 1 : 3 do 1 : 3,5. Najväčšiu variabilitu uvedeného pomeru mal bukový prales Havešová, kde rozpätie v štádiu optima sa pohybovalo od 1 : 4,5 do 1 : 18, v štádiu rozpadu od 1 : 5,5 do 1 : 14 a v štádiu dorastania od 1 : 3,5 do 1 : 5,5.


**Kľúčové slová**: buk; prales; vývojový cyklus; mŕtve drevo

Poznatky výskumu mŕtveho dreva v bukových pralesoch Slovenska možno zhrnúť nasledovne:

V bukovom pralese Havešová sa hodnota mŕtveho dreva vo vývojovom štádiu optima pohybuje od 40,0 $m^3$/ha do 157,46 $m^3$/ha, čo predstavuje 5,26 %, resp. 18,66 % z celkového množstva objemu živých stromov a nekromasy. V štádiu rozpadu sa hodnota nekromasy za sledované obdobie pohybuje v rozpätí od 58,86 $m^3$/ha do 120,82 $m^3$/ha. V štádiu dorastania je hodnota nekromasy najvyššia a varíruje medzi 118,48 $m^3$/ha a 201,18 $m^3$/ha.

Priemerná hodnota mŕtveho dreva v rámci celého vývojového cyklu pralesa sa pohybuje v celom sledovanom období v rozpätí 14–15 % z celkového objemu živých stromov a nekromasy.

Bukový prales Rožok má hodnoty nekromasy v štádiu optima rozdielne ako v pralese Havešová. Hodnota mŕtveho dreva v tomto štádiu je najnižšia a pohybuje sa v rozpätí od 31,79 $m^3$/ha do 49,77 $m^3$/ha, čo reprezentuje 3,85 %, resp. 5,16 % z celkového objemu živých stromov a nekromasy. Príčina tohto rozdielu je v tom, že pokusná plocha sa nachádza v pokročilej fáze štádia optima, kedy sa už stromy predchádzajúcej generácie buka v pralese nenachádzajú a stromy terajšieho vývojového cyklu sú vo vrchole svojej produkcie. V tejto fáze, ktorá v bukovom pralese trvá približne 20 rokov, je mortalita stromov veľmi malá.

V ostatných štádiach vývojového cyklu tohto pralesa sú absolútne hodnoty nekromasy podobné ako v bukovom pralese Havešová. V štádiu dorastania sa hodnota mŕtveho dreva pohybuje v rozpätí od 102,68 $m^3$/ha do 297,07 $m^3$/ha, v štádiu rozpadu od 191,30 $m^3$/ha do 222,29 $m^3$/ha.

Priemerná hodnota mŕtveho dreva v celom vývojovom cykle pralesa sa pohybuje v rozpätí od 13,14 % do 19,6 % z celkového objemu živých a odumretých stromov.

Bukový prales Kyjov, ktorý bol sledovaný najdlhšie (30 rokov), má podobné charakteristiky mŕtveho dreva ako bukový prales Havešová. Absolútna hodnota mŕtveho dreva v štádiu optima dreva sa pohybuje v rozpätí od 38,32 $m^3$/ha do 164,40 $m^3$/ha, čo predstavuje 7,89 %, resp. 26,38 % z celkového objemu živých a odumretých stromov. Aj v tomto pralese sa TVP 2 nachádza na začiatku štádia optima, kedy ešte dožívajú a odumierajú stromy predchádzajúcej generácie, čím narastá objem nekromasy. V štádiu rozpadu sa absolútna hodnota nekromasy pohybuje v rozpätí od 66,5 $m^3$/ha do 220,14 $m^3$/ha. V štádiu dorastania sú tieto hodnoty vyššie a pohybujú sa v rozpätí od 126,38 $m^3$/ha do 247,81 $m^3$/ha.

Priemerná hodnota nekromasy vypočítaná z celého vývojového cyklu bukového pralesa z celkového objemu živých a odumretých stromov sa pohybuje v rozpätí od 15,57 % do 29,41 %.

*Corresponding author:*

Prof. Ing. MILAN SANIGA, DrSc., Technická univerzita, Lesnícka fakulta, T. G. Masaryka 24, 960 53 Zvolen, Slovenská republika
tel.: + 421 45 520 62 34, fax: + 421 45 533 26 54, e-mail: saniga@vsld.tuzvo.sk

# Brief evaluation of new provenance plots of Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco)

J. CAFOUREK

*Tišice Forest Nurseries, s.r.o., Tišice, Czech Republic*

**ABSTRACT**: Exotic species take up the area of about 35,000 ha in forests of the Czech Republic, that means about 1.5% of the forested area. The share 7% is considered as the upper limit of the area to be planted with exotic species in the Czech Republic's forestry. Douglas fir should take up a half of this area. The present area of Douglas fir in the CR forests is 3,950 ha. Suitability of Douglas fir provenances for the conditions of CR is investigated on research provenance plots. There have been seven research plots of the area 5.60 ha until now on which 87 provenances are studied. Newly established provenance plots should provide further results describing suitability of new provenances for the needs of the CR forestry. But Act No. 114/1992 passed by the Czech National Council is a limiting factor.

**Keywords**: exotic species; Douglas fir; provenance plots; introduction

Douglas fir is the most important introduced tree species for the forestry of Central Europe. It is due to its very good growth characteristics and its wood of universal use. By its volume production at 100 years of age it outyields the pine and beech by nearly 100% and the spruce by more than 30%.

Douglas fir has some advantageous silvicultural characteristics such as great regenerative capacity; it maintains a favorable humus form on soils of Cambisol type, it tolerates arid areas better than spruce or durmast oak. It should be grown at medium-rich sites of fresh oak stands or fir-beech stands.

An elementary precondition of successful introduction is the choice of a suitable provenance for the given region and site. This fact is explicitly documented by the present experience in Douglas fir growing particularly in Western Europe.

Trials were established on different plots in order to acquire further knowledge concerning the suitability of Douglas fir use and its tolerance to climatic conditions of some sites, especially in forest region 33 – Předhoří Českomoravské vrchoviny. Another, even though a complementary finding due to the short time that has elapsed from the establishment of trials was the basic assessment of growth characteristics of tested provenances at juvenile age.

## MATERIAL AND METHODS

Operational and pilot plots were established one after another to verify theoretical assumptions in operating conditions and operating nursery trials. The plots were established gradually at a pace how the planting stock to be tested was produced.

The first plot was established at Bílá Skála locality (formerly Jaroměřice Forest District, currently Třebíč FD) in 1997. Plants produced from seed supplied to the Czech Republic under the project Canadian Forest were used. It was the planting stock that was received by Budišov Forest Nursery from the Canadian party – from British Columbia.

Another plot was established at Slavonice locality (Český Rudolec FD) in 1999. Douglas fir plants produced from the seed supplied from Canada as a part of this PhD thesis were used. Besides seedings of Canadian provenances seed specimens from local stands supplied by a seed production plant of the firm LČR (Forests of the Czech Republic) at Týniště nad Orlicí were used. Local stands were selected by taking into account the forest region where verification was carried out.

The last plot was established at Zálesí locality (managed by the firm Městské lesy Znojmo) in 2000. Similar provenances like on Český Rudolec plot in 1999 were planted; but three different methods (A, B, C) of planting stock growing were tested for each lot (provenance).

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## A SURVEY OF LOCALITIES, BRIEF DESCRIPTION OF PLOTS

### Jaroměřice nad Rokytnou FD, Dukovany – Bílá Skála forest range (planted in 1997)

The plot was established in natural forest region 33 Předhoří Českomoravské vrchoviny at a locality in Jaroměřice Forest District of the firm LČR (currently Třebíč FD), Dukovany forest range, cadaster of Jamolice commune. Its local name is Bílá Skála, and the plot is included in stand division 75 A 1c (stand 611 A at the time of establishment) according to a new Forest Management Plan (FMP 2000–2009). The plot height above sea level is 300 m. Linden-trees were planted on the margins of this plot with Douglas fir.

Another reason for selection of this plot is that in neighboring compartment (76) there is a stand division with Douglas fir at the age of 100 years, having above-average growth characteristics (breast-height diameter 50 cm, height 35 m, mean stem volume 3.35 $m^3$ i.b.). Detailed evaluation of this stand division was made within the research project *Douglas Fir Growth in the CSR* (ŠIKA, VINŠ 1978).

Note: For reasons of material unification, the original designation of the plot – Jaroměřice-Dukovany is mostly used in the text, tables and documentation.

### Český Rudolec FD, Slavonice locality (planted in 1999)

The plot was established in natural forest region 16 – Českomoravská vrchovina at a locality in Český Rudolec FD of the firm LČR, Slavonice forest range, cadaster of Slavonice commune. The plot is in close proximity of natural forest region 33 – Předhoří Českomoravské vrchoviny (2 km). It is included in stand division 560 H 0 according to the effective FMP (1999–2008). The plot height above sea level is almost 600 m. The plot is situated in a vast complex of forests near the frontier with Austria. It consists of two parts on a very moderate arid NE slope. Surrounding stands (mostly spruce ones) are of average and better quality with good canopy.

The established plot is 1.00 ha in size (2 plots of 0.50 ha at a distance of 300 m), situated on a moderate slope of north-east exposure, the forest type is classified as 5 K 1 (*Abieto-Fagetum* with *Deschampsia*). The locality can be characterized as an acid site where the aggressive growth of weeds is problematic.

### Městské lesy Znojmo, Hostěhrádky-Zálesí locality (planted in 2000)

The plot was established in 2000 at a site where an overmature oak stand with linden and pine admixture was felled. This plot is managed by the firm Městské lesy Znojmo (Znojmo Municipal Forests), Hostěhrádky forest range, it is designated as 23 A 15 in accordance with the effective FMP (1996–2005). The plot is situated on a very moderate slope in two parts distant 80 m from each other. A southern exposure of the plot prevails. The plot height above sea level ranges from 390 to 410 m. The total plot size is 1.00 ha.

## EXPERIMENTAL DESIGN

The experimental design was determined by some assumptions defined in advance and by limiting factors. These criteria were selected:

- To establish the plot in an region where good-quality stands or stand divisions of Douglas fir already exist (plot Jaroměřice, Dukovany);
- To choose the plot at a site where moisture deficit is a limiting factor, desiccating site (plot Znojmo, Zálesí);
- To provide a possibility of verifying the tolerance to climatic factors, mainly to frost or physiological drought (plot Český Rudolec, Slavonice).

Another reason why the plot Jaroměřice, Dukovany was chosen is that in neighboring compartment (76) there is a stand division with Douglas fir at the age of 100 years, having above-average growth characteristics (breast-height diameter 50 m, height 35 m, mean stem volume 3.35 $m^3$ i.b.). Detailed evaluation of this stand division was made within the research project *Douglas Fir Growth in the CSR* (ŠIKA, VINŠ 1978).

Plot establishment at the locality Český Rudolec, Slavonice in the given region was intended to verify Douglas fir tolerance to frosts or to investigate physiological damage (spring overtranspiration, etc.).

One of the experimental objectives was to verify the growth and possibilities of Douglas fir growing at localities with imminent moisture deficit and poor supply of minerals. Drought is a limiting factor for most species on these fertile but desiccating sites. The locality Znojmo, Zálesí was chosen for planting.

To eliminate site and other factors, all plantings of provenances were arranged in 4 replications on all plots. The number of planted provenances, plant number and spacings on the particular plots were adjusted to the size of plot taking into account the amount of plants and type of provenances as follows.

On the plot Jaroměřice, Dukovany 28 plants at a 1.25 × 2.25 m spacing were set out within one square (9 × 9 m). Twenty lots having enough plants to be set out were selected from the 25 originally sown provenances. Three specimens of provenances from Vancouver region and two specimens from Kamloops region were not planted. On the contrary, a specimen of currently supplied (merchantable) seed from Prince George locality was included as a comparative standard.

On the plot Český Rudolec, Slavonice 25 provenances at 4 replications were planted: 2 × 1m spacing, square size 1 are (10 × 10 m), 50 plants per replication.

On the plot Znojmo, Zálesí 8 (24) provenances were planted produced by different methods of growing. The same planting design as on Český Rudolec plot was used. A total of 4,800 plants were set out.

Table 1. A list of DG provenances – Canadian Forest, planting in spring 1997, Dukovany locality, stand 75 A 1c (611 A)

| Provenance No. | Specimen No. | Provenance name | Region | Altitude (m) | North latitude | West longitude |
|---|---|---|---|---|---|---|
| 1 | **8492** | **Little Lk** | **C** | **900** | **52°37'** | **121°41'** |
| 2 | 404 | Mt. Benson | V | 610 | 49°08' | 124°04' |
| 3 | 424 | Hitl 60-Lo | V | 610 | 48°49' | 123°56' |
| 4 | 1019 | Devine-Bla | V | 900 | 50°34' | 122°32' |
| 5 | 1022 | Gordon R H | V | 579 | 48°52' | 124°22' |
| 6 | 1270 | Shawatum C. | V | 1,006 | 49°06' | 121°05' |
| 7 | 6282 | Saanichton | V | 612 | 49°15' | 123°53' |
| 8 | 6362 | Saanichton | V | 612 | 49°15' | 123°53' |
| 9 | 6513 | Quinsam | V | 519 | 49°08' | 124°24' |
| 10 | 6921 | Dewdney | V | 765 | 49°21' | 121°14' |
| 12 | 6942 | Quinsam | V | 507 | 49°07' | 124 04' |
| 15 | 31951 | East of Othello | V | 373 | 49°22' | 121°22' |
| 16 | 32401 | Bella Coola | V | 150 | 52°25' | 126°15' |
| 17 | **25780** | **Green Mtn** | **G** | **850** | **53°57'** | **122°28'** |
| 18 | **5006** | **Hospital Creek** | **N** | **1,050** | **51°21'** | **116°57'** |
| 19 | **10205** | **Blackwater Ridge** | **N** | **1,200** | **51°30'** | **117°15'** |
| 20 | **19913** | **Busk Cr** | **N** | **875** | **49°37'** | **117°08'** |
| 21 | **33124** | **Akolkolex** | **N** | **550** | **50°51'** | **118°02'** |
| 22 | **8273** | **Mamit Lake** | **K** | **1,070** | **50°15'** | **120°47'** |
| 24 | **30663** | **Dutch Lake** | **K** | **600** | **51°37'** | **120°00'** |
| **Standard** | **25780** | **Prince George** | **MGR** | **700** | **53°50'** | **122°54'** |

**var. *glauca***

## PROVENANCES

The choice of provenances was partly influenced by the planting stock (seed) available for verification. The lots of provenances identified in Tables 1–3 were used. The variety *glauca* is color-shaded in documentation materials for illustration.

Both the variety green Douglas – so called *viridis* and blue Douglas – so called *glauca* were represented in the trial on the plot Jaroměřice, Dukovany. Twelve provenances (57%) belong to var. *viridis* – a coastal one and nine provenances to an inland variety.

The structure of provenances used on other plots is similar – see the lists of provenances; in addition, both plots contain provenances coming from certified local stands of Douglas fir in which some selection has already been made and where better adaptation to local climatic conditions can be expected.

## METHODS OF EVALUATION

Basic assessments were made to evaluate field trials aimed at practical verification of nursery results, i.e. assessment of provenance mortality or survival, health assessment and measurement of height growth. Current mathematical and statistical methods were used for data processing according to modified methodical instructions for biological and breeding trials. Basic mathematical characteristics were calculated such as arithmetic mean, standard error of arithmetic mean, standard deviation, coefficient of variation. Analyses of variance or Duncan's test were used to determine differences in height growth. Variability of mean heights on the plots was evaluated by analysis of variance according to the model: $y_{ij}$ = trial mean + $p_i + o_j + e_{ij}$.

The unknown variables in this equation (model) are defined as follows:

$y_{ij}$ = value of *i*-th provenance at *j*-th replication,
$p_i$ = effect of *i*-th provenance,
$o_j$ = effect of *j*-th replication,
$e_{ij}$ = experimental error.

Tree heights were measured on two plots: Dukovany and Slavonice. Height growth was measured in each live plant to the nearest 1 cm. Only survival after the first growing season was investigated on Zálesí plot. Tree health was parallelly assessed on Dukovany plot by this simple scale:

1 – healthy, fully vital tree,
2 – less vital tree, without signs of damage,
3 – tree with unhealthy symptoms, declining or damaged.

Qualitative traits were transformed by the function arc sine, and a contingency table was used to assess the health of individual parts.

The results of assessments carried out on the plots were arranged in tables and represented graphically – see the Appendixes. Statistical program STATGRAPH ver. 3 was used for data processing.

Table 2. A list of DG provenances – Český Rudolec FD, Slavonice locality, stand 560 H

| Provenance No. | Specimen No. | Provenance name | Altitude (m) | North latitude | West longitude *)East longitude |
|---|---|---|---|---|---|
| 1 | 236/95 | Pelhřimov | 550 | 49°25' | 15°14'*) |
| 2 | **AL B** | **Adams Lake** | **600** | **51°25'** | **119°30'** |
| 3 | 0404 | Mt. Benson | 610 | 49°08' | 124°04' |
| 4 | 6362 | Saanichton | 610 | 49°15' | 123°53' |
| 5 | 217/95 | Žďár nad Sázavou | 570 | 49°43' | 15°50'*) |
| 6 | **10205** | **Blackwater Ridge** | **1,200** | **51°30'** | **117°15'** |
| 7 | **AL A** | **Adams Lake** | **600** | **51°29'** | **119°29'** |
| 8 | 1270 | Shawatum C. | 1,000 | 49°06' | 121°05' |
| 9 | 7276 | Nanaimo | 925 | 48°55' | 123°52' |
| 10 | **5006** | **Hospital Creek** | **1,050** | **51°21'** | **116°57'** |
| 11 | 216/95 | Žďár nad Sázavou | 560 | 49°43' | 15°48'*) |
| 12 | 7410 | Powell River | 850 | 49°54' | 123°53' |
| 13 | **FSJ B** | **Fort St. James** | **800** | **54°30'** | **124°20'** |
| 14 | **FSJ A** | **Fort St. James** | **800** | **54°30'** | **124°18'** |
| 15 | 448/91 | Náměšť nad Oslavou | 340 | 49°12' | 16°09'*) |
| 16 | 447/91 | SLŠ Písek | 400 | 49°17' | 14°11'*) |
| 17 | **140 MH** | **140 Mile House** | **1,000** | **51°45'** | **121°20'** |
| 18 | 6282 | Saanichton | 610 | 49°15' | 123°15' |
| 19 | **TV** | **Turtle Valley** | **650** | **50°46'** | **119°29'** |
| 20 | **26281** | **Coalmont Road** | **1,000** | **49°30'** | **120°42'** |
| 21 | 0424 | Hitll 60-Lo | 610 | 49°15' | 123°14' |
| 22 | **306663** | **Dutch Lake** | **600** | **51°37'** | **120°00'** |
| 23 | 459/86 | Jaroměřice | 300 | 49°08' | 16°15'*) |
| 24 | 57/95 | Jaroměřice | 300 | 49°08' | 16°15'**) |
| 25 | **30699** | **Clearwater** | **600** | **51°33'** | **119°45'** |

**var. *glauca***

## RESULTS OF ASSESSMENTS

### MORTALITY

The results of survival and/or mortality were processed for each plot separately; they have different weights because the plots are of different age. Nevertheless, they are the most valuable information on a potential use of Douglas fir for evaluation of provenance trials and especially after the survival was assessed in the first years after planting.

Assessments on the oldest plot Dukovany were made in the autumn 2000, that means after 4 years since planting. A total of 2,352 trees were set out, after four years there were 1,231 vital individuals on the plot, i.e. 52.3% of all planted trees (Table 4). Preliminary comparison did not show any substantial and statistically significant differences between the varieties. In 9 provenances of the variety *glauca* 53.6% of planted trees survived (540 individuals), in 12 provenances of the variety *viridis* 691 individuals survived, i.e. 51.8%. The provenance planted as a standard – Prince George (No. 25) appears to be the best: 75% of planted trees survived (Fig. 1). More than two thirds of the trees were vital in provenance 04 (Devine-Bla) from Vancouver region. On the contrary, two provenances of var. *glauca* (No. 19 – Blackwater Ridge and No. 22 – Mamit Lake) were among the worst, similarly like two provenances of green Douglas No. 2 – Mt. Benson and No. 6 – Shawatum C. Provenance No. 7 – Saanichton was the absolutely worst of all because its survival amounts to 38% only. The analysis of variance (Table 5) transformed for mortality assessment indicated that neither effect of provenance nor effect of replication was significant, that means the plot is a homogeneous site. The effect of replications was absolutely negligible. For this reason Duncan's test for identification of particular provenances was not made.

On the second plot Český Rudolec, where the inventory was taken during height measurements, the results of survival were much better and more favorable. An amount of 3,850 plants out of 5,000 plants set out in spring 1999, i.e. 77%, survived in spring 2001 (after termination of winter 2000). In spring 2000, when the first assessment of the plot was made, 3,994 trees survived, i.e. almost 80%. The health of the remaining surviving plants was very good, therefore the originally envisaged health assessment was not made. Differences between the provenances were large. Similarly like on Dukovany plot,

Table 3. A list of DG provenances – Městské lesy Znojmo, Zálesí locality, stand 23 A15

| Provenance No. | Specimen No. | Provenance name | Altitude (m) | North latitude | West longitude *)East longitude |
|---|---|---|---|---|---|
| 1 | 5006 A | | | | |
| 2 | **5006 B** | **Hospital Creek** | **1,050** | **51°21'** | **116° 57'** |
| 3 | **5006 C** | | | | |
| 4 | **45986 A** | | | | |
| 5 | 45986 B | Jaroměřice nad Rokytnou | 300 | 49°08' | 16°15'*) |
| 6 | 45986 C | | | | |
| 7 | 46003 A | | | | |
| 8 | 46003 B | Náměšť nad Oslavou | 340 | 49°12' | 16°09'*) |
| 9 | 46003 C | | | | |
| 10 | 1270 A | | | | |
| 11 | 1270 B | Shawatum C. | 1,000 | 49°06' | 121°05' |
| 12 | 1270 C | | | | |
| 13 | **26281 C** | | | | |
| 14 | **26281 B** | **Coalmont Road** | **1,000** | **49°30'** | **120°42'** |
| 15 | **26281 A** | | | | |
| 16 | 7276 A | | | | |
| 17 | 7277 B | N | 925 | 48°55' | 123°52' |
| 18 | 7278 C | | | | |
| 19 | 25783 A | | | | |
| 20 | 25784 B | Green Mtn. | 850 | 53°57' | 122°28' |
| 21 | 25785 C | | | | |
| 22 | **30699 A** | | | | |
| 23 | **30700 B** | **Clearwater** | **600** | **51°33'** | **119°45'** |
| 24 | **30701 C** | | | | |

var. *glauca*

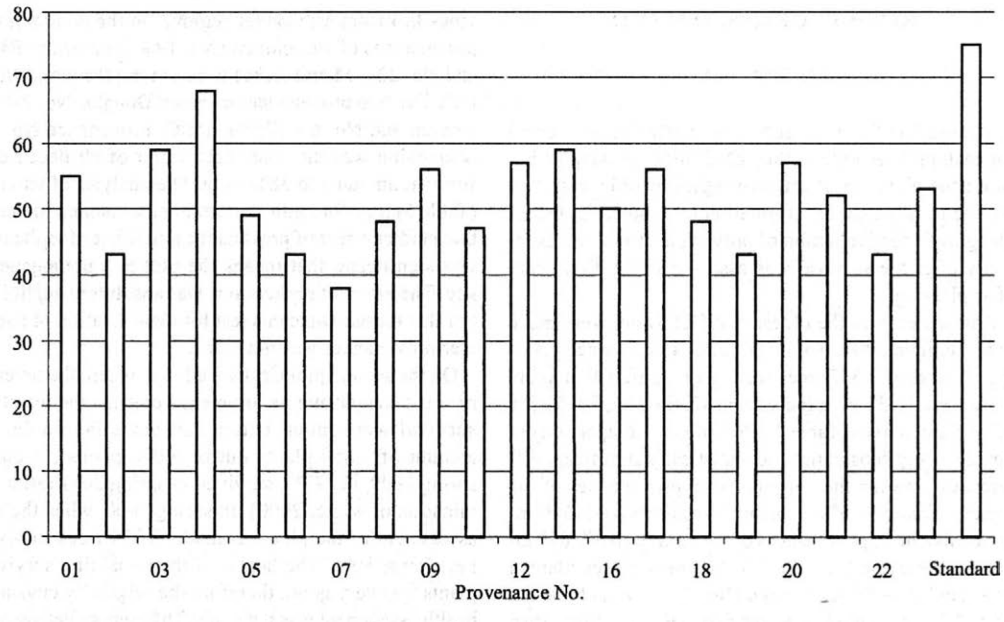


Fig. 1. Dukovany – DG – vital trees in % (autumn 2000)

Table 4. Dukovany – DG – vital trees (autumn 2000)

| Provenance No. | 1st replication | | | 2nd replication | | | 3rd replication | | | 4th replication | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Plants set out | Vital plants | (%) | Plants set out | Vital plants | (%) | Plants set out | Vital plants | (%) | Plants set out | Vital plants | (%) | Plants set out | Vital plants | (%) |
| 1 | 28 | 7 | 25 | 28 | 20 | 71 | 28 | 16 | 57 | 28 | 19 | 68 | 112 | 62 | 55 |
| 2 | 28 | 11 | 39 | 28 | 10 | 36 | 28 | 16 | 57 | 28 | 11 | 39 | 112 | 48 | 43 |
| 3 | 28 | 10 | 36 | 28 | 18 | 64 | 28 | 15 | 54 | 28 | 23 | 82 | 112 | 66 | 59 |
| 4 | 28 | 21 | 75 | 28 | 19 | 68 | 28 | 19 | 68 | 28 | 17 | 61 | 112 | 76 | 68 |
| 5 | 28 | 10 | 36 | 28 | 13 | 46 | 28 | 14 | 50 | 28 | 18 | 64 | 112 | 55 | 49 |
| 6 | 28 | 16 | 57 | 28 | 15 | 54 | 28 | 13 | 46 | 28 | 4 | 14 | 112 | 48 | 43 |
| 7 | 28 | 13 | 46 | 28 | 14 | 50 | 28 | 10 | 36 | 28 | 5 | 18 | 112 | 42 | 38 |
| 8 | 28 | 23 | 82 | 28 | 13 | 46 | 28 | 15 | 54 | 28 | 3 | 11 | 112 | 54 | 48 |
| 9 | 28 | 10 | 36 | 28 | 20 | 71 | 28 | 13 | 46 | 28 | 20 | 71 | 112 | 63 | 56 |
| 10 | 28 | 11 | 39 | 28 | 15 | 54 | 28 | 11 | 39 | 28 | 16 | 57 | 112 | 53 | 47 |
| 12 | 28 | 17 | 61 | 28 | 19 | 68 | 28 | 20 | 71 | 28 | 8 | 29 | 112 | 64 | 57 |
| 15 | 28 | 24 | 86 | 28 | 15 | 54 | 28 | 17 | 61 | 28 | 10 | 36 | 112 | 66 | 59 |
| 16 | 28 | 9 | 32 | 28 | 12 | 43 | 28 | 19 | 68 | 28 | 16 | 57 | 112 | 56 | 50 |
| 17 | 28 | 12 | 43 | 28 | 12 | 43 | 28 | 21 | 75 | 28 | 18 | 64 | 112 | 63 | 56 |
| 18 | 28 | 16 | 57 | 28 | 14 | 50 | 28 | 12 | 43 | 28 | 12 | 43 | 112 | 54 | 48 |
| 19 | 28 | 13 | 46 | 28 | 12 | 43 | 28 | 3 | 11 | 28 | 20 | 71 | 112 | 48 | 43 |
| 20 | 28 | 12 | 43 | 28 | 20 | 71 | 28 | 14 | 50 | 28 | 18 | 64 | 112 | 64 | 57 |
| 21 | 28 | 18 | 64 | 28 | 11 | 39 | 28 | 15 | 54 | 28 | 14 | 50 | 112 | 58 | 52 |
| 22 | 28 | 6 | 21 | 28 | 11 | 39 | 28 | 15 | 54 | 28 | 16 | 57 | 112 | 48 | 43 |
| 24 | 28 | 16 | 57 | 28 | 13 | 46 | 28 | 16 | 57 | 28 | 14 | 50 | 112 | 59 | 53 |
| Standard | 28 | 22 | 79 | 28 | 20 | 71 | 28 | 21 | 75 | 28 | 21 | 75 | 112 | 84 | 75 |
| | | | | | | | | | | | Total | | 2,352 | 1,231 | 52 |

Table 5. Dukovany – DG

Analysis of variance for vital trees (autumn 2000)

| Source of variability | $N$ | Sum of squares | Mean square | $F$ | Critical $F$ for $p = 1 - \alpha$ | |
|---|---|---|---|---|---|---|
| | | | | | $\alpha = 0.05$ | $\alpha = 0.01$ |
| Provenance | 20 | 0.7174 | 0.0359 | 1.1611 – | 1.75 | 2.20 |
| Replication | 3 | 0.0158 | 0.0053 | 0.1707 – | 8.57 | 26.31 |
| Residual | 60 | 1.8535 | 0.0309 | | | |
| Total | 83 | 2.5867 | | | | |

Český Rudolec FD, Slavonice forest range

ANVA for height growth of DG provenances (spring 2000)

| Source of variability | $N$ | Sum of squares | Mean square | $F$ | Critical $F$ for $p = 1 - \alpha$ | |
|---|---|---|---|---|---|---|
| | | | | | $\alpha = 0.05$ | $\alpha = 0.01$ |
| Provenance | 20 | 0.7174 | 0.0359 | 2.66 ++ | 1.67 | 2.06 |
| Replication | 3 | 0.0158 | 0.0053 | 0.21 – | 8.56 | 26.28 |
| Residual | 60 | 1.8535 | 0.0309 | | | |
| Total | 83 | 2.5867 | | | | |

Znojmo – DG

ANVA for vital trees (autumn 2000)

| Source of variability | $N$ | Sum of squares | Mean square | $F$ | Critical $F$ for $p = 1 - \alpha$ | |
|---|---|---|---|---|---|---|
| | | | | | $\alpha = 0.05$ | $\alpha = 0.01$ |
| Provenance | 23 | 3.3955 | 0.1476 | 3.8327 ++ | 1.68 | 2.08 |
| Replication | 3 | 0.7486 | 0.2495 | 6.4778 ++ | 2.74 | 4.07 |
| Residual | 69 | 2.6578 | 0.0385 | | | |
| Total | 95 | 6.8019 | | | | |

the highest losses were observed in provenance No. 3 – Mt. Benson with only 44.5% surviving trees. In the other provenances the survival rate ranged from 61% (provenance 17 – 140 Mile House) to 94.5% (provenance 14 – Fort St. James). Taking into account recurrent spring droughts (both in 1999 and 2000) and high temperatures immediately after planting this plantation appears to be successful. The differences in survival rates between the lots were at a significance level.

Considerably different results were obtained by mortality assessment on the plot Znojmo, Zálesí. Only this parameter was assessed on the plot because the bulk of the trees did not have any increments due to extreme rainfall deficit in the spring season. Sprouted annual shoots often dried. On the plot where 4,800 plants were set out, 3,126 live individuals were recorded (Table 5) even though their health was not optimum in all cases; this number accounted for 78.15% of all planted trees. Differences between the provenance lots were large. The highest loss was determined in provenance 3 Hospital Creek: only 37% of individuals survived (Table 6). The best was provenance 13 – Coalmont Road with lowest mortality below 10%. Using modified models the analysis of variance showed highly significant differences not only between the provenances but also between the replications (Table 5). Inclusion of provenances in the groups with similar survival patterns is indicated by Duncan's test. It is to note that the ocular assessment in the field can hardly reveal any markedly different part of the plot, perhaps except the margin of the 1st replication that is situated at the highest place of the plot. A dominant effect on survival in the first year after planting was apparently exerted by availability of groundwater or at least by slower desiccation of the soil profile.

## HEIGHT GROWTH

The procedure of height growth assessment was similar to the assessment of plant mortality. All plots were assessed separately because each plot was established in a different year and by planting different provenances.

Tree heights were measured twice on the oldest plot Jaroměřice, Dukovany. The first measurement in the autumn 1998 was terminated prematurely – it was prevented by weed competition and bad orientation due to small heights of plants. The second measurement was made in the autumn 2000: total height and tree height achieved in 1999 were measured.

Table 6. Znojmo – DG

Vital trees (autumn 2000) – plot from 2000 (spring)

| Provenance No. | 1st replication | | | 2nd replication | | | 3rd replication | | | 4th replication | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Plants set out | Vital plants | (%) | Plants set out | Vital plants | (%) | Plants set out | Vital plants | (%) | Plants set out | Vital plants | (%) | Plants set out | Vital plants | (%) |
| 1 | 50 | 4 | 8 | 50 | 20 | 40 | 50 | 35 | 70 | 50 | 33 | 66 | 200 | 92 | 46 |
| 2 | 50 | 20 | 40 | 50 | 7 | 14 | 50 | 18 | 36 | 50 | 38 | 76 | 200 | 83 | 42 |
| 3 | 50 | 27 | 54 | 50 | 34 | 68 | 50 | 2 | 4 | 50 | 10 | 20 | 200 | 73 | 37 |
| 4 | 50 | 23 | 46 | 50 | 38 | 76 | 50 | 45 | 90 | 50 | 45 | 90 | 200 | 151 | 76 |
| 5 | 50 | 28 | 56 | 50 | 31 | 62 | 50 | 41 | 82 | 50 | 49 | 98 | 200 | 149 | 75 |
| 6 | 50 | 32 | 64 | 50 | 22 | 44 | 50 | 42 | 84 | 50 | 37 | 74 | 200 | 133 | 67 |
| 7 | 50 | 14 | 28 | 50 | 13 | 26 | 50 | 20 | 40 | 50 | 38 | 76 | 200 | 85 | 43 |
| 8 | 50 | 10 | 20 | 50 | 20 | 40 | 50 | 18 | 36 | 50 | 29 | 58 | 200 | 77 | 39 |
| 9 | 50 | 12 | 24 | 50 | 9 | 18 | 50 | 38 | 76 | 50 | 34 | 68 | 200 | 93 | 47 |
| 10 | 50 | 28 | 56 | 50 | 8 | 16 | 50 | 41 | 82 | 50 | 32 | 64 | 200 | 109 | 55 |
| 11 | 50 | 24 | 48 | 50 | 32 | 64 | 50 | 39 | 78 | 50 | 37 | 74 | 200 | 132 | 66 |
| 12 | 50 | 39 | 78 | 50 | 34 | 68 | 50 | 37 | 74 | 50 | 48 | 96 | 200 | 158 | 79 |
| 13 | 50 | 46 | 92 | 50 | 44 | 88 | 50 | 48 | 96 | 50 | 44 | 88 | 200 | 182 | 91 |
| 14 | 50 | 42 | 84 | 50 | 44 | 88 | 50 | 41 | 82 | 50 | 33 | 66 | 200 | 160 | 80 |
| 15 | 50 | 35 | 70 | 50 | 43 | 86 | 50 | 38 | 76 | 50 | 49 | 98 | 200 | 165 | 83 |
| 16 | 50 | 43 | 86 | 50 | 13 | 26 | 50 | 34 | 68 | 50 | 37 | 74 | 200 | 127 | 64 |
| 17 | 50 | 43 | 86 | 50 | 37 | 74 | 50 | 45 | 90 | 50 | 48 | 96 | 200 | 173 | 87 |
| 18 | 50 | 32 | 64 | 50 | 45 | 90 | 50 | 43 | 86 | 50 | 45 | 90 | 200 | 165 | 83 |
| 19 | 50 | 23 | 46 | 50 | 36 | 72 | 50 | 31 | 62 | 50 | 37 | 74 | 200 | 127 | 64 |
| 20 | 50 | 47 | 94 | 50 | 42 | 84 | 50 | 34 | 68 | 50 | 46 | 92 | 200 | 169 | 85 |
| 21 | 50 | 40 | 80 | 50 | 37 | 74 | 50 | 23 | 46 | 50 | 39 | 78 | 200 | 139 | 70 |
| 22 | 50 | 18 | 36 | 50 | 22 | 44 | 50 | 36 | 72 | 50 | 36 | 72 | 200 | 112 | 56 |
| 23 | 50 | 41 | 82 | 50 | 42 | 84 | 50 | 28 | 56 | 50 | 38 | 76 | 200 | 149 | 75 |
| 24 | 50 | 22 | 44 | 50 | 36 | 72 | 50 | 24 | 48 | 50 | 41 | 82 | 200 | 123 | 62 |

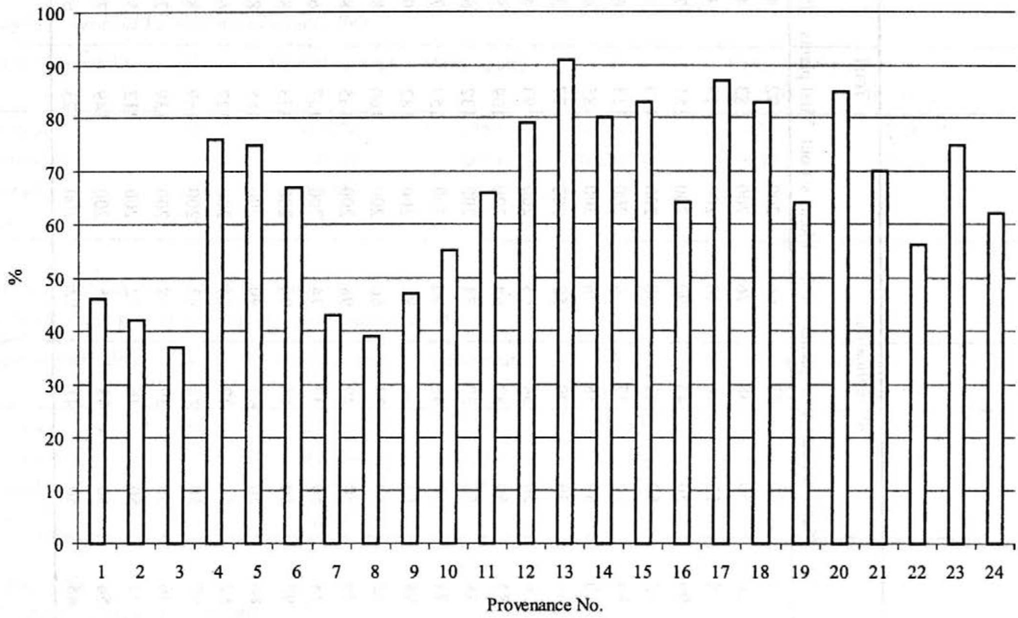


Fig. 2. Znojmo – DG – vital trees in % (autumn 2000)

Average height on the plot in 2000 was found to be just below 60 cm (59.92 cm) and the height difference ranged from 40.72 cm (provenance 18 – Hospital Creek) to 126.24 cm (standard provenance – Prince George). Average height values in 1999 were lower by 15 cm (average height 44.12 cm). A difference between minimum and maximum height measured within a provenance was large (e.g. the difference is more than 250 cm in provenance 05 – Gordon R H – Fig. 1). It was not caused by slower growth in all cases. Weed competition had a dominant effect on this plot in the first years after planting (it was quite a rich site, older and partly weed-infested

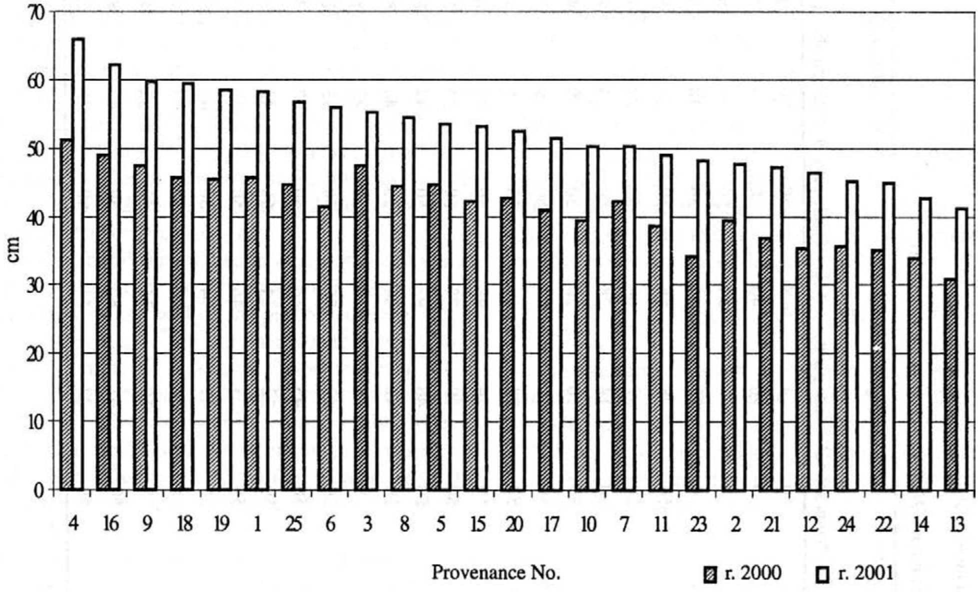


Fig. 3. Český Rudolec FD, Slavonice forest range – mean heights

Table 7. Český Rudolec FD, Slavonice forest range

The results of evaluation of DG height growth – plot from 1999, basic characteristics (spring 2000)

| Provenance No. | *n* | $\bar{x}$ (cm) | *sx* (cm) | $s\bar{x}$ (cm) | *Vk* (%) |
|---|---|---|---|---|---|
| 1 | 156 | 45.56 | 9.60 | 0.77 | 21.06 |
| 2 | 153 | 39.31 | 13.08 | 1.06 | 33.27 |
| 3 | 91 | 47.30 | 12.41 | 1.30 | 26.24 |
| 4 | 169 | 51.12 | 8.43 | 0.65 | 16.48 |
| 5 | 169 | 44.75 | 8.80 | 0.68 | 19.66 |
| 6 | 155 | 41.50 | 9.32 | 0.75 | 22.45 |
| 7 | 134 | 42.22 | 14.38 | 1.24 | 34.06 |
| 8 | 158 | 44.31 | 9.65 | 0.77 | 21.78 |
| 9 | 190 | 47.53 | 11.75 | 0.85 | 24.73 |
| 10 | 137 | 39.51 | 9.97 | 0.85 | 25.24 |
| 11 | 182 | 38.66 | 7.87 | 0.58 | 20.35 |
| 12 | 175 | 35.43 | 9.62 | 0.73 | 27.14 |
| 13 | 171 | 30.76 | 8.54 | 0.65 | 27.77 |
| 14 | 190 | 33.87 | 6.36 | 0.46 | 18.76 |
| 15 | 190 | 42.12 | 9.72 | 0.70 | 23.07 |
| 16 | 168 | 49.01 | 12.84 | 0.99 | 26.19 |
| 17 | 128 | 40.91 | 11.37 | 1.00 | 27.78 |
| 18 | 137 | 45.55 | 10.43 | 0.89 | 22.89 |
| 19 | 159 | 45.36 | 12.69 | 1.01 | 27.97 |
| 20 | 169 | 42.56 | 10.80 | 0.83 | 25.37 |
| 21 | 151 | 36.81 | 8.20 | 0.67 | 22.28 |
| 22 | 161 | 35.24 | 8.68 | 0.68 | 24.63 |
| 23 | 176 | 34.10 | 6.97 | 0.53 | 20.45 |
| 24 | 143 | 35.74 | 12.06 | 1.01 | 33.74 |
| 25 | 182 | 44.68 | 9.20 | 0.68 | 20.60 |

clearcut area and weaker plants were used), some plants were damaged by game but their regeneration was satisfactory.

The analysis of variance of height growth showed a statistically highly significant effect of provenance on height growth and an insignificant effect of replication in both years. Duncan's test used to evaluate the effect of the particular provenances makes it possible to identify only the standard provenance Prince George at a 99% significance level, which was substantially different from the other provenances. Smaller differences were determined at a 95% significance level when some more slowly growing provenances of the variety *glauca* were identified.

It is to state from height growth assessment on the plot Český Rudolec, Slavonice in spring 2000 (height growth in 1999) as well as in early spring 2001 (total height for 2000) that the values of height growth were close to the values on Dukovany plot although the latter plot was planted two years ago. The average height on Slavonice plot was 52.38 cm at the end of the growing season 2000 (Fig. 2). After growth termination in the autumn 1999 it was 41.36 cm. The difference between the years is not very large, but extremely dry May and June in 2000 should be taken into account, when the rainfall sum at this locality amounted only to 14% of the long-term average. Nevertheless, Douglas fir vitality was very good and stable. Height variability (between the lowest and the highest plant in a given replication and within the provenance) was also stable, which is documented by low values of standard error and standard deviation and stable coefficients of variation.

Provenance No. 4 – Saanichton with average height 65.88 cm in 2000 and provenance No. 16 from a Czech stand in the area of the Secondary Forestry School Písek with height 62.18 cm are among the best and fastest growing provenances. On the contrary, most slowly growing are provenances No. 13 and No. 14 (Fort St. James) with average height a little above 41 and 42 cm, respectively. The varieties *viridis* are fastest growing provenances while the varieties *glauca* are the most slowly growing ones (Table 7, Fig. 3).

The analysis of variance of height growth in 1999 (measurements in spring 2000) demonstrated a significant effect of provenance at a 99% significance level and an insignificant effect of replications (Table 5). Similarly like on Dukovany plot, the plot in question is very homogeneous. The analysis of variance of spring 2001 measurements was not made. To identify the particular provenances, Duncan's test was made in 2000. It demonstrated a smooth distribution at a significance level, but it is not of great importance for the time being with respect to the definition of fast or slowly growing provenances.

No height measurements were carried out on the third plot Znojmo, Zálesí established in 2000 – see the abovementioned reasons.

## QUALITATIVE TRAITS

As for the qualitative traits, only health and/or vitality could be assessed on the plot Jaroměřice, Dukovany over the years of observation. It was not possible to assess other traits such as stem form, foliage, existence of Lammas shoots or frost tolerance due to the age and condition of trees.

The health (vitality) was assessed by the above-mentioned method. It was difficult to identify the causes of damage or wilting in slowly growing trees or in trees with hardly any increments on the plot influenced by negative impacts of weed competition and its irregular elimination on growth and consequently on mortality or health, in addition to moisture deficit. Therefore the simplest scale possible was chosen for reliable classification.

The health assessment through transformation of qualitative traits by the function arc sine indicated the negative effect of provenance, and mainly the negative effect of replications. The effect of provenance is closely above the 95% significance level, and the effect of replications slightly exceeds the 99% significance level.

It is evident that significance partly decreases for the most frequently represented class (1 - healthy, vital). The effect of provenance is insignificant and the effect of replications is significant at a 95% significance level. In general, it is not possible to identify var. *glauca* or *viridis* as worse and better ones (less vital or more vital) even though the provenances of *glauca* are less vital because their growth is slower and they have been influenced by adverse factors for a longer time. Among the most vital provenances with highest number of trees included in class 1 (or 2) are provenances 03 – Hitll 60-Lo, 10 – Dewdney, 16 – Bella Coola and standard provenance – Prince George.

No such assessment was made on Český Rudolec plot because in an experimental polygon (8 squares) there were only 9 trees that could be included in other class than 1 – vital. This number accounted for less than 3% of the test sample. The same situation on the whole plot was confirmed by walking about the plot and by ocular assessment.

## SUMMARY ASSESSMENT OF ESTABLISHED PLOTS

A base for further objective assessment of chances to grow Douglas fir in this region was created by the establishment of provenance plots in natural forest region 33 – Předhoří Českomoravské vrchoviny or in its close surroundings. No Douglas fir plots of similar type have been established in this region until now, and the collection of planted provenances is large.

The first practical findings from the established plots can be summarized as follows:

Douglas fir plantations are promising to grow well at similar sites. In general, Douglas fir is very sensitive to manipulation during lifting and planting and its responses to adverse factors are spontaneous. Evaluation of this series of plots shows the highest vitality of Douglas fir plants on the plot Český Rudolec – Slavonice, where the mortality rate is about 23% two years after planting and the growing trees are in a very good physical condition.

A similar mortality rate (22%) was determined on the youngest plot established in 2000 (Znojmo, Zálesí), but plants on this plot were not in such a good condition; therefore it is to expect that losses will increase this year. Nevertheless, the mortality of Douglas fir plantings was lowest among all tree species planted in this region in the same year. The mortality rate of pine and oak amounted to more than 35% as reported by employees of the firm Městské lesy Znojmo, being still higher in larch and spruce. Mortality was significantly influenced by a huge rainfall deficit and spring drought accompanied by high spring temperatures. The highest losses were recorded on the plot Jaroměřice, Dukovany, amounting to nearly 50% on average. It is to note that this plot has the most favorable soil conditions for Douglas fir but the impacts of two factors were extremely negative: strong weed infestation and weak (often nonstandard) plants that were used. As it was necessary to set out plants of the given population on the plot at a time to provide for the same starting conditions for all provenances, nothing else could be done.

It is to state that average height growth lags behind the growth of Douglas fir in other regions; in recent years it has been considerably influenced by moisture deficit in the whole territory of the region concerned. Nevertheless, the best individuals achieve total heights above 200 cm on the oldest plot, and average values per provenance are close to 1 m, the fastest growing trees on other plots are assumed to be still taller in comparison with so called starting heights (i.e. heights at planting).

Height growth, survival and physiological condition are the most important traits at juvenile age. It can be assumed from the first evaluation that the growth rate of the provenances of the variety *viridis* from coastal regions is higher but the differences are not significant enough in most cases to confirm the hypothesis reliably. Provenances from the certified Czech stands that have been planted on plots Český Rudolec, Slavonice and Znojmo, Zálesí also appear to be in good shape.

As for Douglas fir health and vitality, preliminary knowledge is available because only one plot – Jaroměřice, Dukovany was evaluated. The trees on the other plot were mostly in good condition. Vitality is basically influenced by local macroclimatic and microclimatic factors, most of them cannot be influenced by man. The vitality of provenances of the variety *glauca* is somewhat lower on this plot as a result of slower growth. Neither frost injuries nor damage due to potential phy siological drought was observed with some negligible exceptions. The effect of replications was evident in the lower part of the plot (moisture = more vital and aggressive weeds).

## DISCUSSION

A suitable origin of planting stock, that means also of forest tree species, is crucial for successful regeneration or introduction. It is rather a complicated problem in forest tree species because reliable and verified findings are available after a long time only, and the findings from one region can hardly be generalized and fully applied in other regions.

Older Douglas fir stands and research plots in the CR are mostly situated at locations from 300 to 600 m above sea level. There are several important and very successful older stands of Douglas fir in natural forest region 33 – Předhoří Českomoravské vrchoviny, but it has not been possible to verify and reliably identify their origin, no research plots are available. Therefore the trial was located into this relatively large forest region.

In none of the Czech trials established until now has the classification of Douglas fir provenances to two varieties – *viridis* (coastal Douglas fir) and *glauca* (inland one) been investigated. A contribution of this paper is that our trials involved several provenances of the inland variety, which in contrast to the green form has higher tolerance to early frosts, winter desiccation and drought. On the other hand, more dynamic growth, considerably higher production, later flushing and resistance to needle cast are typical of coastal Douglas fir. Losses in Douglas fir plantations are mainly caused by winter desiccation. The provenances from Oregon and Washington (USA) coasts suffer most. Very good growth and variable damage in relation to extreme climatic conditions were observed in provenances from lower locations of the Cascades in northern Washington. Tolerance to winter desiccation and very good growth especially in harsh climatic conditions were reliably demonstrated in provenances from the inland southern part of British Columbia (ŠIKA 1982). Such verification should continue on the established plots, particularly in periods with potential climatic abnormalities.

In his report on Douglas fir provenance research ŠIKA (1988) recommended to establish medium-term research plots with well-tried provenances of Douglas fir and to combine these plantings with the progeny of Czech old well-tried (certified) stands. He also argued that in spite of high costs and time consumption the establishment of such trials was irreplaceable. It is to agree with this opinion, progenies coming from seed orchards or clone archives, both the Czech and Canadian (U.S.) ones, could also be used for plantings in future.

Practical experience has been confirmed that losses are considerably higher on plots of the type extensive clearcut (Dukovany plot) than on plots with narrow cut (Slavonice, Zálesí) (SCHOBER et al. 1983; ŠIKA 1982, etc.). It was proved beyond any doubt that strong plants with well-developed root system must be used for regeneration of older plots.

## CONCLUSION

The results of provenance trials confirmed high variability of Douglas fir growth, mortality and resistance to adverse factors, not only between the provenances but also within some provenances. The choice of suitable provenances is difficult due to high variability, on the other hand it is a good basis for selection.

As for the adverse factors, the highest losses were caused by moisture deficit, and weed competition was also a crucial factor on Dukovany plot. The best results were obtained in the provenances of var. *viridis*, even though the differences are statistically insignificant for the time being. The potential good characteristics of var. *glauca* could not be confirmed because no larger climatic fluctuations occurred from planting to spring 2001 and its higher tolerance to drought was not demonstrated at a significance level. The hitherto findings of negative correlations between the growth and tolerance of provenances to extreme climatic conditions (physiological overtranspiration, late frost, etc.) have not been confirmed because such situations did not occur in the period of observation, so the established trials have not been affected.

The results of height growth are similar, even though Douglas fir growth on the oldest plot substantially lags behind our expectation taking into account the starting conditions. The provenances of Czech certified stands, which are a part of the planting on the plot Český Rudolec, Slavonice as well as on the plot Znojmo, Zálesí, show average or slightly above-average growth.

Investigations on these outdoor plots should continue by handing them over to forest research institutions or forest schools. The data acquired and processed until now are the first contribution to verify the chances of potential Douglas fir use in the natural forest region Předhoří Českomoravské vrchoviny and to reduce the risks of planting provenances of unsuitable origin.

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# Stručné zhodnocení nových provenienčních ploch douglasky tisolisté (*Pseudotsuga menziesii* [Mirb.] Franco)

J. CAFOUREK

*Školky Tišice, s.r.o., Tišice, Česká republika*

**ABSTRAKT**: V lesích České republiky rostou cizokrajné dřeviny na ploše asi 35 000 ha, což je asi 1,5 % plochy lesů. Jako horní hranice se pro uplatnění cizokrajných dřevin v lesním hospodářství České republiky uvažuje podíl 7 %. Z tohoto podílu připadá asi polovina na douglasku tisolistou. V současnosti je douglaska tisolistá v lesích ČR zastoupena plochou 3 950 ha. Vhodnost provenienci douglasky tisolisté pro podmínky ČR se zkoumá na výzkumných provenienčních plochách. Až dosud jde o sedm výzkumných ploch na ploše 5,6 ha, na nichž je sledováno celkem 87 provenienci. Nově založené provenienční plochy mají přinést další výsledky o vhodnosti nových provenienci pro potřeby lesního hospodářství v ČR. Limitujícím faktorem je však Zákon ČNR č. 114/1992 Sb.

**Klíčová slova**: cizokrajné dřeviny; douglaska tisolistá; provenienční plochy; introdukce

Cílem založení pokusů na jednotlivých plochách bylo získat doplňující poznatky o vhodnosti využití douglasky a její odolnosti ke klimatickým podmínkám vybraných stanovišť, a to především v lesní oblasti 33 – Předhoří Českomoravské vrchoviny.

První plocha byla založena právě v přírodní lesní oblasti 33 – Předhoří Českomoravské vrchoviny na lokalitě Lesní správy Lesů České republiky, s. p., Jaroměřice (dnes Třebíč), revír Dukovany, katastr obce Jamolice. Místní označení je Bílá Skála, podle nového LHP (2000–2009) je plocha zařazena do porostní skupiny 75 A 1c (v době založení porost 611 A). Nadmořská výška plochy je 300 m. Jedná se o plochu o výměře 0,95 ha.Výsadba na této ploše se uskutečnila v dubnu roku 1997.

Druhá plocha byla založena v přírodní lesní oblasti 16 – Českomoravská vrchovina na lokalitě LS LČR Český Rudolec, revír Slavonice, katastr obce Slavonice. V těsném sousedství (2 km) plocha sousedí s PLO 33 – Předhoří Českomoravské vrchoviny. Podle platného LHP (1999–2008) je plocha zařazena do porostní skupiny 560 H 0. Nadmořská výška této plochy se blíží 600 m. Vlastní založená plocha má výměru 1 ha (dvě plochy po 0,5 ha vzdálené od sebe 300 m). Výsadba se uskutečnila rovněž v měsíci dubnu roku 1999.

Třetí a doposud poslední plocha byla založena v roce 2000 na místě smýceného přestárlého porostu dubu s příměsí lípy a borovice. Jedná se o plochu, která je v obhospodařování Městských lesů Znojmo, polesí Hostěrádky, označení podle platného LHP (1996–2005) je 23 A 15. Plocha se nachází na velmi mírném svahu ve dvou částech od sebe vzdálených 80 m. Expozice plochy je převážně jižní. Nadmořská výška ploch kolísá v rozmezí 390–410 m n. m., velikost plochy je 1 ha.

Na ploše Jaroměřice, Dukovany bylo v rámci jednoho čtverce (9 × 9 m) vysazeno 28 sazenic ve sponu 1,25 × 2,25 m. Z 25 původně vysetých provenienci bylo vybráno 20 partií, které měly dostatek sazenic pro výsadby. Nebyly vysazeny tři vzorky provenienci z regionu Vancouver a dva vzorky z regionu Kamloops. Naopak jako srovnávací standard byl přiřazen vzorek běžně dodávaného osiva (tzv. obchodního) z lokality Prince George.

Na ploše Český Rudolec, Slavonice bylo vysazeno celkem 25 provenienci ve čtyřnásobném opakování. Použitý spon byl 2 × 1 m, velikost čtverce 1 a (10 × 10 m), počet sazenic v jednom opakování 50 kusů.

Na ploše Znojmo, Zálesí bylo vysazeno 8 (24) provenienci získaných z různých způsobů pěstování. Princip výsadby byl stejný jako na ploše Český Rudolec. Celkem bylo vysazeno 4 800 sazenic.

Na ploše Jaroměřice, Dukovany je v pokusu zastoupena jak varieta douglasky zelené – tzv. *viridis*, tak douglasky sivé (modré) – tzv. *glauca*. Celkem 12 provenienci (57 %) je variety zelené – pobřežní a devět provenienci je variety vnitrozemské.

Na dalších plochách je struktura použitých provenienci obdobná, ale navíc jsou obě plochy doplněny o provenience pocházející z uznaných domácích porostů douglasky, u kterých již proběhla určitá selekce a kde lze předpokládat především lepší adaptaci na místní klimatické poměry.

Na ploše Dukovany se uskutečnilo vyhodnocení na podzim roku 2000, po čtyřech letech od výsadby. Na plochu bylo vysazeno celkem 2 352 stromů, po čtyřech letech bylo zaznamenáno na ploše 1 231 rostoucích jedinců, což představuje 52,3 % všech vysazených stromů. Při stručném porovnání bylo zjištěno, že rozdíly mezi jednotlivými varietami nejsou podstatné a statisticky významné. U devíti provenienci variety *glauca* přežívá 53,6 % vysazených stromů (540 kusů), u 12 provenienci variety *viridis* přežívá 691 jedinců, tj. 51,8 %. Nejlepší provenience je provenience vysazená jako standard – Prince George (č. 25), kde přežívá 75 % vysazených stromů. Více než dvě třetiny stromů rostou i u provenience 04 (Devine-Bla) z regionu Vancouver. Mezi nejhorší provenience patří dvě provenience var. *glauca* (č. 19 – Blackwater Ridge a č. 22 – Mamit Lake) stejně jako dvě provenience douglasky zelené (č. 2 – Mt. Benson a č. 6 – Shawatum C.). Úplně nejhorší byla provenience 7 – Saanichton, kde přežívá pouhých 38 % stromů.

Na Českém Rudolci byly výsledky přežívání podstatně příznivější. Z 5 000 vysazených sazenic na jaře 1999 jich na jaře 2001 (po skončení zimy 2000) přežilo 3 850, tj. 77 %. Na jaře 2000, kdy proběhlo první hodnocení plochy, přežívalo 3 994 stromů, tj. téměř 80 %. Zbývající přežívající sazenice jsou vesměs ve velmi dobrém zdravotním stavu, proto se původně uvažované hodnocení zdravotního stavu neprovádělo. Rozdíly mezi jednotlivými proveniencemi jsou značné. Největší ztráty vykazuje stejně jako na ploše Dukovany provenience číslo 3 – Mt. Benson, kde roste pouze 44,5 % vysazených stromů. U ostatních proveniencí se procento ujímavosti (přežívání) pohybuje od 61 % (provenience 17 – 140 Mile House) do 94,5 % (provenience 14 – Fort St. James).

Hodnocení mortality na ploše Zálesí poskytlo velmi rozdílné výsledky. Zde se provedlo pouze toto hodnocení, neboť na uvedené ploše vzhledem k extrémnímu nedostatku srážek v jarním období většina stromů neměla prokazatelně žádný přírůst. Vyrašené letorosty často úplně uschly. Na ploše, kde bylo vysazeno 4 800 sazenic, bylo evidováno 3 126 živých jedinců (tab. 6), i když ne vždy v optimálním zdravotním stavu, což představovalo 78,15 % všech vysazených stromů. Rozdíly mezi jednotlivými partiemi proveniencí byly značné. Největší ztráty zde vykazuje provenience 3 – Hospital Creek, kde přežívá pouhých 37 % jedinců. Naopak mezi nejlepší provenience patří provenience 13 – Coalmont Road, kde je mortalita nejmenší a činí méně než 10 %.

Na ploše Dukovany se provedla dvě měření výšek: první měření na podzim roku 1998, druhé na podzim 2000; při tomto hodnocení se měřila celková výška a výška stromu dosažená i v roce 1999.

Bylo zjištěno, že průměrná výška na ploše v roce 2000 je těsně pod 60 cm (59,92 cm) a výšková diference průměrné výšky se pohybuje od 40,72 cm (provenience 18 – Hospital Creek) do 126,24 cm (provenience standardní – Prince George). V roce 1999 byly průměrné hodnoty výškového růstu o 15 cm nižší (průměrná výška byla 44,12 cm). Výrazná diferenciace je mezi nejmenší a největší výškou naměřenou v rámci provenience (např. u provenience 05 – Gordon R H je rozdíl přes 250 cm). Při hodnocení výškového růstu, které bylo prováděno na ploše Český Rudolec, Slavonice jak na jaře 2000 (výškový růst v roce 1999), tak v předjaří 2001 (celková výška za rok 2000), lze konstatovat, že zjištěné hodnoty výškového růstu se již blíží hodnotám plochy Dukovany, a to přesto, že tato plocha je vysazena o dva roky dříve. Průměrná výška plochy Slavonice tak dosáhla po skončení vegetační sezony 2000 hodnoty 52,38 cm. Po skončení růstu na podzim 1999 to bylo 41,36 cm.

Mezi nejlepší a nejrychleji rostoucí provenience patří provenience č. 4 – Saanichton, u které dosahovala v roce 2000 průměrná výška 65,88 cm, a provenience č. 16 z českého porostu na SLŠ Písek 62,18 cm. Naopak mezi nejpomaleji rostoucí se řadí provenience 13 a 14 (Fort St. James), kde průměrná výška jen těsně překračuje 41, resp. 42 cm. Nejrychleji rostoucí provenience jsou variety *viridis*, naopak nejpomaleji rostou provenience variety *glauca*.

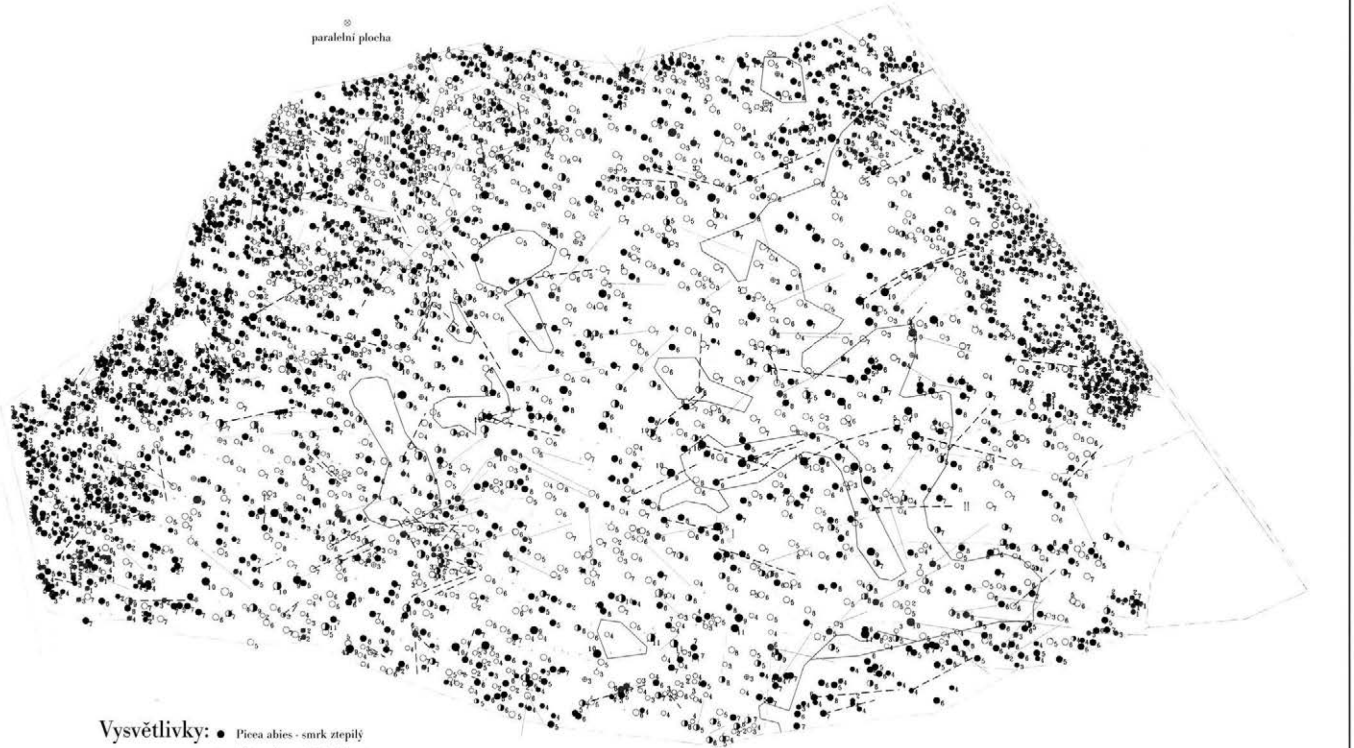
Na třetí ploše, která byla založena v roce 2000 (Znojmo, Zálesí), se žádné výškové šetření neprovádělo.

Výškový růst je společně s mortalitou a fyziologickým stavem nejdůležitějším znakem v juvenilním věku. Na základě prvních zhodnocení je možné předpokládat, že provenience variety *viridis* z pobřežních oblastí mají větší rychlost růstu, ale zatím ve většině případů nejsou rozdíly natolik průkazné, aby bylo možné hypotézu spolehlivě potvrdit. Dobře se jeví i provenience pocházející z uznaných českých porostů, které jsou vysazené na ploše Český Rudolec, Slavonice a Znojmo, Zálesí.

*Corresponding author:*

Ing. JOSEF CAFOUREK, Myslibořice 175, 675 52 Lipník u Hrotovic, Česká republika
tel.: + 420 206 69 81 23, fax: 420 206 69 81 22, e-mail: cafourek@trnet.cz

# MILEŠICE 1972 – 1996




Vysvětlivky:

- ● Picea abies - smrk ztepilý
- ◑ Abies alba - jedle bělokorá
- ○ Fagus sylvatica - buk lesní
- ⊕ Acer pseudoplatanus - javor klen
- ⊗ Sorbus aucuparia - jeřáb ptačí
- ležící kmen tvrdý
- ležící kmen nahnilý
- ležící kmen rozpadlý
- vývrat
- tloušťková třída 4 = 35 - 44 cm
- stromy, které dosáhly v období 1972 - 1996 $d_{1,3}$ = 10 cm
- stromy odumřelé v období 1972 - 1996

- zlom
- pahýl
- souše
- dvoják
- dvoják s pahýlem
- pařez
- strom s chůdovitými kořeny

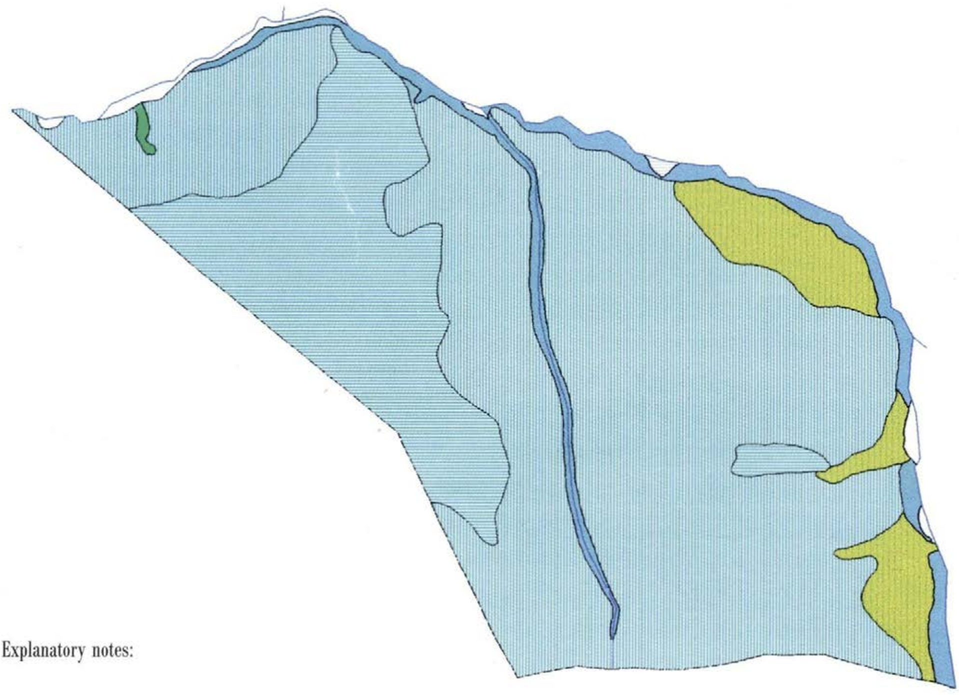
- hranice lesního typu
- hranice skupin zmlazení
- ⊗ trvalá typologická plocha

Originally pure European beech stand (originating in shelterwood felling – the eastern part of the nature reserve) starts to differentiate without human intervention. Natural regeneration of European beech appears in gaps originating in dead individuals of the main storey (the ending stage of "optimum" – maturity)

The continuous subdominant European beech level reached the height of 10–15 m near the spring area of the brook near the southern edge of the nature reserve. The main storey – gradually becoming thinner – enables light sufficient for the development of the new generation (stage of disintegration – natural regeneration phase)

Dead dominant silver firs differentiate the subdominant European beech level when falling down. The possibility of concrete individuals to succeed in the natural selection is not proportional to their growth abilities

# RAZULA – MAP OF FORESTS TYPES



Explanatory notes:

| | | |
|---|---|---|
| 5B1 – rich fir - beech stand with woodruff undergrowth | | 14,96 ha |
| 5B6 – rich fir - beech stand with maple admixture | | 4,74 ha |
| 5D6 – enriched fir - beech stand with butterbur undergrowth | | 1,62 ha |
| 5F1 – slope fir - beech stand with fern undergrowth | | 1,30 ha |
| 5V0 – wet fir - beech stand | | 0,04 ha |
| 5L1 – moutain stream ash - alder stand | | 0,20 ha |
| 5J3 – talus elm - maple stand with fern undergrowth | | 0,02 ha |
| TOTAL | | 22,88 ha |

TopoL 22. 9. 1999

1 : 5000

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

# RAZULA – NATURAL REGENERATION 1972

Explanatory notes:

| | | |
|---|---|---|
| [crosshatched] | the area originating in shelterwood felling (at present without natural regeneration) | 2,21 ha |
| [green] | beech 100, h. 2 - 6 m, thick natural regeneration | 16,17 ha |
| [dark speckled] | beech 100, h. 2 - 6 m, thin natural regeneration | 2,58 ha |
| [light] | beech 100, h. 8 - 13 m | 1,92 ha |
| | TOTAL | 22,88 ha |

Topol 22. 9. 1999

1 : 5000

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

# RAZULA – NATURAL REGENERATION 1995

Explanatory notes:

| | | |
|---|---|---|
| [dark green] | beech 100, h. 1 - 6 m | 1,56 ha |
| [green] | beech 100, h. 5 - 10 (12) m | 5,44 ha |
| [light green] | beech 100, h. 10 - 16 m | 10,39 ha |
| [hatched] | beech 100, h. 15 + m | 5,31 ha |
| | TOTAL | 22,70 ha |

TopoL 22. 9. 1999

1 : 5000

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# BOUBÍN 1972-1996

**Legend:**

| | |
|---|---|
| ○ | European beech - Fagus sylvatica |
| ● | Norway spruce - Picea abies |
| ◑ | silver fir - Abies alba |
| ⊕ | sycamore maple - Acer pseudoplatanus |
| ◒ | Scotch elm - Ulmus scabra |
| ⊗ | European mountain ash - Sorbus aucuparia |
| ⦶ | European birch - Betula verrucosa |
| | European aspen - Populus tremula |
| | willow - Salix sp. |
| | footpath |
| | forest type boundary line |
| | regeneration area boundary line in 1996 |
| | stream |
| 8 | permanent typological plot |
| | stub |
| | fracture |
| | dead standing tree |
| | forked tree with stub |
| | live tree with stilt roots |
| | live tree with burr |
| | live tree with prominently curved stem |
| | trees, that died in the period 1972-1996 |
| | live trees that, reached d.b.h. = 10 cm in the period 1972-1996 |
| | lying hardwood |
| | lying touchwood |
| | lying disintegrated wood |
| | windthrow |
| ●5 | diameter class 5 = 45-54 cm |
| ⊞ | landmark |

## BOUBÍN - natural regeneration in 1972

**Legend:**

| | | |
|---|---|---|
| | European beech (Fagus sylvatica) 10 ... 1 - 2m | 11,17 ha |

## BOUBÍN - natural regeneration in 1988

**Legend:**

| | | |
|---|---|---|
| | European beech (Fagus sylvatica) 10 ... 0 - 1m | 1,26 ha |
| | European beech (Fagus sylvatica) 10 ... 1 - 2m | 7,46 ha |
| | European beech (Fagus sylvatica) 10 ... 2 - 7m | 3,78 ha |
| | TOTAL | 12,50 ha |

## BOUBÍN - natural regeneration in 1996

**Legend:**

| | | |
|---|---|---|
| | European beech (Fagus sylvatica) 10 ... 0 - 0.5m | 0,17 ha |
| | European beech (Fagus sylvatica) 10, Norway spruce (Picea abies) + ... 0,5 - 1m | 0,73 ha |
| | European beech (Fagus sylvatica) 10, Norway spruce (Picea abies) +, European mountain ash (Sorbus aucuparia) + ... 1 - 2m | 3,06 ha |
| | European beech (Fagus sylvatica) 10 ... 2 - 4m | 6,88 ha |
| | European beech (Fagus sylvatica) 10 ... 4m and taller | 3,09 ha |
| | TOTAL | 13,93 ha |

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Rozšiřuje Ústav zemědělských a potravinářských informací, referát odbytu, Slezská 7, 120 56 Praha 2, tel.: + 420 2 27 01 03 85, e-mail: finance@uzpi.cz