Acknowledgements
We wish to thank Prof. S. BRULLO for providing the samples of Quercus virginiana. We also thank the reviewers for their useful comments.

References

Altitudinal Adaptation of Norway Spruce (Picea abies (L.) Karst.)
Progenies Indicates Small Role of Introduced Populations
in the Karkonosze Mountains

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Summary
It is believed that many of the Norway spruce stands in Karkonosze Mts. are of foreign origin. To determine what is the real share of such stands, eighteen were ecotypically identified based on the phenology and growth of progeny. The characters, observed or measured in 2 distant nurseries were: bud set index (in the first and second growing season), bud flushing index (second growing season), diameter and height (after the second and fifth growing season) as well as height increment, crown diameter and roots dry matter (after the fifth growing period). It appears that most of the investigated stands fit well into the altitudes at present occupied by them in the Karkonosze Mts. Even the poorest adapted populations show average altitudinal adaptations of 129 m (156 m), which fit easily the tolerance zones accepted for the seed transfer. It is strongly recommended that spruce stands in Karkonosze Mts. be regenerated in a natural way and that local seed resources be used for artificial regeneration.

Key words: Picea abies, ecotype identification, progeny characters, ecological adaptation, regeneration, West Sudety Mts.

FDC: 165.5; 181.2; 232.1; 174.7 Picea abies; (234.5) (458).

Introduction
There exists a belief, corresponding with the opinion of RUBNER (1866), that in Karkonosze Mts. ("Riesengebirge" in German) Norway spruce stands located above 1000 m elevation (upper mountain zone) are native and those located below (lower mountain zone) are of foreign origin. MATUSZKIEWICZ, W. and MATUSZKIEWICZ, A. (1967) as well as SOKOLOWSKI (1968) write, however, that some spruce stands in the lower zone of these mountains are of natural, local origin. On the other hand ZOLL (1958) as well as PEKINA and SAMEK (1958) suggest that numerous spruce stands in the upper zone of the Karkonosze Mts. have been established artificially, whith the use of imported seeds.

70 Silvae Genetica 44, 2-3 (1995)
The suspicion that Norway spruce stands in Karkonosze Mts. consist, at least partially, of introduced origins seems justified, for in this region artificial regeneration relying on imported seed and plant material of unknown origin was fairly common, especially in the period 1840 to 1925 (BOUVAREL, 1974; FANTA, 1974; SCHMIDT-VOGT, 1975; LUDEMANN, 1978). Until the foreign, unadapted ecotypes are recognized, the indigenousness (or adaptedness) of all stands may be questioned, with serious consequences for silviculture in this area. The author was confronted with the problem of Norway spruce ecotypes when studying natural regeneration of this species in the Karkonosze National Park, where the utilization of spruce self-sowing was officially forbidden, despite its vitality (MODRZYSKI, 1978, 1979).

The purpose of this study was: 1. To identify the ecotype of 18 Norway spruce stands, to determine what proportion of stands in the Karkonosze Mts. are poorly adapted, and 2. To formulate some silvicultural recommendations for this region.

**Material and Methods**

For the study 20 Norway spruce stands were chosen on the map, if they met the conditions that they were over 50 years old and well distributed throughout the entire investigated area (15°28’E to 15°51’E and 50°45’N to 50°50’N). Two of these stands were later eliminated, because of insufficient cone bearing. From the remaining 18 mother stands (Table 1) cones were collected in the autumn of 1976.

The altitude of the center of the collection plot in the stand was measured by means of an aneroid altimeter.

Seeds from the mother populations were sown (in the spring of 1977) in 2 nurseries: Morawina and Rakownia. Morawina (nursery 1) is located at 51°15’N, 18°06’E and 180 m altitude; average annual temperature (during the 5 years of the experiment): 7,7°C and precipitation: 628 mm. Rakownia (nursery 2) is located at 52°32’N, 17°05’E and 110 m altitude; average annual temperature: 7,9°C and precipitation: 535 mm. Both climatic and nutritional conditions were for the young spruce trees more favorable in nursery 1 (Morawina).

The seed was sown in drills 20 cm apart. Two year old seedlings were transplanted at a spacing of 30 cm x 40 cm. Both sowing and transplanting was in the same plot design, a latin rectangle with three replicates.

During the first and second growing season observations were made on terminal bud setting, and at the beginning of the second growing season - on terminal bud flushing, following in general the method proposed by HOLZER (1975). Bud set observations were made at 10 day intervals, from mid-July to the beginning of October. The number of seedlings with brown bud scales was related to the total number of seedlings in the plot. Percentages from the observations in all 3 plots (replicates of the same population) were added and the sum was divided by the number of plots and the number of observations in the annual cycle. This became the bud set index, characterizing each specific population in the given nursery. The bud flushing index was calculated in a similar way. On the average 204 seedlings were observed per plot.

After the second growing period, root collar diameter and height of 50 randomly selected seedlings were measured in each plot. After the fifth growing season the root collar diameter, total height, current height-increment and crown diameter of 24 trees were measured in each plot. Additionally dry weight of root system of 10 trees per population and nursery was recorded.

Natural regeneration occurring wild in the stands was estimated by a method described earlier (MODRZYSKI, 1989).

Statistical parameters were estimated using the JMP program, version 2.0.5. (SAS Institute Inc., Cary, NC, USA). Also a graphical method of estimating altitudinal deviations for the investigated populations was applied. It is based on the assumption that mother stands 5 and 7 (lower zone) as well as 14 and 16 (upper zone) are indigenous because of their age (Table 1) which guarantees that they have been established before the year 1830 (i.e. before artificial regeneration started).

**Table 1. -- Some data on the location and age of the mother populations.**

<table>
<thead>
<tr>
<th>Population</th>
<th>Compt. number</th>
<th>Altitude (m)</th>
<th>Exposition and slope</th>
<th>Mean age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>122 g</td>
<td>870</td>
<td>N</td>
<td>8° 124</td>
</tr>
<tr>
<td>2</td>
<td>112 c</td>
<td>705</td>
<td>NE</td>
<td>10° 107</td>
</tr>
<tr>
<td>3</td>
<td>43 b</td>
<td>720</td>
<td>NNW</td>
<td>20° 104</td>
</tr>
<tr>
<td>4</td>
<td>130 d</td>
<td>847</td>
<td>NNW</td>
<td>15° 133</td>
</tr>
<tr>
<td>5</td>
<td>46 d</td>
<td>855</td>
<td>N</td>
<td>10° 159</td>
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<tr>
<td>6</td>
<td>141 f</td>
<td>890</td>
<td>NNE</td>
<td>15° 110</td>
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<tr>
<td>7</td>
<td>45 k</td>
<td>895</td>
<td>NE</td>
<td>5° 150</td>
</tr>
<tr>
<td>8</td>
<td>180 i</td>
<td>955</td>
<td>NEE</td>
<td>18° 108</td>
</tr>
<tr>
<td>9</td>
<td>188 b</td>
<td>970</td>
<td>N</td>
<td>15° 102</td>
</tr>
<tr>
<td>10</td>
<td>49 a</td>
<td>980</td>
<td>NEE</td>
<td>10° 132</td>
</tr>
<tr>
<td>11</td>
<td>26 d</td>
<td>1038</td>
<td>N</td>
<td>28° 131</td>
</tr>
<tr>
<td>12</td>
<td>195 d</td>
<td>1082</td>
<td>NEE</td>
<td>10° 83</td>
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<tr>
<td>13</td>
<td>148 J</td>
<td>1085</td>
<td>N</td>
<td>22° 92</td>
</tr>
<tr>
<td>14</td>
<td>67 f</td>
<td>1136</td>
<td>N</td>
<td>10° 178</td>
</tr>
<tr>
<td>15</td>
<td>157 c</td>
<td>1189</td>
<td>N</td>
<td>15° 135</td>
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<td>16</td>
<td>10 a</td>
<td>1190</td>
<td>N</td>
<td>32° 149</td>
</tr>
<tr>
<td>17</td>
<td>201 R</td>
<td>1195</td>
<td>NEE</td>
<td>8° 143</td>
</tr>
<tr>
<td>18</td>
<td>19 f</td>
<td>1235</td>
<td>NEE</td>
<td>30° 132</td>
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</tbody>
</table>

*) Compartment number in the Karkonosze National Park

**Results**

The bud setting index at both nurseries and in both observation years followed a very similar pattern (Fig. 1). Statistical parameters for all combinations of location and growing period indicate a highly significant relationship between this character of the progeny and the altitude of mother stands.

The relationship between bud flushing index of the progeny and the altitude of mother populations (Fig. 1) was significant in both nurseries.

Height and diameter of progeny populations, both after second (Fig. 2) and fifth (Fig. 3) growing period show a significant regression on altitude of mother populations. The differentiation of progeny populations however was greater in the 5-year old material and there were some changes in ranking compared with the 2-year old trees. There was a highly significant relationship between height increment and crown diameter of the 5-year old spruce-trees and the altitude of their mother populations (Fig. 3).

When estimating altitudinal deviations, data from both nurseries and different observation years were combined, since no interactions between populations, nurseries and years were observed for bud set index or between populations and nurseries for growth traits and bud flushing index.

The graphically estimated deviations usually show quite random values for the same population in different characters (Table 2). The deviations averaged over all studied characters...
range from –156 m to +125 m. Extreme deviations for any trait were from –546 to +416.

The ability of mother populations to regenerate naturally ranged from 10.0 to 14.5 on a 0 to 17 scale which indicates a rather high regeneration potential.

Discussion

Many authors have shown that Norway spruce ecotypes adapted to higher altitudes cease growth and set bud earlier than those adapted to lower altitudes (Gietz, 1976; Schmidt-Vogt, 1978; Dornling, 1979; Holzer, 1988). In this study, spruce bud populations showed a close relationship between the progeny bud set index and the altitude of mother stands, which would indicate good ecological adaptation.

The bud flushing index exhibited a relatively little differentiation in the same material. It is not clear whether high-altitude ecotypes flush later (Moulaud, 1971; Garten, 1980; Holzer, 1984) or earlier (Schmidt, 1961; Rohmmeier, 1964; Schmidt-Vogt, 1977) than low-altitude ones. Therefore this character cannot be recommended for the identification of spruce ecotypes in the mountains.

Schmidt-Vogt (1977), Holzer (1981) and Nather (1988) claim that spruce seedling heights decrease with increasing altitude of the origin. This was also observed in the material studied, which would indicate that the investigated populations are mostly well adapted to the sites occupied presently by the mother stands.

The similar decrease in other investigated progeny traits (diameter, height increment and crown diameter) with the increase in origin altitude confirms the generally good adaptation of the studied populations to the altitudes at which they now occur (Holzer, 1966, 1975, 1981, 1988; Bouvarel, 1974; Nather, 1988).

It appears that decrease in growth parameters of the populations originating from higher altitudes (apart from shorter growing period) may result from higher respiration and lower assimilation rates (Schmidt, 1979; Tranquillini et al., 1980; Kleinschmitt et al., 1981). It seems that in the process of adaptation to the more severe environmental conditions of higher altitudes, spruce populations gain on hardness at the expense of growth.

The poorer adapted populations (showing the highest average deviations in table 2) were: 1, 15, 13, 17 and 11. But even highest average deviations of +125 m to –156 m, scarcely exceeded half of the range of tolerance zones proposed for seed transfer in the mountains by Rohmmeier (1984): 250 m to 300 m, Pravdin and Rostovtsev (1979): 150 m to 250 m, or Holzer (1985): 200 m to 300 m. It cannot be excluded however, that the 2 stands eliminated from the study because of very poor cone bearing behaved differently because of foreign origin and lack of adaptation.
Figure 3. – Relationship between height, diameter, height increment and crown diameter of 5-year old spruce trees grown in 2 different nurseries and the altitude of mother populations.

Table 2. – Altitudinal deviations (m) estimated graphically for the studied populations.

<table>
<thead>
<tr>
<th>Population</th>
<th>Bud setting index</th>
<th>Flushing index</th>
<th>Diameter</th>
<th>Height</th>
<th>Diameter</th>
<th>Height</th>
<th>Height increment</th>
<th>Crown diameter</th>
<th>Roots dry matter</th>
<th>Average</th>
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<tbody>
<tr>
<td>1</td>
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<td>-92</td>
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<td>-276</td>
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<td>-156</td>
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<tr>
<td>2</td>
<td>-14</td>
<td>-78</td>
<td>+88</td>
<td>+12</td>
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<td>+208</td>
<td>+100</td>
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<td>+546</td>
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</tr>
<tr>
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<td>+84</td>
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<td>+84</td>
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<td>-84</td>
<td>+96</td>
<td>+104</td>
<td>-50</td>
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</tr>
</tbody>
</table>

*) Numbers 1, 2 and 5 denote the 1st, 2nd and 5th growing period.
It may seem a paradox that populations 15 and 17, located close to the timberline (about 1250 m) appear adapted to higher altitudes. FIRNAS (cited in RUNNER and REINHOLD, 1953) claims, however, that until the 16th century the timber line in Karkonosze Mts. was 150 m to 200 m higher than today.

The spruce ecotypes transferred into drastically alien environments can be completely destroyed, e.g. by frost, snow or wind (RUNNER, 1936; ZOLL, 1958; ROHMEIDER, 1964; SCHMIDT-VOGT, 1975, 1977). This may be what happened to some ecotypes imported to the Karkonosze Mts.. Usually, however, the introduced spruce populations have a chance of adaptation to the new site. Norwegian spruce populations, characterized by very high variability and heterozygosity (LUNDBRO, 1978; KLEIN-SCHMITT et al., 1981; GERTHSCHE, 1985; GOMORY and PAULS, 1995) may undergo an effective selection during one generation. The offspring of these populations are usually significantly different from the mother populations, especially in terms of ecologically important characteristics (BOUVAEL, 1974; HOLZER, 1988). The effectiveness of this process is increased by the inflow of pollen from neighboring native stands.

KRITSCH (1992) claims that environmental tolerance and adaptability to Norway spruce is much higher than that of Scots pine.

Thus, the high plasticity and adaptability of Norway spruce would probably make the general good adaptation of stands in Karkonosze Mts. in spite the possible foreign origin of some of them.

The results obtained suggest that valuable gene resources of the highly endangered spruce stands in Karkonosze Mts. should be protected. The author has established in the vicinity of Kepro (much less polluted than the Sudety Mts.) an archive of the ecotypes identified in this study.

Conclusions

1. The investigated Norwegian spruce populations show, in general, good adaptation to the sites occupied by them in the Karkonosze Mts. and siliculturally they may be treated as indigenous.

2. Of 5 populations which show poorest adaptation, 4 have an inclination to higher, and 1 to lower altitude. Their average altitudinal deviations (125 m to 156 m) fit easily into the tolerance zones accepted in siliculture for seed transfer in the mountains (150 m to 300 m).

3. Because spruce stands in the Karkonosze Mts. generally behave like native ecotypes, and show high regeneration potential, they should be regenerated naturally wherever possible.

4. Seeds for artificial regeneration can be obtained in all seed producing adult spruce stands of the Karkonosze Mts. and used within the tolerance zones, because their adaptation seems satisfactory.

5. Gene resources of local Norway spruce ecotypes in the Karkonosze Mts. deserve conservation.

Literature


SCHMIDT-VOGT, H.: Analyse der Fichtenbestände nach Provenienzen und deren
Performance of 43 Pinus pinaster Ait. Provenances on 5 Locations in Central Spain

By R. Allia, L. Gil, and J. A. Pardo

(Received 13th September 1993)

Summary

The paper presents results of a 5-location all range Pinus pinaster provenance study in Spain, conducted in four-replicated complete block design provenance tests. Total height, diameter, survival and stem form were analysed at age 19 years. An analysis of variance over locations was made and two methods of studying stability of provenances were used, correlation and joint regression analysis.

For stem form, provenance was the most important effect, and site was statistically not significant. For height and diameter, site was the predominant effect, but high provenance-site interaction was present. Significance of interaction and implications on the use of the species were discussed.

Key words: Provenance x environment interaction, provenances experiments, genotypic stability, Pinus pinaster.

Introduction

Maritime pine (Pinus pinaster Ait.) is one of the most important forest species in the Occidental Mediterranean basin and the Atlantic coastal region of Southern Europe. It grows in natural stands on an extremely wide range of soil types and a variety of climatic conditions which characterize the plains, coastal regions and mountain slopes in an altitudinal range of about 2,000 meters.

Maritime pine is commonly planted at all conditions within its range and was extensively used in production and protection plantings. In Spain, 780,000 ha were afforested with this species between 1940 and 1982.

The performance of maritime pine provenances has been studied on numerous occasions, mainly in Atlantic climates, (Rycoff and Witch, 1947; Sweet and Thulin, 1963; Hopkins, 1964; Molina, 1965; Bellefontaine, 1975, 1979; Matziris, 1982); and it is considered a highly plastic species (Harris, 1966; Butcher, 1974; Matziris, 1982) in the sense that the best genotypes or provenances usually display superior performance in a wide variety of conditions. On some occasion the species has been cited as an example of stability (Zobel et al., 1987).

However, when the diversity of locations tested or the number of provenances involved increase, stability ceases to be a general feature. Susceptibility to frost (Bouvarel, 1960; Illy, 1966) and drought (Guillon and Kremer, 1982; Sarraute, 1982; Nguyen and Lamant, 1989) varies according to provenance, and therefore performances in diverse conditions are not homogeneous.

Because of the great genetic variability displayed in this species, which has been subdivided into 18 elementary geographical races (Barréant and Marqueau, 1988), and the different performance of provenances, it is necessary to study the behaviour of maritime pine in mediterranean conditions.

This paper examines the performance of 43 provenances of Pinus pinaster in 5 sites in West-Central Spain, located in mediterranean phytoclimates. The importance of the factors site and provenance are analysed, likewise the interaction of these, for survival, height, diameter and stem form. Stability of the provenances for each of the traits is also examined.

Material and Methods

A series of trials was planted at 5 locations in 1967 with 1-0 seedlings for the purpose of evaluating performance of maritime pine provenances. Figure 1 shows the location of the provenance tests under analysis, and details of the sites included in this study are presented in Table 1.

Each plantation followed a randomized complete block design with 16-tree plots and 4 replications. Spacing was 2.5 m x 2.5 m. They include as many as 52 provenances of the species, 40 of which were chosen for this study.

Seeds were collected both in natural stands and plantations (Table 2), covering the entire range of the species (Figure 1).

Three response variables were measured on each surviving tree in each plot: i.e. height (HTOT), diameter at breast height (DBH) and stem form (FORM, on a subjective scale from 1-good quality- to 9-poor quality- according to straightness and verticality), and the survival (SUR) of each plot was evaluated. Acebo, Cabañeros and Riofrío plantations were measured 18 years after planting, and Miravete and Espinosa tests were measured after 19 years. For height and diameter in Acebo,