Fober, H., Giertych, M.

DIFFERENTIATION OF SPRUCE SEEDLINGS OF POLISH PROVENANCE IN RELATION TO THE NITROGEN CONCENTRATION IN THE MEDIUM AND COMPETITION WITH GRASS

(Zróżnicowanie siewek świerka polskich proweniencji w zależności od stężenia azotu w pożywce i stopnia konkurencji z trawą)

| Introduction | | | 230 |
|---|---------|------|-----|
| Material and Methods | | | 232 |
| Results | | | 235 |
| Seeds | | a . | 235 |
| Grass | | | 237 |
| Seedlings in the Nursery | | | 237 |
| Seedlings in the Greenhouse | | | 238 |
| Special Characters | | | 238 |
| The Color of Seedlings | | | 239 |
| The Height of Seedlings | | | 240 |
| The Number of Lateral Shoots | | | 244 |
| The Length of Lateral Shoots | | | 246 |
| The Number of Buds in Seedlings | | | 247 |
| The Percentage of Seedlings with Apical Buds | | | 249 |
| The Dry Weight of Seedlings | | | 249 |
| The Dry Weight of Seedlings Growing in Competition with Gra | ass . | | 254 |
| The Percentage of Nitrogen in Seedlings Grown Without Comp | etition | from | |
| Grass | | | 257 |
| Discussion | | | 261 |

Introduction

Long-term experiments involving comparison of spruce populations in Europe as well as in North America show with great consistency the high sylvicultural value of Polish provenances (Bouvarel and Lemoine, 1957; Dietrichson, 1961, 1964; Fröhlich, 1960, 1966; Gathy, 1957, 1960a, 1960b; Holst, 1963; Langlet, 1959, 1960, 1963; Nanson, 1964; Rubner, 1957, Schönbach, 1957, Slabaugh and Rudolf, 1956, Troeger, 1958; Vincent and Vincent, 1964; and Vinš, 1963). These international experiments covered very few Polish provenances and the results concern essentially only those from the Forest District Istebna and Brody Żarskie, occasionally Białowieża, the Masurian Lake District, and the Sudeten. A more thorough knowledge of spruce from a larger number of stands in Poland and better determination of the range of the sylviculturally most suitable races is useful both for the needs of our own forestry and the opportunities for exports of seeds and seedlings to countries with poor local races and requiring imports of higher-quality spruce. Seeds make up even now an important item in our exports, but it is confined to seeds from Istebna and the neighboring forest districts because we know next to nothing about the usefulness of spruce from the other regions of Poland.

Knowledge of the economic value of individual tree races requires years of field experiments and the relevant work must therefore be planned for long periods in advance. Nevertheless there is the possibility, still untested but very probable, that early trials based on greenhouse experiments run under strictly uniform and strictly controlled conditions, may yield at least some general data on the usefulness of particular races. This kind of trials run with seedlings will afford us information on the quality differences between seedlings of different provenances which is not unimportant from the economic point of view because it is often the quality of the seedlings that determines the quality of the future plantation. This kind of studies will show whether the differences found between seedlings persist and whether the results recorded now will correlate with those recorded after years for mature trees in field experiments.

In the present work it is attempted to define the variations of such qualities of Polish spruce as can be observed in seedlings under the conditions of relatively brief experiments.

Growth characters were investigated in the first place, i.e. the height of the plants, the dry weight of particular parts, the proportions of the total dry weight accounted for by the leaves and roots, the length of lateral shoots, etc. Next, the studies concerned the developmental characters, such as the presence of the apical bud, the number of lateral buds, and the number of side shoots as well as such other qualities as the content and percentage of nitrogen and the color of leaves. These qualities may be affected by different environmental factors, and not necessarily in the same way for the entire geographical race. Therefore, for the sake of better insight into the interracial differentiation, the experimental conditions must be made different, but strictly controlled, to correspond to the variations met with at large. The number of such variations is restricted in this kind of experiments by the space available in greenhouses and the time-consuming character of the laboratory analyses and calculations. In experiments with seedlings of 20 provenances, run in triplicate, 12 environmental variations were found to be practicable. Two variables were introduced: (1) the nitrogen content in the medium, four levels, and (2) competition with grass, three grades. As a further stage other variables, specifically different compositions of mineral nutrients, are envisaged for future experiments.

Planned in this way, the experiments will not only show the range of variation between the provenances but should also reveal the effect of the variables on the physiological qualities of spruce irrespective of provenance. The response of spruce to competition from grass and how it is affected by the concentration of nitrogen in the medium are little known physiological-ecological problems which the present work may help to clarify a little.

Material and Methods

Seeds of the 20 different geographical races of spruce (Picea abies Karst.) were used in the experiments. They were collected between October 20, 1964, and February 13, 1965, from natural, or probably natural, populations in the northeastern and southern range of the species in Poland and, in addition, from a few isolated stands beyond the natural range (Sławki, Miedzyrzec, Konstancjewo, and Hawa). The particular provenances represent tree-stands at different altitudes. Thus, the provenance Chochołowska Valley comes from the altitude of 1400 m in the Tatra Mountains, whereas the provenance Brody comes from the altitude of 80 m, in the river valley of Nysa Łużycka. The geographical races covered by our experiments are listed in detail in Table 1 and Fig. 1, with our seed catalog number, geographical latitude and longitude, and altitude recorded in the former. The seeds were collected from presumably native trees during felling operations by taking the same number of cones from at least ten trees selected at random. Removed from the cones at the Institute of Dendrology the seeds were then stored in jars at 3°C. Those set aside for the determinations of dry weight and nitrogen content were dried 24 hrs in a desiccator at 100°C. The determinations concerned only full seeds, separated from empty ones and other impurities in methanol. The dry weight was determined by weighing on an analytical balance, with each provenance represented by two samples of 100 each. Drying was done in 24 hrs because the weight readings were the same as after 48 hrs. The weighed samples were each ground in a mortar and dried for another 24 hrs before determinations of nitrogen by the Kjeldahl method (Piper, 1957).

The nitrogen determinations were made in quadruplicate for each provenance and the results were accepted as reliable only when all four were in good agreement (with the deviation from the mean not exceeding 0.8 percent).

The principal experiments with seedlings were started between the 8th and the 10th of December, 1965. The seeds of each geographical race were sown in 36 pots, 20 in each. The jars were filled with technical sand over a 1.5 cm deep layer of gravel. There was a total of 720 pots in an experiment (20 provenances \times 36). Batches of 20 and 5 seeds of grass (*Poa annua* L.) were added each to 12 pots of every provenance to create competition for the spruce seedlings. Throughout the time of the experiments the grass was trimmed weekly to the

height of the spruce seedlings. The number of grass plants in individual pots was checked and possible losses were replaced.

All pots were set up in blocks of 60 each, i.e., 20 with three degrees of competition per block. The pots in the blocks as well as the blocks themselves were



Fig. 1. The natural geographical distribution of spruce in Poland with the sources of the seeds used in the experiments indicated.

fully randomized and then the blocks were regularly watered each three with one of four different media, so that the experiment was run in triplicate. The media differed in the content of ammonium nitrate (NH_4NO_3). The nitrogen concentration was accordingly 140 mg/l, 70 mg/l, 35 mg/l, and 0 mg/l for the media 1N, $\frac{1}{2}N$, $\frac{1}{4}N$, and 0N respectively. The remaining elements were present in the media in constant amounts, namely KH_2PO_4 , $MgSO_4$, and KCl each in amounts of 2 ml of a 1 M solution per liter of the medium, and $CaCl_2$ and $FeSO_4$ in amounts of 3 ml and 1 ml respectively. Furthermore, the pH was adjusted to 6.2 with versenic acid (EDTA) and a solution of microelements of the composition given by Hoagland was added to the media. The spruce seedlings were watered twice a week with

233

http://rcin.org.pl

about 10 ml of the nutrient per pot, and on the remaining days with distilled water, whereby the effective concentration of the nutrient medium was reduced by about two-thirds. Table 2 gives the concentration of the particular elements in the full medium, the real concentration in the pots, and the concentration of these elements reported as optimum by Ingestad (1959).

Table 1

| No. | Source locality | Geogr. lat. | Geograph, long. | Alt. |
|----------|---------------------|-------------|-----------------|------|
| 1 | 2 | 3 | 4 | 5 |
| S-16-96 | Brody | 51°42′ | 14°53′ | 80 |
| S-15-98 | Kowary | 50°48′ | 15°52′ | 625 |
| S-03-99 | Istebna | 49°33′ | 18°52′ | 630 |
| S-04-101 | Rycerka | 49°32′ | 19°00′ | 530 |
| S-09-104 | Wetlina | 49°08′ | 22°30′ | 700 |
| S-10-107 | Bliżyn | 51°05′ | 20°42′ | 320 |
| S-14-109 | Konstancjewo | 53°11′ | 19°08′ | 90 |
| S-07-110 | Iława | 53°39′ | 19°34′ | 116 |
| S-11-113 | Myszyniec | 53°22′ | 21°09′ | 120 |
| S-11-114 | Sławki | 53°03′ | 21°07′ | 130 |
| S-07-115 | Borki | 54°06′ | 22°05′ | 155 |
| S-07-116 | Przerwanki | 54°08′ | 22°04′ | 150 |
| S-01-117 | Gołdap | 54°20′ | 22°24′ | 150 |
| S-01-118 | Suwałki | 53°59′ | 23°07′ | 170 |
| S-01-119 | Augustów | 53°54′ | 23°11′ | 130 |
| S-01-120 | Białowieża | 52°40′ | 23°47′ | 160 |
| S-01-121 | Zwierzyniec | 52°43′ | 23°47′ | 160 |
| S-05-122 | Międzyrzec | 52°03′ | 22°57′ | 154 |
| S-15-125 | Stronie Sląskie | 50°18′ | 16°55′ | 870 |
| S-04-133 | Chochołowska Valley | 49°13′ | 19°48′ | 1400 |

List of the Geographical Races of Spruce Used in the Experiments

The plants began to be watered with the media on December 31, 1965, after they had received only distilled water for 20 consecutive days. On March 21, 1966, the number of seedlings per pot was reduced to five. The grass cut on February 16 was kept for determinations of fresh and dry weight and nitrogen content. The

Table 2

The Concentration of Particular Elements in the Medium, in mg per liter

| | N | Р | K | Mg | Ca | Fe | S |
|--|-----|----|-----|----|-----|----|----|
| Full medium, 1N | 140 | 62 | 156 | 48 | 120 | 56 | 64 |
| Effective concentration in the pots | 47 | 21 | 52 | 16 | 40 | 19 | 21 |
| Concentration recommended by Ingestad (1959) | 50 | 10 | 50 | 15 | 40 | 1 | 20 |

determinations were made for 24 samples, i.e. for four different media at two degrees of competition, all in triplicate. In July the color of the seedlings was estimated according to the 1938 Horticultural Colour Chart, in which the colors of the spectrum are numbered from 1 to 64, green being assigned the numbers from 53 (bluish green) to 63 (yellow-green).

The greenhouse experiments were concluded in July 1966, when the following data were recorded: (1) the number of seedlings per pot, (2) the height of seedlings, (3) the number of seedlings with apical buds, (4) the number of buds per seedling, and (5) the sum total of the length of the lateral shoots and their number.

The seedlings were removed from the pots together with the sand, which was then carefully shaken off, the roots were washed in distilled water, and the plants were dried in a dessicator at 100°C. The dry weight was determined with an accuracy of up to 0.2 mg for the whole plants, the leaves, the shoots, and the roots. The fresh weight was not determined since this would consume too much time and would involve great errors due to evaporation (720 samples would take at least two months to weigh).

All the data were processed statistically and only those found to be statistically significant are recorded in the present.

Results

Seeds

An average 32.7 percent of the dry weight is accounted for by the seed coat and the remaining 67.3 percent by the endosperm and embryo. Possible deviations in individual provenances do not exceed 0.9 percent (as based on four provenances). Since the separation of the seed coat is very time-consuming the analyses were made for whole seeds thoroughly ground in a porcelain mortar and well mixed. The percentage of the dry weight accounted for by nitrogen is 0.7 in the seed coat and 5 in the endosperm and embryo, the average for the whole seed ranging thus from 3.4 to 3.9, depending on the provenance. The average weight of a single husked seed varies between the geographical races from 6.8 mg to 10.3 mg, with the seeds from Konstancjew having the lowest weight and those from Rycerka the highest one, followed closely by those from Istebna (9.4 mg). The two last-named geographical races represent the forest complexes of Beskid Śląski and Beskid Żywiecki, which are not far apart, and the seeds differ substantially in weight from those of the other provenances.

It also needs to be noted that the other geographical races from the Sudeten and the Carpathian mountain ranges as well have rather heavy seeds, weighing over 8 mg. In the northeastern range of spruce in Poland the seeds average 7.35 mg versus 8.55 mg in the southern range. The relevant values for the individual provenances vary from 7.0 mg to 8.0 mg in the northeastern range, and from 7.7 mg to 10.3 mg in the southern range. This essentially confirms the data reported by Tyszkiewicz (1952), which were correspondingly 6–7.5 mg and 7–10 mg.

Upon drying at 100°C the seeds lost an average of 6.7 percent of their weight. The differences recorded depended on the geographical race. Seeds from Stronie Śląskie lost only 5.6 percent in weight, whereas those from Istebna lost as much as 8.7 percent. All the other provenances fitted within this range. However, irrespective of the differences in loss upon drying the provenances considered fell into the same order by the dry weight of seeds as they did by the fresh weight. The average dry weight of a single seed grain varies between the geographical races from 6.3 mg to 9.5 mg (Table 3).

Table 3

| Source | Dry wt mg | Nitrogen content | | |
|---------------------|--------------|------------------|------|--|
| Source | Diy wi., ing | dry wt., % | mg | |
| 1 | 2 | 3 | 4 | |
| Brody | 7.43 | 3.86 | 0.29 | |
| Kowary | 8.33 | 3.52 | 0.29 | |
| Istebna | 8.58 | 3.88 | 0.33 | |
| Rycerka | 9.51 | 3.63 | 0.35 | |
| Wetlina | 7.39 | 3.80 | 0.28 | |
| Bliżyn | 7.13 | 3.80 | 0.27 | |
| Konstancjewo | 6.31 | 3.78 | 0.24 | |
| Iława | 7.63 | 3.55 | 0.27 | |
| Myszyniec | 6.79 | 3.55 | 0.24 | |
| Sławki | 6.49 | 3.50 | 0.23 | |
| Borki | 6.60 | 3.60 | 0.24 | |
| Przerwanki | 6.51 | 3.51 | 0.23 | |
| Gołdap | 7.16 | 3.68 | 0.26 | |
| Suwałki | 6.73 | 3.82 | 0.26 | |
| Augustów | 6.53 | 3.60 | 0.24 | |
| Białowieża | 7.18 | 3.41 | 0.24 | |
| Zwierzyniec | 7.37 | 3.67 | 0.27 | |
| Międzyrzec | 8.43 | 3.72 | 0.31 | |
| Stronie Śląskie | 7.69 | 3.59 | 0.28 | |
| Chochołowska Valley | 7.53 | 3.28 | 0.25 | |

The Nitrogen Content and Dry Weight of Seeds from Different Sources

The nitrogen content, in terms of dry weight, varies within the range of 3.3–3.9 percent (Table 3). It was highest in the seeds from Istebna and lowest in those from Chochołowska Valley, in which it was as low as 3.28 percent according to Duncan's test and conspicuously different from all the others, as if constituting an altogether separate group.

By weight, the nitrogen content of the seeds of individual provenances obviously depends on its percentual content and the weight of the seeds, the latter being the more important owing to its greater differentiation. The by-weight content of nitrogen is lowest in the seeds from Sławki, which together with those of 16 other provenances constitute a single group marked by nitrogen contents varying within a range as narrow as 0.23–0.29 mg per average seed (Table 3).

The differences become more noticeable only with the seeds from Międzyrzec and Istebna, which have nitrogen contents of 0.31 mg and 0.33 mg respectively. The seeds from Rycerka proved to be the richest in nitrogen, averaging 0.35 mg of the element apiece.

The nitrogen content of the seeds was correlated with the geographical latitude of their site of origin. In the more northern latitude this content was lower than in the south. The analysis of the multiple regression revealed a marked correlation between the weight of the seeds and their nitrogen content (r = 0.95). The correlation between the geographical latitude and the weight of the seeds (r = -0.70) is somewhat greater than it is with the nitrogen content of the seeds (r = -0.67) but the standard partial regression coefficient is respectively -0.74and -0.04, which means that the geographical latitude is correlated with the nitrogen content *via* the dry weight of seeds.

Grass

An analysis of the grass cut on February 16, 1966, i.e. after 68 days of the experiment, yielded the following data. The average fresh weight of the grass diminishes with the degree of competition and concentration of nitrogen in the medium. All the pots with five grass plants in each yielded a total crop of 67 g of fresh grase, whereas the pots with 20 grass plants in each yielded a total of 138 g. A fourfold increase in the number of grass plants thus produced in this case barely a twofold increase in the fresh weight of grass. With higher concentrations of nitrogen in the particular media the increase in the fresh weight of the grass became almost proportionate. Thus, the pots watered with medium 0N yielded a total of 37 g of grass, and those watered with the media $\frac{1}{4}$ N, $\frac{1}{2}$ N and 1N gave respectively 44 g, 60 g, and 65 g of fresh weight. Upon drying at 100°C the loss of weight was about 85 percent.

The percentage of nitrogen in the grass grew with its concentration in the medium and was for the particular media 3.89, 4.18, 4.49, and 5.03 respectively. With the competition of five grass plants and 20 plants it was respectively an average 4.65 and 4.14.

Seedlings in the Nursery

Analyses of one-year seedlings of spruce grown in a composted forest nursery failed to reveal any correlation whatever between the qualities of the seeds and those of the seedlings. This concerns both the dry weight and the percentage of nitrogen. An analysis of the variations in dry weight and nitrogen content did not reveal any statistically significant differences between the particular provenances, since the differences between the multiplicates of the experiments were many times greater. Probably the course of the experiment was adversely affected by an uneven composting of the nursery, so that all the genetically determined differences between the provenances were obliterated in the one-year seedlings.

Seedlings in the Greenhouse

Special Characters

As regards special morphological characters of spruce seedlings grown in the greenhouse we must note in the first place the failure of cotyledons to separate (Fig. 2) and the so-called albinism (white seedlings, achlorophyllous). The former



Fig. 2. Seedlings with cotyledons sticking together. Seeds from Stronie Śląskie.

was observed in seedlings of Stronie Śląskie provenance; it was seen in almost all the pots and concerned roughly 16 percent of seedlings in this population. It was conspicuous in the early stage of seedling development and disappeared with time, preventing the normal development only in a few cases (Fig. 2). "Albinism" was seen only in two provenances, Gołdap and Wetlina, in which it affected 0.46 percent and 0.51 percent of the seedlings respectively. Yellow seedlings also were observed in these provenances, but they turned green after a time. Albino forms arise from crossing two aurea forms (Langner, 1952) or from their self-pollination. Since the aurea forms are rare, our albinos were very likely the result of the self-pollination of a single aurea-type tree in each of the two geographical reces here concerned. Self-pollination of an *aurea*-type individual will produce 25 percent of albinos and 50 percent of aurea forms. Consequently, each albino represented four seedlings from self-pollination. As will be recalled, the seeds were collected proportionately from ten trees. Assuming that the percentage of self-pollination is the same in all trees and that the albinos came from a single tree in each tree stand, every albino represented $4 \times 10 = 40$ individuals resulting from self-pollination. Hence the seeds of provenances Goldap and Wetlina can be presumed to have included respectively $0.46\% \times 40 = 18.4$ percent and $0.51\% \times 40 = 20.4$ percent of seeds produced by self-pollination. Consequently, in spruce stands, some 20 percent of seeds must be presumed to come from self-pollination. The results obtained by Sarvas (1962) for Pinus silvestris and by Fowler (1965) for Pinus banksiana were similar.

The mortality of seedlings as determined in the pots directly before the end of the experiments depended in the first place on the competition and next on the concentration of nitrogen. In the pots with the highest competition it averaged as much as 14 percent, at a lesser competition (five grass plants per pot) 8 percent, and without competition barely 1.5 percent. The nitrogen concentration in the media had a slight effect on mortality and only in the presence of grass. Therefore the analysis of variance revealed a statistically significant interaction between the nitrogen concentration and competition. Higher nitrogen concentration increased the seedling mortality, probably through promoting the growth of the grass competing with spruce.

The Color of Seedlings

The color of spruce seedlings changes significantly with the concentration of nitrogen in the media. With lesser concentrations it changed from bluish green to pale green and eventually yellow green. In figures it averaged with the particular media respectively 55.6, 57.6, 58.0, and 59.5 (according to the Horticultural Color Chart, 1938), the last figure being for medium 0N and designating the palest green. The color of the seedlings was very significantly affected by the presence of grass and averaged in figures 57.5 without competion, 60.8 with competition from five grass plants, and 60.9 with competition from 20 grass plants. The average color numbers for the particular provenances and nitrogen concentrations are recorded in Table 4. The color was significantly different in spruce seedlings from Chocho-lowska Valley, in which it was the most intensive bluish green. All the remaining

provenances made up a single group and differed not significantly from one another. As regards the interaction of the nitrogen concentration and competition, which was significant, it is probably due to the fact that the former influences the color

Table 4

| Source locality | Color | Percentage with apical buds |
|---------------------|-------|--------------------------------|
| 1 | 2 | 3 |
| Brody | 60.4 | 58.4 |
| Kowary | 59.5 | 76.4 |
| Istebna | 59.9 | 60.4 |
| Rycerka | 59.7 | 67.1 |
| Wetlina | 59.9 | 89.3 |
| Bliżyn | 59.8 | 58.5 |
| Konstancjewo | 59.9 | 60.9 |
| Iława | 59.8 | 67.6 |
| Myszyniec | 59.7 | 76.1 |
| Sławki | 59.8 | 76.1 |
| Borki | 59.9 | 80.7 |
| Przerwanki | 59.9 | 71.3 |
| Gołdap | 59.6 | 73.6 |
| Suwałki | 59.8 | 77.1 |
| Augustów | 59.9 | 71.7 |
| Białowieża | 59.8 | 75.0 |
| Zwierzyniec | 59.7 | 78.5 |
| Międzyrzec | 59.7 | 69.9 |
| Stronie Śląskie | 59.6 | 73.5 |
| Chochołowska Valley | 58.7 | 76.4 |

Color of Seedlings and Percentage of Seedlings with an Apical Bud by Provenances. Overall Averages Irrespective of Nitrogen Supply and Competition

only in the absence of competition. Competition in general, therefore, affects the color of seedlings more markedly, obviously tending to make the green more yellow, than does the degree of competition (5 or 20 grass plants per pot in the present experiments).

The Height of Seedlings

The height of spruce seedlings depends on the nitrogen concentration in the medium (Fig. 3), competition (Fig. 4), and the geographical race (Fig. 5). The most pronounced effect is that of competition, but it depends on the nitrogen concentration because there is a statistically significant interaction between the two. Thus,



Fig. 3. The effect of the nitrogen content in the medium (0N, $\frac{1}{2}$ N, $\frac{1}{2}$ N, and 1N) on the growth of seedlings. Seeds from Białowieża.

Table 5

Average Height of Seedlings, in cm, Grown Without Competition from Grass

| Guardan Japalita | Content of nitrogen in the medium | | | | | | |
|---------------------|-----------------------------------|-------|-------|------|--|--|--|
| Source locality | ON | 1/4 N | 1/2 N | 1 N | | | |
| 1 | 2 | 3 | 4 | 5 | | | |
| Brody | 5.6 | 7.5 | 12.2 | 13.1 | | | |
| Kowary | 5.6 | 7.8 | 7.9 | 8.3 | | | |
| Istebna | 5.3 | 8.7 | 10.5 | 11.1 | | | |
| Rycerka | 5.7 | 6.3 | 9.7 | 10.3 | | | |
| Wetlina | 4.7 | 6.2 | 5.7 | 7.1 | | | |
| Bliżyn | 6.0 | 6.5 | 10.7 | 9.6 | | | |
| Konstancjewo | 5.3 | 6.8 | 9.1 | 11.1 | | | |
| Iława | 5.5 | 7.3 | 10.1 | 11.5 | | | |
| Myszyniec | 5.3 | 7.2 | 9.3 | 8.4 | | | |
| Sławki | 5.0 | 6.7 | 8.1 | 8.1 | | | |
| Borki | 4.7 | 6.9 | 7.7 | 9.5 | | | |
| Przerwanki | 5.6 | 7.1 | 10.1 | 12.1 | | | |
| Gołdap | 5.1 | 7.2 | 9.5 | 8.4 | | | |
| Suwałki | 5.0 | 7.0 | 9.9 | 12.4 | | | |
| Augustów | 4.8 | 7.0 | 9.6 | 12.1 | | | |
| Białowieża | 5.3 | 6.7 | 10.5 | 12.5 | | | |
| Zwierzvniec | 5.4 | 7.1 | 8.9 | 8.5 | | | |
| Miedzyrzec | 4.9 | 7.9 | 10.4 | 9.1 | | | |
| Stronie Ślaskie | 4.8 | 7.9 | 9.9 | 8.8 | | | |
| Chochołowska Valley | 3.8 | 4.2 | 5.1 | 6.1 | | | |



Fig. 4. The effect of the nitrogen content in the medium (0N, $\frac{1}{4}$ N, $\frac{1}{2}$ N, and 1N) and competition from grass (5 and 20 plants) on the growth of spruce seedlings. http://rcin.org.pl

Table 6

| Seuree locality | Competit | Averages | | | |
|---------------------|----------|----------|-----|----------|--|
| Source locality | 0 | 5 | 20 | Averages | |
| 1 | 2 | 3 | 4 | 5 | |
| Brody | 9.6 | 5.0 | 4.5 | 6.4 | |
| Kowary | 7.4 | 4.7 | 4.5 | 5.5 | |
| Istebna | 8.9 | 5.0 | 4.7 | 6.2 | |
| Rycerka | 8.0 | 4.8 | 4.6 | 5.8 | |
| Wetlina | 5.9 | 4.4 | 4.4 | 4.9 | |
| Bliżyn | 8.2 | 4.7 | 4.5 | 5.8 | |
| Konstancjewo | 8.1 | 4.7 | 4.6 | 5.8 | |
| Iława | 8.6 | 5.1 | 4.7 | 6.1 | |
| Myszyniec | 7.5 | 4.8 | 4.8 | 5.7 | |
| Sławki | 7.0 | 4.3 | 4.2 | 5.2 | |
| Borki | 7.2 | 4.6 | 4.3 | 5.4 | |
| Przerwanki | 8.7 | 4.9 | 4.7 | 6.1 | |
| Gołdap | 7.5 | 4.9 | 4.6 | 5.7 | |
| Suwałki | 8.6 | 4.7 | 4.7 | 6.0 | |
| Augustów | 8.4 | 4.8 | 4.5 | 5.9 | |
| Białowieża | 8.7 | 4.7 | 4.4 | 5.9 | |
| Zwierzyniec | 7.5 | 4.7 | 4.7 | 5.6 | |
| Międzyrzec | 8.1 | 4.6 | 4.2 | 5.6 | |
| Stronie Śląskie | 7.9 | 4.8 | 4.4 | 5.7 | |
| Chochołowska Valley | 4.8 | 3.7 | 3.6 | 4.0 | |

The Effect of Competition on the Height, in cm, of Spruce Seedlings. Averaged Irrespective of the Nitrogen Supply



Fig. 5. Seedlings from different sources (Chochołowska Valley, Konstancjewo, Międzyrzec, and Brody) grown under exactly similar conditions, with medium $\frac{1}{2}N$ as the nutrient.

http://rcin.org.pl

seedlings completely deprived of nitrogen do not show any differences in growth at different competitions, whereas when the nitrogen supply is rich, the differentiation is very marked. Only the seedlings of the Chochołowska Valley race differed from the others significantly in their small height. The other provenances made up a single group, in which only the extreme differences in height proved to be statistically significant. The differences are in evidence only between seedlings growing without competition from grass (Table 5). In the presence of grass there are no significant growth differences either between the geographical races or the different degrees of competition. Thus, irrespective of the degree of competition taken for comparisons, the seedlings growing in its absence are roughly 71 percent higher. The mean heights of the seedlings of different provenances and at different degrees of competition are recorded in Table 6. It is worthwhile to note that Brody seedlings, which grow best of all without competition, grow by an average 53 percent less

| Com | petition (No. | | Nitrogen | Avortagios | | |
|------------------|---------------|-------|----------|------------|----------|-----|
| of grass plants) | 0N | 1/4 N | 1/2 N | 1 N | Averages | |
| 12. | 1 | 2 | 3 | 4 | 5 | 6 |
| | 0 | 5.2 | 7.0 | 9.2 | 9.9 | 7.8 |
| | 5 | 4.7 | 4.6 | 4.7 | 4.8 | 4.7 |
| | 20 | 4.7 | 4.3 | 4.4 | 4.5 | 4.5 |
| Aver | ages | 4.9 | 5.3 | 6.1 | 6.4 | 5.7 |
| | | | | | | |

The Effect of Competition and Nitrogen Supply on the Height,

Table 7

high in the presence of 20 grass plants, whereas for the poorly growing Chochołowska Valley seedlings the corresponding figure is only 26 percent. This is undoubtedly due to the fact that the differences in height are due to differences in the length of the shoot above the cotyledon node, whereas the hypocotyl length seems to be unaffected either by competition or the nitrogen concentration. The variation in height in relation to the competition and nitrogen concentration in the media is recorded in Table 7.

The Number of Lateral Shoots

Analysis of variance shows the number of the lateral shoots to depend on all the experimental variables, including third-order interaction, i.e. that of nitrogen concentration, competition, and provenance. Competition was the most important factor, reducing the number of lateral shoots to one-thirtieth on average. But the effect was independent of the degree of competition, i.e. the number of grass plants in a pot. Higher nitrogen concentrations usually increased the number of side shoots, but the response varied greatly between the provenances. One group of the



Fig. 6. The relation between the mean number of lateral shoots per seedling and the nitrogen content of the medium for two different groups of geographical races.

geographical races produced the maximum number of lateral shoots already at one-half the optimum nitrogen concentration in the medium ($\frac{1}{2}N$), whereas the other races reached the maximum only on the full medium (1N) (Fig. 6).

http://rcin.org.pl

245

According to Duncan's test all the provenances fall into two partly overlapping groups, with the lateral shoots being fewest in the montane races Wetlina and Chochołowska Valley and most numerous in Przerwanki and Brody. The average

Table 8

| Source locality | | Averages | | | |
|---------------------|-----|----------|-------|-----|-----|
| | 0N | 1/4 N | 1/2 N | 1 N | |
| 1 | 2 | 3 | 4 | 5 | 6 |
| Brody | 0,2 | 0.9 | 3.1 | 4.5 | 2.2 |
| Kowary | 0.1 | 1.3 | 1.3 | 2.4 | 1.3 |
| Istebna | 0.1 | 0.6 | 1.7 | 2.0 | 1.1 |
| Rycerka | 0.0 | 0.4 | 2.3 | 2.7 | 1.4 |
| Wetlina | 0.1 | 0.5 | 0.7 | 1.2 | 0.6 |
| Bliżyn | 0.3 | 0.6 | 2.5 | 2.6 | 1.5 |
| Konstancjewo | 0.1 | 0.5 | 1.5 | 3.9 | 1.5 |
| Iława | 0.0 | 1.1 | 2.8 | 2.7 | 1.7 |
| Myszyniec | 0.1 | 0.7 | 1.7 | 1.6 | 1.0 |
| Sławki | 0.1 | 0.7 | 2.7 | 2.8 | 1.6 |
| Borki | 0.2 | 0.7 | 0.7 | 2.8 | 1.1 |
| Przerwanki | 0.1 | 0.2 | 3.6 | 5.3 | 2.3 |
| Gołdap | 0.1 | 0.2 | 1.1 | 2.7 | 1.0 |
| Suwałki | 0.0 | 0.3 | 2.0 | 3.7 | 1.5 |
| Augustów | 0.2 | 0.9 | 2.2 | 4.1 | 1.9 |
| Białowieża | 0.3 | 0.3 | 1.0 | 4.1 | 1.4 |
| Zwierzyniec | 0.2 | 0.5 | 1.3 | 0.9 | 0.7 |
| Międzyrzec | 0.0 | 0.3 | 2.3 | 3.0 | 1.4 |
| Stronie Śląskie | 0.4 | 0.5 | 1.8 | 2.8 | 1.4 |
| Chochołowska Valley | 0.1 | 0.2 | 0.5 | 1.7 | 0.6 |
| Averages | 0.1 | 0.6 | 1.8 | 2.9 | 1.4 |

| Mean | Number | of | Lateral | Shoots | per | Seedling | in | the | Absence | of |
|------|--------|----|---------|--------|--------|----------|----|-----|---------|----|
| | | | | Compe | tition | n | | | | |

number per seedling varied between the particular provenances from 0.2 to 0.8.

The precise variation in relation to the nitrogen content of the media is given by provenances in Table 8.

The Length of Lateral Shoots

When the length of the lateral shoots of the seedlings is considered, the difference between seedlings with grass and without it becomes even more pronounced. Thus the analysis of variation shows a highly significant influence of competition and a significant influence of the nitrogen concentration and interaction of the two variables. In the presence of competition (20 and 5 grass plants) the nitrogen supply does not affect the growth of the side shoots, whereas without competition the sum total of the length of the lateral shoots is directly proportionate to the amount of nitrogen in the medium, as is shown in Fig. 7. In this respect the provenances did not differ significantly.



Fig. 7. The effect of the nitrogen content of the medium on the sum total of the lengths of lateral shoots.

The Number of Buds in Seedlings

The number of buds in seedlings is affected most by the competition of grass. As competition increases, the number of buds diminishes. The competition of five grass plants cuts this number by an average 28 percent, and that of 20 grass plants by another 9 percent. The response to a change in the degree of competition varies between the provenances, as is shown by the statistically significant interaction between the two experimental variables. The number of buds in seedlings growing in the presence or absence of competition from grass is recorded for the particular provenances in Table 9. Also statistically significant is the interaction between competition and the nitrogen supply; the data are recorded in Table 10.

On the whole there is a certain relation between the number of buds and the size of seedlings (small seedlings can have only one bud) and the intensity of growth at the end of the experiment (the seedlings which grew most vigorously had active

Table 9

| Contra la calita | Comp | Avatages | | |
|---------------------|------|----------|------|----------|
| Source locality | 0 | 5 | 20 | Averages |
| 1 | 2 | 3 | 4 | 5 |
| Brody | 1.28 | 0.92 | 0.72 | 0.97 |
| Kowary | 1.83 | 1.13 | 1.04 | 1.33 |
| Istebna | 1.18 | 0.96 | 0.84 | 0.99 |
| Rycerka | 1.40 | 1.00 | 0.84 | 1.08 |
| Wetlina | 1.17 | 1.09 | 1.07 | 1.11 |
| Bliżyn | 1.33 | 0.96 | 0.69 | 0.99 |
| Konstancjewo | 1.35 | 0.85 | 0.82 | 1.01 |
| Iława | 1.37 | 1.02 | 0.93 | 1.11 |
| Myszyniec | 1.90 | 1.12 | 0.99 | 1.34 |
| Sławki | 1.33 | 1.08 | 0.92 | 1.11 |
| Borki | 1.77 | 1.20 | 1.10 | 1.36 |
| Przerwanki | 1.65 | 1.19 | 0.98 | 1.27 |
| Gołdap | 2.08 | 1.09 | 0.96 | 1.38 |
| Suwałki | 1.60 | 1.28 | 1.02 | 1.30 |
| Augustów | 1.12 | 1.09 | 0.80 | 1.00 |
| Białowieża | 1.90 | 1.10 | 0.95 | 1.32 |
| Zwierzyniec | 1.56 | 1.08 | 0.87 | 1.17 |
| Międzyrzec | 1.35 | 0.96 | 1.02 | 1.11 |
| Stronie Śląskie | 1.23 | 1.18 | 1.01 | 1.14 |
| Chochołowska Valley | 0.95 | 0.89 | 0.98 | 0.94 |

Mean Number of Buds per Seedling in Relation to Competition. Averaged Irrespective of the Nitrogen Supply

Table 10

The Effect of Competition and Nitrogen Content in the Medium on the Number of Buds per Seedling, Averaged for All 20 Provenances Jointly

| Nitrogen content in the medium | Com of g | Averages | | |
|-----------------------------------|-------------|----------|------|-----------|
| | 0 | 5 | 20 | - 10 - 1- |
| ON | 1.29 | 1.13 | 1.07 | 1.16 |
| 1/4 N | 1.31 | 1.07 | 0.98 | 1.12 |
| 1/2 N | 1.53 | 1.07 | 0.95 | 1.18 |
| 1 N | 1.73 | 0.97 | 0.71 | 1.14 |
| Averages | 1.47 | 1.06 | 0.93 | 1.15 |

side shoots and not buds). As a consequence the least and the most vigorously growing seedlings belonged both to the group of provenances marked by a small number of buds.

The Percentage of Seedlings with Apical Buds

The percentage of seedlings with apical buds on the ultimate day of the experiment depended on competition, the nitrogen concentration, and the provenance. Furthermore, the interaction of the nitrogen concentration and the competition from grass also had a statistically significant effect (Table 11). The presence of grass causes an increase in the number of seedlings with apical buds, but there is no difference between the degrees of competition (5 or 20 grass plants per pot). Higher concentrations of nitrogen in the medium reduce the percentage of seedlings with apical buds from 89 for medium 0N to 57 for the maximum nitrogen concentration. Thus an increase in the percentage of seedlings with an apical bud, i.e. a decrease in the percentage of growing seedlings, occurs under the conditions of nitrogen deficiency (medium 0N) and competition. Duncan's test divides all the geographical

Table 11

| Nitrogen content | Comp of g | petition rass pla | Averages | |
|------------------|--------------|----------------------|----------|----|
| in the medium | 0 | 5 | 20 | |
| 0 N | 81 | 93 | 94 | 89 |
| 1/4 N | 45 | 94 | 87 | 75 |
| 1/2 N | 28 | 87 | 84 | 66 |
| 1 N | 34 | 76 | 60 | 57 |
| Averages | 47 | 88 | 81 | 72 |

The Effect of Competition and Nitrogen Supply on the Percentage of Seedlings with Apical Buds, Averaged for all 20 Provenances Jointly

races into four groups. Wetlin seedlings show the highest proportion of apical buds. The next group comprises 12 geographical races with 74-81 percent of seedlings with apical buds. It includes the provenances Białowieża, Chochołowska Valley, Stronie Śląskie, and others. Three geographical races — Międzyrzec, Iława, and Rycerka — make up the third group. The percentage of seedlings with apical buds is least in the provenance Bliżyn, which together with Brody, Konstancjewo, and Istebna makes up the last, fourth, group. The percentage of seedlings with apical buds in the particular geographical races is recorded in Table 4. The figures are inversely proportionate to the height of the seedlings, which is due to the failure of seedlings with apical buds to grow.

The Dry Weight of Seedlings

The statistical analysis of this quality was made for the seedlings of all the geographical races growing without the competition of grass, and for the five most interesting races — Brody, Istebna, Gołdap, Białowieża, and Chochołowska

Valley — with consideration of all the experimental variables, competition included. The first analysis revealed a significant influence of the site of origin and nitrogen concentration. According to Duncan's test all the geographical races fall into two partly overlapping groups with consideration of the averages at all the nitrogen concentrations (Table 12). The extreme values are those for the provenances Brody and Chochołowska Valley.

Table 12

| | | Dry weigh | t, in mg | | Dry wt. |
|---------------------|--------------------|-----------|----------|--------|---------------------------|
| Source locality | whole seedlings | leaves | roots | shoots | roots-to- leaves ratio |
| 1 | 2 | 3 | 4 | 5 | 6 |
| Brody | 312.3 | 124.6 | 133.0 | 54.7 | 1.41 |
| Kowary | 232.2 | 83.8 | 107.7 | 40.7 | 1.53 |
| Istebna | 278.4 | 110.6 | 120.4 | 47.4 | 1.32 |
| Rycerka | 277.3 | 109.4 | 121.2 | 46.7 | 1.36 |
| Wetlina | 179.8 | 61.4 | 84.9 | 33.8 | 1.69 |
| Bliżyn | 245.6 | 99.9 | 104.5 | 41.4 | 1.23 |
| Konstancjewo | 230.6 | 87.6 | 100.8 | 42.2 | 1.46 |
| Iława | 260.7 | 103.8 | 112.9 | 44.0 | 1.33 |
| Myszyniec | 233.2 | 88.2 | 102.0 | 43.1 | 1.49 |
| Sławki | 240.2 | 97.0 | 104.1 | 39.1 | 1.32 |
| Borki | 229.6 | 86.3 | 103.2 | 40.2 | 1.53 |
| Przerwanki | 263.7 | 106.5 | 107.7 | 49.5 | 1.32 |
| Gołdap | 224.9 | 84.8 | 101.6 | 38.6 | 1.51 |
| Suwałki | 258.9 | 106.0 | 104.7 | 47.7 | 1.33 |
| Augustów | 276.9 | 115.1 | 112.8 | 48.8 | 1.37 |
| Białowieża | 267.1 | 104.1 | 111.5 | 51.5 | 1.49 |
| Zwierzyniec | 221.0 | 85.6 | 102.1 | 37.7 | 1.53 |
| Międzyrzec | 260.8 | 107.6 | 112.4 | 40.1 | 1.25 |
| Stronie Śląskie | 254.1 | 98.0 | 111.9 | 45.9 | 1.45 |
| Chochołowska Valley | 137.9 | 45.7 | 66.5 | 25.6 | 2.48 |
| Averages | 244.3 | 95.3 | 106.3 | 42.9 | 1.47 |

Mean Dry Weight of Spruce Seedlings Grown in the Absence of Competition and its Distribution Between Different Parts, Averaged Irrespective of the Nitrogen Supply

Obviously there is a strong correlation between the dry weight of the seedlings of the particular provenances and their average height (r = 0.094). There is none between the dry weight of the seedlings and that of the seeds within the particular provenances (r = 0.16). But there is a marked correlation between the dry weight of seedlings and the proportion of nitrogen in the seeds from which they are obtained (r = 0.84).

For the provenances from the southern range (Brody, Kowary, Stronie Śląskie, Istebna, Rycerka, Chochołowska Valley, Bliżyn, and Wetlina) the dry weight of seedlings is inversely correlated with the altitude of the site of origin.



Fig. 8. The effect of the nitrogen content of the medium on the average dry weight of seedlings.

Table 13

| The Effe | ct o | of Nitro | gen Sup | ply | on | the Dry | Wei | ght of | Leaves | s (n | ng p | er |
|-----------|------|----------|---------|-----|-----|---------|-----|--------|---------|------|------|-----|
| seedling) | of | Spruce | Grown | in | the | Absence | of | Comp | etition | of | Gra | iss |

| Source locality | Nitro | ogen conten | t in the me | edium |
|---------------------|-------|-------------|-------------|-------|
| Source locality | 0 N | 1/4 N | 1/2 N | 1 N |
| 1 | 2 | 3 | 4 | 5 |
| Brody | 31.9 | 68.5 | 171.7 | 226.3 |
| Kowary | 28.9 | 81.5 | 107.8 | 117.1 |
| Istebna | 31.9 | 90.1 | 163.7 | 156.9 |
| Rycerka | 37.3 | 52.9 | 150.0 | 197.3 |
| Wetlina | 19.1 | 68.5 | 61.1 | 96.9 |
| Bliżyn | 38.9 | 63.1 | 158.5 | 139.3 |
| Konstancjewo | 27.9 | 56.7 | 92.3 | 173.4 |
| Iława | 28.9 | 72.8 | 132.3 | 181.4 |
| Myszyniec | 21.4 | 74.4 | 128.4 | 128.6 |
| Sławki | 27.7 | 70.5 | 133.7 | 156.2 |
| Borki | 19.7 | 72.6 | 102.5 | 150.3 |
| Przerwanki | 34.1 | 63.5 | 136.2 | 192.0 |
| Gołdap | 24.0 | 62.9 | 124.5 | 127.6 |
| Suwałki | 21.4 | 69.3 | 142.2 | 192.8 |
| Augustów | 19.1 | 77.7 | 144.5 | 219.3 |
| Białowieża | 18.5 | 62.4 | 139.3 | 196.0 |
| Zwierzyniec | 25.9 | 73.9 | 115.2 | 110.6 |
| Międzyrzec | 34.6 | 90.1 | 145.7 | 159.9 |
| Stronie Śląskie | 28.7 | 78.8 | 129.0 | 148.7 |
| Chochołowska Valley | 13.1 | 24.8 | 41.1 | 103.9 |
| Averages | 26.6 | 68.8 | 126.0 | 185.8 |

The dry weight of the seedlings does not increase in proportion to the concentration of nitrogen in the media (Fig. 8). As can be seen in the graph, the increase is slight at concentrations upward of $\frac{1}{2}N$.

The dry weight of leaves (without competition from grass). As with the dry weight of whole seedlings, the statistically most significant effect was that of the nitrogen concentration in the medium, with the provenance and the interaction of the two variables coming next (Table 13).

With the particular nitrogen concentrations in the media the dry weight of leaves averaged 26.6 mg, 68.8 mg, 126.0 mg, and 158.7 mg. The mean dry weight of leaves is recorded by provenances in Table 12. It should be noted that as with the other qualities the extreme values mark the provenances Brody and Chochołowska Valley.

The dry weight of roots (without competition from grass). The differences in the dry weight of the roots are due first and foremost to the concentration of nitrogen in the media and exist also between the provenances. There is interaction

Table 14

| Source locality | Nitro | ogen conten | t in the me | edium |
|---------------------|-------|-------------|-------------|-------|
| Source locality | 0N | 1/4 N | 1/2 N | 1 N |
| 1 | 2 | 3 | 4 | 5 |
| Brody | 63.4 | 89.6 | 205.7 | 173.5 |
| Kowary | 58.6 | 110.9 | 147.5 | 113.7 |
| Istebna | 66.9 | 106.0 | 180.0 | 128.6 |
| Rycerka | 66.6 | 87.1 | 167.9 | 163.2 |
| Wetlina | 46.1 | 101.3 | 88.9 | 103.4 |
| Bliżyn | 56.4 | 100.1 | 148.2 | 113.2 |
| Konstancjewo | 57.8 | 90.2 | 104.9 | 150.2 |
| Iława | 56.9 | 96.3 | 151.8 | 146.6 |
| Myszyniec | 50.2 | 97.7 | 144.0 | 116.2 |
| Sławki | 59.3 | 94.1 | 145.1 | 117.7 |
| Borki | 47.3 | 102.5 | 134.2 | 128.6 |
| Przerwanki | 63.0 | 80.4 | 145.6 | 142.0 |
| Gołdap | 56.3 | 92.0 | 133.7 | 124.5 |
| Suwałki | 45.7 | 95.1 | 136.8 | 141.2 |
| Augustów | 46.7 | 85.0 | 157.8 | 161.6 |
| Białowieża | 46.0 | 100.5 | 126.5 | 173.0 |
| Zwierzyniec | 59.0 | 100.1 | 129.6 | 119.6 |
| Międzyrzec | 62.9 | 120.6 | 132.6 | 134.1 |
| Stronie Śląskie | 59.3 | 115.9 | 136.4 | 136.2 |
| Chochołowska Valley | 44.4 | 56.1 | 70.9 | 94.4 |
| Averages | 55.6 | 96,1 | 139.4 | 134.1 |

The Effect of Nitrogen Supply on the Dry Weight of Roots (mg per seedling) of Spruce Grown Without Competition from Grass

of the two variables (Table 14). For most provenances and for the mean in the whole experiment the dry weight of the roots of seedlings reaches the peak with the medium $\frac{1}{2}$ N, whereas with the full medium 1 N it is already a little less. In the remaining provenances the roots are heaviest with medium 1N. The mean values for all the geographical races and all nitrogen concentrations in the medium are given in Table 12.

The dry weight of shoots (without competition from grass). This characteristic depends on the concentration of nitrogen in the medium and varies between the provenances. As in the case of the other dry weight measurements, the extreme values were recorded for the same provenances (Table 12).

The roots-to-leaves dry weight ratio (without competition from grass). As shown in Table 15 this ratio varies. It depends very much on the nitrogen concentration in the medium and differs between the geographical races. The roots exceed the leaves in dry weight with the medium 0N and on the average with all the media,

Table 15

| The] | Effec | t of Ni | trogen | Supply | on on | the | Dry | Weight | Ro | ots-to-Leaves |
|-------|-------|---------|---------|--------|-------|------|-----|---------|----|---------------|
| Ratio | in | Spruce | Seedlin | ngs Gi | own | in | the | Absence | of | Competition |
| | | | | fr | om (| Gras | S | | | |

| Source locality | Nitro | ogen conten | t in the me | edium |
|---------------------|-------|-------------|-------------|-------|
| Source locality | 0N | 1/4 N | 1/2 N | 1 N |
| 1 | 2 | 3 | 4 | 5 |
| Brody | 2.32 | 1.32 | 1.24 | 0.76 |
| Kowary | 2.07 | 1.67 | 1.30 | 1.09 |
| Istebna | 2.11 | 1.23 | 1.10 | 0.85 |
| Rycerka | 1.77 | 1.64 | 1.18 | 0.84 |
| Wetlina | 2.47 | 1.55 | 1.68 | 1.07 |
| Bliżyn | 1.51 | 1.62 | 0.96 | 0.81 |
| Konstancjewo | 2.21 | 1.64 | 1.15 | 0.86 |
| Iława | 1.97 | 1.40 | 1.15 | 0.81 |
| Myszyniec | 2.49 | 1.33 | 1.13 | 1.01 |
| Sławki | 2.16 | 1.30 | 1.04 | 0.77 |
| Borki | 2.43 | 1.41 | 1.44 | 0.86 |
| Przerwanki | 1.94 | 1.49 | 1.08 | 0.75 |
| Gołdap | 2.45 | 1.46 | 1.10 | 1.03 |
| Suwałki | 2.13 | 1.46 | 0.99 | 0.72 |
| Augustów | 2.50 | 1.12 | 1.10 | 0.74 |
| Białowieża | 2.51 | 1.58 | 0.94 | 0.90 |
| Zwierzyniec | 2.47 | 1.38 | 1.13 | 1.13 |
| Międzyrzec | 1.85 | 1.38 | 0.92 | 0.86 |
| Stronie Śląskie | 2.31 | 1.51 | 1.05 | 0.91 |
| Chochołowska Valley | 3.43 | 2.35 | 2.09 | 0.90 |
| Averages | 2.26 | 1.49 | 1.19 | 0.88 |

but with the higher concentrations often the reverse is true. The relatively highest dry weight of roots was recorded for the two montane provenances, Chochołowska Valley and Wetlina.

Increased nitrogen supply depresses the average roots-to-leaves ratio. It promotes the development of the assimilation apparatus more than roots, because where nitrogen is readily available a smaller root system suffices to provide the plant with the necessary mineral salts.

Furthermore, the analysis of regression revealed a statistically significant correlation (r = -0.80) between the dry weight of seedlings and the ratio of roots to leaves. This correlation is negative in individual provenances, which shows that the differences in dry weight between the provenances concern first and foremost the organs of assimilation.

The Dry Weight of Seedlings Growing in Competition with Grass

The analysis of variance based on the five most interesting geographical races — Istebna, Brody, Gołdap, Białowieża, and Chochołowska Valley — revealed a statistically significant influence of all the experimental variables, including the

Table 16

| Competition | Nitr | | | | |
|-------------|------|-------|-------|-------|----------|
| plants) | 0 N | 1/4 N | 1/2 N | 1 N | Averages |
| 0 | 93.2 | 178.9 | 328.7 | 375.2 | 244.2 |
| 5 | 45.6 | 39.0 | 38.6 | 47.9 | 42.7 |
| 20 | 36.7 | 29.4 | 26.7 | 24.7 | 29,3 |
| verages | 58.4 | 82.4 | 131.5 | 149.5 | 105.4 |

The Effect of Competition from Grass and Nitrogen Supply on the Dry Weight (mg per seedling) of Spruce, Averaged for Five Provenances Jointly

interaction of the third degree (provenance, medium, and competition). The effect of nitrogen supply and competition on the dry weight of seedlings is shown in Table 16. When the seedlings were on the nitrogen-free medium (0N), competition from five grass plants depressed their dry weight by 51 percent, and in the case of the full medium (1N) even by 87 percent. A fourfold increase of competition (20 grass plants) reduced the dry weight of seedlings only by another 10 percent with the medium 0N, and by 6 percent with the medium 1N. Thus, in the presence of competition from 20 grass plants, the dry weight of seedlings declines with an increase in the nitrogen supply, which means that the latter intensifies the negative effect of competition from grass on the growth of spruce seedlings.

The ratio of the aerial part to the roots grows with the supply of nitrogen and competition (Table 17). This means that the proportion of the dry weight of

seedlings accounted for by the root system diminishes when competition and the concentration of nitrogen in the medium increase. These two variables do not interact, but there is an interesting relation between them, on which some light can be shed only by a detailed analysis of the absolute weight of the particular parts of the plant.

Table 17

| Competition | Nitre | Average | | | |
|-----------------------|-------|---------|-------|------|----------|
| (NO. OF grass plants) | 0 N | 1/4 N | 1/2 N | 1 N | Averages |
| 0 | 0.66 | 1.00 | 1.26 | 1.68 | 1.15 |
| 5 | 1.81 | 2.30 | 2.46 | 2.62 | 2.30 |
| 20 | 1.92 | 2.51 | 3.03 | 3.20 | 2.67 |
| Averages | 1.46 | 1.94 | 2.25 | 2.50 | 2.04 |

The Effect of Competition from Grass and Nitrogen Supply on the Dry Weight Aerial Parts-to-Roots Ratio, Averaged for Five Provenances Jointly

How the particular parts share in the dry weight of seedlings growing in competition with grass (20 grass plants per pot) and also the proportion of aerial parts to the roots are compiled for the different media in Table 18. As the tabulation shows, the dry weight of all parts of the seedlings declines as the supply of nitrogen grows. This decline is definitely more pronounced for the roots, than for the other parts of the plants (leaves and shoots), hence the absolute value of the ratio of the

Table 18

The Effect of the Nitrogen Supply on the Dry Weight of the Individual Parts of Spruce Grown in the Presence of Maximum Competition (20 grass plants), Averaged for Five Provenances Jointly in Terms of mg per Seedling

| | Nitrogen content in the medium | | | | | | |
|-----------------------------|--------------------------------|-------|-------|------|--|--|--|
| Parts of seedlings | 0 N | 1/4 N | 1/2 N | 1 N | | | |
| Whole seedling | 36.7 | 29.4 | 26.7 | 24.7 | | | |
| Leaves | 13.6 | 11.7 | 10.1 | 10.6 | | | |
| Shoots | 10.4 | 9.0 | 9.5 | 8.2 | | | |
| Roots | 12.8 | 8.8 | 7.0 | 5.8 | | | |
| Aerial parts-to-roots ratio | 1.9 | 2.5 | 3.0 | 3.2 | | | |

aerial parts to the roots increases parallelly with the concentration of nitrogen in the media. In the absence of grass the same effect was obtained in the reverse way, namely by increasing the nitrogen supply the organs of assimilation were made to grow faster than the root system (Tables 13 and 14).

Competition from grass reduces the dry weight of seedlings to about one-seventh (Table 19), but differences in the intensity of this competition (5 or 20 grass plants per pot) do not affect this reduction significantly. The conspicuous differences between the provenances in the dry weight of seedlings growing in the absence of grass (the extreme values differ by a factor of more than 2) and the absence of these differences in the provenance and competition. In Table 19 the dry weight of seedlings growing in the absence of grass ranges from 138 mg to 312 mg per

Table 19

| Source locality | of | Averages | | |
|---------------------|-------|----------|------|-------|
| | 0 | 5 | 20 | _ |
| 0.0 1 | 2 | 3 | 4 | 5 |
| Brody | 312.3 | 44.1 | 29.5 | 128.6 |
| Kowary | 232.2 | 43.5 | 30.9 | 102.2 |
| Istebna | 278.4 | 52.4 | 36.0 | 122.3 |
| Rycerka | 277.3 | 49.2 | 34.3 | 120.3 |
| Wetlina | 179.7 | 40.3 | 36.4 | 85.5 |
| Bliżyn | 245.6 | 43.0 | 32.1 | 106.9 |
| Konstancjewo | 230.6 | 37.0 | 30.0 | 99.2 |
| Iława | 260.7 | 43.4 | 35.1 | 113.1 |
| Myszyniec | 233.2 | 41.5 | 30.4 | 101.7 |
| Sławki | 240.3 | 33.2 | 24.1 | 99.2 |
| Borki | 229.6 | 38.1 | 26.5 | 98.1 |
| Przerwanki | 263.7 | 46.4 | 28.9 | 113.0 |
| Gołdap | 224.9 | 42.0 | 30.8 | 99.2 |
| Suwałki | 258.9 | 36.3 | 29.3 | 108.2 |
| Augustów | 276.8 | 40.7 | 28.7 | 115.4 |
| Białowieża | 267.1 | 42.8 | 28.3 | 112.7 |
| Zwierzyniec | 221.0 | 41.4 | 32.4 | 98.3 |
| Międzyrzec | 260.8 | 45.7 | 31.2 | 112.6 |
| Stronie Śląskie | 254.1 | 40.6 | 31.5 | 108.7 |
| Chochołowska Valley | 137.9 | 32.4 | 22.1 | 64.1 |
| Averages | 244.3 | 41.7 | 30.4 | 105.5 |

Dry Weight of Spruce, in mg per Seedling, in Relation to Competition, Averaged Irrespective of Nitrogen Supply

seedling, which makes for a difference of over 100 percent. With the competition of five grass plants the range of the differences between the provenances is barely 32–52 mg per seedling, and with the highest competition, 20 grass plants per pot this range becomes as small as 22–36 mg per seedling. It is characteristic that the Wetlina provenance, which in the absence of competition had the second-lowest dry weight of seedlings, had the highest dry weight when grown in competition with

20 grass plants. Similarly, the provenance Zwierzyniec also has a relatively low dry weight in the absence of competition and a rather high one in its presence. With the other geographical races the order of succession remained rather unchanged. Similar differences between the provenances are revealed by the analyses of the dry weights of the shoots, leaves, and roots.

The Percentage of Nitrogen in Seedlings Grown Without Competition from Grass

The concentration of nitrogen in spruce seedlings changes in direct proportion to that in the medium and, depending on the latter, attains the percentages 1.01, 1.30, 1.43, and 1.89, when calculated in terms of averages. The provenances also differ in their nitrogen percentage. According to Duncan's test they fall into three groups: (1) Chochołowska Valley, (2) Wetlina, and (3) all the remaining prove-

Table 20

| Source locality | Con | Averages | | |
|---------------------|------|----------|------|------|
| | 0 | 5 | 20 | |
| 1 | 2 | 3 | 4 | 5 |
| Brody | 1.19 | 0.68 | 0.84 | 0.90 |
| Kowary | 1.45 | 0.72 | 0.78 | 0.98 |
| Istebna | 1.34 | 0.74 | 0.89 | 0.99 |
| Rycerka | 1.32 | 0.74 | 0.85 | 0.97 |
| Wetlina | 1.68 | 0.79 | 0.77 | 1.08 |
| Bliżyn | 1.34 | 0.74 | 0.88 | 0.99 |
| Konstancjewo | 1.36 | 0.73 | 0.64 | 0.91 |
| Iława | 1.32 | 0,69 | 0.71 | 0.91 |
| Myszyniec | 1.44 | 0.79 | 0.85 | 1.03 |
| Sławki | 1.37 | 0.72 | 0.86 | 0.98 |
| Borki | 1.46 | 0.77 | 0.82 | 1.02 |
| Przerwanki | 1.46 | 0.77 | 0.82 | 1.02 |
| Gołdap | 1.38 | 0.75 | 0.89 | 1.01 |
| Suwałki | 1.30 | 0.72 | 0.75 | 0.92 |
| Augustów | 1.29 | 0.72 | 0.91 | 0.97 |
| Białowieża | 1.33 | 0.69 | 0.75 | 0.92 |
| Zwierzyniec | 1.41 | 0.80 | 0.90 | 1.04 |
| Międzyrzec | 1.36 | 0.71 | 0.86 | 0.98 |
| Stronie Śląskie | 1.34 | 0.74 | 0.81 | 0.96 |
| Chochołowska Valley | 2.00 | 0.95 | 0.88 | 1.28 |
| Averages | 1.41 | 0.75 | 0.82 | 0.99 |

Nitrogen Percentage of Spruce Seedlings in Relation to Competition from Grass, Averaged Irrespective of Nitrogen Supply nances. The first two groups have the highest but significantly different nitrogen percentages, and the third group have the lowest nitrogen content, with the extreme values in this group having been recorded in the provenances Przerwanki and Brody. The averages for each provenance are compiled in Table 20.

The analysis of regression indicates a clear-cut correlation (r = -0.91) between the percentage of nitrogen in the seedlings and their dry weight. A high dry weight goes together with a lower percentage of nitrogen, which shows the provenances concerned to utilize better their nitrogen uptake for growth, in contrast to poorly growing seedlings with a high percentual content of nitrogen. There is also a significant negative correlation (r = -0.50) between the nitrogen concentration in seedlings and in seeds. For the provenances from the southern range (Brody, Kowary, Stronie Śląskie, Istebna, Rycerka, Chochołowska Valley, Bliżyn, and Wetlina) there is also a correlation (r = 0.85) between their nitrogen concentration and the altitude of their sites of origin.

The percentage of nitrogen in spruce seedlings (without competition from grass). Since the supply of nitrogen was the same in all pots throughout the duration of the experiment, there were no statistically significant differences in the by-weight content of nitrogen between the geographical races and the overall average was 3.60 mg per seedling (Table 21). However, the average nitrogen content of seedlings grew in proportion to the concentration of this element in the media from 0.96 mg through 2.48 and 4.31 mg to 6.66 mg.

The correlation of the nitrogen content of seedlings with their dry weight is distinct (r = 0.091) and the seedlings with a higher average dry weight have a higher absolute content of nitrogen, notwithstanding the lower percentual content previously referred to. Therefore, in the case of the provenances Chochołowska Valley and Brody, for which the extreme dry weight values were recorded, we find a more than twofold difference in the mean dry weight of seedlings, whereas the average nitrogen content per seedling differs by a factor of barely 1.4. There is a slight but statistically significant (r = 0.40) correlation between the absolute content of nitrogen in seedlings and in seeds.

The nitrogen content of the seedlings watered with the nitrogen-free medium exceeded that of the seeds by the values recorded in Table 21. This indicates some additional small sources of nitrogen in our experiments.

The relation of nitrogen uptake to the dry weight of roots (without competition from grass). The proportion of the nitrogen absorbed by the seedling (the difference between the nitrogen in the seedling and in the seed) to the dry weight of the roots, which provides us with a rough estimate of the efficiency of nitrogen absorption by the roots, depends chiefly on the available amount of the element in the medium. It increases more or less linearly with the concentration of nitrogen in the media. The average calculated for all the provenances jointly rises from 1.23 through 2.33 and 3.48 to 4.87 and is thus for medium 1 N about four times what it is for medium 0N. The geographical races differ significantly in the proportion of nitrogen uptake to the dry weight of the roots (Table 21).

Table 21

Nitrogen in Spruce Seedlings (in mg apiece) Averaged Irrespective of Medium, Nitrogen Absorbed by Seedlings (in mg apiece) Grown on Medium 0 N, and the Ratio of the Nitrogen Absorbed to the Dry Weight of Roots Averaged Irrespective of Medium, All for Seedlings Grown in the Absence of Competition from Grass

| Source locality | Nitrogen per seedling | Nitrogen absorbed when in medium 0 N | Ratio of nitrogen absorbed to dry wt. of roots | |
|---------------------|-----------------------------|---|--|--|
| | 2 | 3 | 4 | |
| Brody | 4.04 | 0.71 | 2.46 | |
| Kowary | 3.47 | 0.62 | 2.87 | |
| Istebna | 3.93 | 0.84 | 2.76 | |
| Rycerka | 3.97 | 0.73 | 2.62 | |
| Wetlina | 3.20 | 0.63 | 3.23 | |
| Bliżyn | 3.37 | 0.92 | 2.85 | |
| Konstancjewo | 3.39 | 0.67 | 2.81 | |
| Iława | 3.70 | 0.67 | 2.73 | |
| Myszyniec | 3.58 | 0.69 | 2.96 | |
| Sławki | 3.49 | 0.69 | 2.95 | |
| Borki | 3.57 | 0.62 | 2.92 | |
| Przerwanki | 4.04 | 1.09 | 3.23 | |
| Goldap | 3.31 | 0.60 | 2.70 | |
| Suwałki | 3.65 | 0.50 | 2.79 | |
| Augustów | 3.87 | 0.56 | 2.77 | |
| Białowieża | 3.88 | 0.54 | 2.79 | |
| Zwierzyniec | 3.19 | 0.83 | 2.70 | |
| Międzyrzec | 3.85 | 0.68 | 2.83 | |
| Stronie Śląskie | 3.67 | 0.70 | 2.78 | |
| Chochołowska Valley | 2.89 | 0.51 | 3.58 | |
| Averages | 3.60 | 0.69 | 2.87 | |

The analysis of regression demonstrated a statistically significant correlation (r = -0.88) between this characteristic and the dry weight of whole seedlings. As the latter grows the proportion referred to diminishes, even though the seedlings of the better growing provenances have a smaller percentage of their dry weight accounted for by the roots and have a higher nitrogen content. Therefore the factor decisive for this proportion is the percentual content of nitrogen in seedlings, which is lower in the geographical races with a smaller dry weight. Consequently, a higher dry weight and therefore also greater height of the seedlings of a particular geographical race is not connected with a greater ability of the roots to absorb nitrogen

from the soil or greater capacity for developing a good root system but is the result of a genetically determined ability to use efficiently the nitrogen absorbed for the production of their dry weight.

The nitrogen content and percentage in seedlings growing in competition with grass. The analysis of variance showed this characteristic to be significantly affected by the concentration of nitrogen in the media and by the provenance, very much as in the case of seedlings growing without the competition of grass. Furthermore, the degree of competition also proved to be a statistically significant factor.

Grass in the pots cuts the percentage of nitrogen in spruce seedlings by an average 45 percent, i.e. from 1.41 percent to 0.78 percent. The two degrees of competition (5 and 20 grass plants per pot) make for a statistically significant difference in nitrogen content. The increase in competition from 5 grass plants to 20 raises the nitrogen content in spruce seedlings from 0.74 percent to 0.82 percent on average. An exception from this rule is the provenance Chochołowska Valley (Table 20).

The nitrogen content of seedlings growing with grass shows an increase only with the full nutrient 1N, whereas with the other media it remains more or less constant. This concerns both the lesser and the greater competition (5 and 20 grass plants respectively).

With most of the geographical races concerned the nitrogen content in seedlings diminishes as the nitrogen supply is increased from 0N to $\frac{1}{4}$ N, or from $\frac{1}{4}$ N to $\frac{1}{2}$ N, which does not show in the averages calculated for all the provenances jointly. This decrease is undoubtedly due to an intensified growth of the grass and, consequently, stronger competition. In the presence of grass the individual provenances

Table 22

| Competition (No. of grass plants) | Nitrogen content in the medium | | | | |
|---|--------------------------------|-------|-------|------|----------|
| | 0 N | 1/4 N | 1/2 N | 1 N | Averages |
| 0 | 0.96 | 2.48 | 4.31 | 6.66 | 3.60 |
| 5 | 0.27 | 0.25 | 0.28 | 0.45 | 0.31 |
| 20 | 0.22 | 0.22 | 0.24 | 0.27 | 0.24 |
| Averages | 0.48 | 0.98 | 1.61 | 2.46 | 1.38 |

Nitrogen in Spruce Seedlings (in mg apiece) in Relation to Nitrogen Supply and Competition from Grass, Averaged for all 20 Provenances Jointly

differed in the amount of the nitrogen absorbed, but not in the way they did without competition. Some geographical races (Myszyniec, Bliżyn, Wetlina, Gołdap, Zwierzyniec, Chochołowska Valley) absorbed in comparison with others more nitrogen than would be suggested by their behavior in the absence of competition, whereas other provenances (Brody, Białowieża, Suwałki, Sławki) absorbed less. On average, competition reduced the overal nitrogen content of seedlings by as much as 93 percent, i.e., from 3.63 mg to 0.26 mg; with the two different degrees of competition the per-seedling nitrogen content averaged 0.31 mg and 0.24 mg with 5 and 20 grass plants respectively, as is recorded in Table 22.

Nitrogen uptake in relation to the dry weight of roots in the presence of competition. Competition reduces the value of this proportion to less than one-tenth, viz. to an average of 0.21, whereas in the absence of competition it was for the same geographical races 2.85. The proportion of the nitrogen uptake to the dry weight of roots differs by a statistically significant margin between the two degrees of competition (5 and 20 grass plants) and averages 0.31 and 0.12 respectively. In the presence of the higher competition, therefore, the roots of spruce seedlings have

Table 23

| Competition (No. of grass plants) | Nitrogen content in the medium | | | | |
|---|--------------------------------|-------|-------|------|----------|
| | 0 N | 1/4 N | 1/2 N | 1 N | Averages |
| 0 | 1.18 | 2.26 | 3.09 | 4.86 | 2.85 |
| 5 | 0.05 | 0.07 | 0.21 | 0.92 | 0.31 |
| 20 | 0.05 | 0.00 | 0.11 | 0.32 | 0.12 |
| verages | 0.43 | 0.78 | 1.14 | 2.03 | 1.09 |

The Effect of Nitrogen Supply and Competition from Grass on Nitrogen Absorption by Seedlings in Relation to the Dry Weight of Roots, Averaged for Six Provenances Jointly

an insignificant capacity for absorbing nitrogen, which is close to zero with the lower concentrations of the element in the media (0.05 and 0.00 respectively — Table 23). In the presence of competition there were no differences between the provenances in this respect.

Discussion

In a measure, the differences between the individual geographical races agree with the results of previous international research of this kind. In the first place we should mention the experiments organized by the International Union of Forest Research Organizations (IUFRO) in 1938, which covered also seeds from Istebna (Beskid Śląski range), Białowieża, and Brody on the Nysa Łużycka River. All these seeds produced trees which grew very well on many experimental plots differing in the conditions of climate and habitat, namely in the United States and Canada (Holst, 1963), France (Bouvarel and Lemoine, 1957), Sweden (Langlet, 1960), Belgium (Gathy, 1960), and Czechoslovakia (Vinš, 1963). Out of these three provenances that of Istebna gave the best results; it was designated as No. 10 in the IUFRO experiments. The provenance Brody (known under the German name Pförten and marked No. 8) gave better than average results and proved on some experimental plots to be even superior to all the others. The provenance Białowieża (No. 34), which was the least frequently used in these experiments, also gave on the whole good results. The results here discussed are based only on the preliminary phase of experiments concerning 20-year old material. The Second World War prevented Poland from participating in these experiments, since the material prepared in nurseries was distributed among uncontrolled aforestations in 1940. Nevertheless, the data recorded in the course of these experiments abroad confirm the results of our research on seedlings. Seeds from the same source localities — i.e. Istebna, Brody, and Białowieża — produced the most vigorously growing seedlings with the highest dry weight of all the 20 provenances investigated, whereas the third — Białowieża — was second in this respect only to Rycerka (Beskid Żywiecki range) and Augustów (Table 12).

Next, the qualities of our provenances Borki, Stronie Śląskie, and Kowary can be compared with the results obtained in the German experiments, which covered among other provenances the spruce populations from Borki in Borecka Forest*, Stronie Śląskie in the Kłodzka Basin**, and Piechowice in the Sudeten***, which lies close to Kowary but at a greater altitude. Spruce from Borki grew well in Bavaria, Saxony, and Wurttemberg, but poorly in Thuringia (Troeger, 1958; Schönbach, 1957). Those from Stronie Śląskie were among the best-growing in Thuringia, Wurttemberg, and Saxony (Troeger, 1958; Schönbach, 1957), but among the poorer ones in Bavaria (Rubner, 1957), whereas those from Piechowice grew poorly in all four regions, i.e. Bavaria, Saxony, Thuringia, and Wurttemberg (Troeger, 1958). The three provenances referred to (Borki, Stronie Śląskie, and Kowary) were in our greenhouse experiments rather low in growth and dry weight (Tables 6 and 19) and the good results recorded for them in the German experiments should be attributed to the fact that they were compared with rather poor German populations, which in the IUFRO experiments also scored less than average.

The results recorded in our experiments under uniform greenhouse conditions therefore confirm the data obtained under different conditions of terrain both in the European range of spruce and in North America. This concerns especially the provenances distinguished clearly by good growth under different conditions of climate and habitat, which means good adaptation to widely different conditions. Our experiments thus amount to an overdue "early test" of the provenances already used in past field experiments and can serve for a preliminary evaluation of the usefulness of individual geographical races. Hence it can be surmised that not only the provenances Brody, Istebna, and Białowieża are distinguished by very good qualities but that many other ones from Poland, which behave similarly

*Borken; **Seitenberg; and ***Petersdorf in the German experiments referred to.

under greenhouse conditions, may be highly productive and adaptable in various regions. This applies especially to spruce from the Beskid Żywiecki range (Rycerka) and some other provenances from the northeast, e.g. Augustów and Przerwanki.

The seeds used in the present experiments came from the northeastern and southern range of spruce in Poland as well as from some isolated stands beyond it (Fig. 1), but it is hard to find any kind of correlation between the geographical location of the site of origin and the individual characteristics of a provenance. Those superior in respect of growth properties come from the north as well as the south of the country. All which has been found is only that the seeds from the south are slightly heavier by 16 percent than from the north, which was brought to notice also by Tyszkiewicz (1952); this however, is rather a phenotypic character.

The southern provenances that come from different altitudes (Brody, Kowary, Stronie Ślaskie, Istebna, Rycerka, Chochołowska Valley, Bliżyn, and Wetlina) (Table 1) need to be discussed separately. Thus, the greater the altitude of the site of origin the greater is the percentage of nitrogen in the seedlings grown under uniform greenhouse conditions (Table 20) and the smaller is their height (Table 6) and dry weight (Table 12). A higher nitrogen concentration in seedlings of the alpestrine provenances (1500-2000 m) than of those from less elevated sites (700-1200 m) growing under the same greenhouse conditions is reported also by Kral (1961), who studied spruce from the Alpine range. This correlation does not apply to the lowland spruce from the northeastern range, which show marked differentiation in respect of the qualities considered, whereas there are no major differences in altitude between their sites of origin. The geographical latitude of the site of origin is not correlated either with the concentration of nitrogen in seedlings or other characters. Hence the reports by many authors of a higher nitrogon concentration in seedlings of the northern provenances of Pinus silvestris (Langlet, 1936/37; Gerhold, 1959; Steinbeck, 1965) and Pinus banksiana (Giertych and Farrar, 1962; Morgan and Worral, 1965) grown under uniform conditions in greenhouses were not confirmed for Picea abies seedlings in the present experiments. Therefore the geographical location of individual provenances appears to have no significant effect on the body of morphological and physiological qualities of spruce grown under uniform conditions. An exception is here the already discussed correlations with the altitude of the site of origin of the provenances from the Carpathian and the Sudeten mountain ranges. Not inconceivable, the absence of a correlation with the geography may be due to the possibility that not all the seeds were collected from native tree stands.

The correlations of the growth of seedlings, which suggest certain conclusions, need to be discussed separately. In the provenances whose seedlings show a relatively better growth and therefore greater dry weight the leaves account for a higher proportion of the dry weight of whole seedlings (Table 12). This means that the more productive seedlings utilize relatively more metabolites for the develop-

ment of organs of assimilation. The genetically determined greater vigor of a provenance is associated with a richer development of leaves, i.e. assimilation organs. At the same time the greater absolute development of the root system (Table 12). which shows in the greater dry weight of whole seedlings, makes for a greater absolute uptake of nitrogen, whereas the more effective utilization of this element contributes to higher dry weight increments in the provenances superior in this respect. Consequently, although they have a great capacity for absorbing nitrogen, apparent from the positive correlation between the dry weight of roots and the nitrogen content of seedlings (Tables 12 and 21), the better growing seedlings are distinguished by a less efficient absorption of nitrogen by their roots — a smaller ratio of nitrogen uptake to the dry weight of roots (Table 21) - because this quality is negatively correlated with the dry weight of seedlings. This is probably due to the smaller requirements of the seedlings of these provenances for mineral salts, specifically nitrogen. This is confirmed by the smaller percentual content of nitrogen in the whole plant (Table 20) as well as the lower roots-to-leaves ratio (Table 12). This ratio decreased also as the nitrogen concentration in the media grew (Table 15), which shows a relatively large root system to be connected with the deficiency of nitrogen in the substratum and conversely, a relatively small root system to be the consequence of an adequate nitrogen supply, and confirms low nitrogen requirements in the provenances which gave the well-growing seedlings. Poorly growing seedlings belong to provenances distinguished by a higher roots-toleaves ratio and therefore have a relatively large root system, which absorbs nitrogen more effectively. Consequently the seedlings of these provenances have a higher percentual nitrogen content but grow less vigorously. This concerns especially two alpestrine provenances, Chochołowska Valley and Wetlina, which probably owing to poor soils need a large root system for effective nitrogen uptake. Their growth, however, is limited because under montane conditions it is less important for survival than is the quality of the root system.

The correlation of the dry weight of whole seedlings (Table 12) with the percentual content of nitrogen in seeds (Table 3) shows more vigorously growing seedlings to come from seeds with a higher nitrogen concentration irrespective of their absolute nitrogen content. This means that spruce distinguished by greater vigor provide their seeds better with nitrogen even though the concentration of this element in their vegetative organs (seedlings) is lower. Hence it is an additional character of vigorously growing provenances that their seeds have a high concentration of nitrogen, which is independent of their weight, since the latter is not correlated with the dry weight of the seedlings they produce.

One of the variables of the experiments was the media, specifically their nitrogen concentration. The sand, which was to take the place merely of the mechanical fraction of soil in the experiments, undoubtedly contained a certain amount of nitrogen compounds which provided the seedlings watered with the nitrogen-free medium (0N) with a source of this element. A certain quantity of it may have been contributed to the pots from the atmosphere by bacteria living on the surface of the sand. The principal source of nitrogen for the 0N group of seedlings was the protein of the seeds. The pots averaged each about 5.40 mg of nitrogen (20 seeds with 0.27 mg of nitrogen apiece), whereas at the end of the experiment the seedlings of one 0N pot averaged 4.80 mg of this element. A certain amount of it had obviously been removed from a pot together with spruce seedlings when their number was being reduced to five per pot, but there remained the seeds that had failed to sprout and the roots of the eliminated seedlings. The life and growth of seedlings watered with nitrogen-free medium was ensured over the first months primarily by the nitrogen of the seeds. But this was not enough for normal development in the subsequent months, as was indicated by the pale green of the leaves or absence of increments in these seedlings and their failure to develop apical buds, i.e. manifestations of nitrogen deficiency.

The media $\frac{1}{4}$ N, $\frac{1}{2}$ N, and 1N supplied nitrogen as ammonium nitrate; i.e. as nitrate and ammonium. It was relatively little utilized by the seedlings, at the level of an average 32 percent for all three media; since the utilization is more or less the same for each medium, a large proportion of the nitrogen was washed out from the pots during watering with distilled water. The nitrogen concentration was not excessive in the media, since the seedlings grew better on medium 1N than on the poorer ones.

The dry weight of whole seedlings grew in proportion to the nitrogen concentration in the media up to the level $\frac{1}{2}$ N (Fig. 8). The increase in the dry weight of seedlings that received the full medium (1N) was already a little less, whereas the concentration of nitrogen in the seedlings continued to increase in proportion to that in the medium. With the lower concentrations of nitrogen in the media precisely its scarcity is what restricts growth and its relatively low concentration in the seedlings is under these conditions the consequence of its maximal utilization for vegetative development. The differences in the uptake of nitrogen and its subsequent utilization, which are decisive for the quality of the seedlings of the particular provenances, proved in the present experiments to be statistically significant and relatively large. With nitrogen supplied in full measure the dry weight of some provenances exceeded that of plants grown on a nitrogen-free medium by an average of roughly 500 percent (Augustów and Białowieża), whereas in others it rose barely by 180 percent (Bliżyn and Zwierzyniec).

Since the experiments were run in multiplicates and under largely uniform greenhouse conditions, the inter-racial differences recorded must be considered as due to the heritable characters of the particular spruce populations. These characters concern growth as well as the correlated qualities involving nitrogen management. In practical respects, sylviculture is interested in selecting the most productive spruce populations, which at the same time make the best use of the mineral salts absorbed from the soil. The differences in growth and nitrogen economy that distinguished the seedlings of different provenances in our experiments need not necessarily apply to mature trees, although a correlation of the qualities of seedlings with those of mature trees is very likely. At any rate the characters recorded concern seedlings, and after all growth and the utilization of the available mineral salts are what determines already in the forest nursery or young plantation the survival and general quality of this plantation. The larger and stronger seedlings will succeed more easily in the struggle for space and living conditions in the forest.

In order to follow the development of seedlings under the conditions of competition, an additional variable was introduced in the experiments in the form of competition from grass. The presence of grass was found to inhibit the growth of spruce seedlings (Table 7) and largely obliterate the differences between particular provenances (Table 6). Since grass grows very rapidly to the point of maximum utilization of the space available in a pot, the differences between the lower and the higher degree of competition (5 and 20 grass plants resp.) are small and usually not statistically significant (Table 7). The effect of the competition on the dry weight of whole seedlings and of their particular parts increases with the concentration of nitrogen in the medium (Tables 16 and 18). The absorbing surface of roots being in grass larger and, consequently, the uptake of mineral nutrients more rapid and greater, the development of grass is more profuse when the supply of nutritive compounds is more abundant. The better developed grass restricts and inhibits the development of spruce seedlings more. Consequently, in the presence of competition the dry weight of seedlings is inversely related to the concentration of nitrogen in the medium, whereas, very much like in seedlings growing in the absence of grass, their concentration of nitrogen increases (Table 22) and the share of roots in the whole dry weight dminishes (Table 18) as nitrogen is supplied more abundantly. The trend of the changes in the development of spruce seedlings is the same in the presence of competition from 5 and 20 grass plants. A higher concentration in the medium therefore intensifies competition because it helps to increase the amount of grass in the pots. With the nitrogen-free medium grass felt the nitrogen deficiency more sharply and offered no strong competion to the spruce seedlings, for the latter differed little from those growing in the absence of grass (Table 16). There was no nitrogen for which to compete and other factors were present in excess and were not utilized for growth, which was made possible by the available traces of nitrogen. The competition was most intensive when the full medium was used, because under these circumstances the weight of the spruce seedlings was lowest (Table 16). However, since the seedlings showed a higher nitrogen concentration than they did when the nitrogen-free medium was used, in which case they nevertheless had a higher dry weight, the intensified competition due to the increased nitrogen concentration in the medium is unlikely to have concerned exclusively competition for nitrogen. The nitrogen concentration was lower than that in seedlings grown in the absence of grass but was not critical, since at the lower concentrations of nitrogen in the medium its content in the seedlings

was still lower and the seedlings bigger. Therefore it must be presumed that the intensified competition brought about by the increased supply of nitrogen caused some factor other than nitrogen to become critical for the growth of spruce seedlings. An antagonistic effect of grass roots on the roots of spruce is rather unlikely, because watering of spruce seedlings with the concentrated washings of grass roots had no effect whatever. What may have been involved is competition for some other mineral component, air, oxygen in the substratum, or simply space. When the concentration of N, P. S, or Fe is critically low for growth, the ratio of the aerial parts of a plant to the roots diminishes (Ingestad, 1959), whereas in our experiments it grew (Table 17). When K is deficient, spruce seedlings do not lack apical buds (Ingestad, 1959). In our experiments competition raised the number of seedlings with an apical bud (Table 11), but an increase in the nitrogen supply in the presence of competition reduced the number of buds per plant (Table 10) as well as the number of seedlings with an apical bud (Table 11), hence the increased competition due to a greater abundance of nitrogen did not involve potassium. Water was supplied according to need so as to keep the soil always moist, and therefore it could not have been the factor restricting the growth of spruce seedlings. A deficiency of air also is rather out of question, although it is not impossible that within the grass cluster in which the spruce seedlings were growing (Fig. 4) the carbon dioxide needed for photosynthesis could become locally exhausted. Oxygen deficiency in the substratum also was a possibility, because distilled water was used. However, the most likely explanation of the stunted growth of spruce seedlings associated with a better supply of nitrogen is competition with grass for space for the roots in the pots. The pots were so thoroughly filled with grass roots that it was hard to imagine where the roots of the spruce seedlings were to find room.

The results here discussed give ground for the suspicion that nitrogen fertilizers for spruce seedlings grown in soil favorable for weeds may be harmful, because they will promote the growth of weeds. *Poa annua* does not grow in spruce habitats, but other grasses, which do grow in spruce plantations and sod the soil may very likely have a similar effect on spruce as has the grass used in our experiments.

The authors' sincere gratitude for the execution of the technical part of the project is due to laboratory assistants Alicja Szubertówna and Zofia Ziętówna.

The research was in part supported under Agreement FG-Po-174 with the US Department of Agriculture, US Public Law 480.

LITERATURE CITED

[2] Dietrichson, J., Breeding for Frost Resistance - Silv. Genet. Vol. 10, 1961, p. 172-179.

267

http://rcin.org.pl

Bouvarel, P., Lemoine M., L'expérience internationale sur les provenances d'epicéa (*Picea excelsa* Link.) — Silv. Genet. Vol. 6, 1957, p. 91–97.

- [3] Dietrichson, J., Proveniensproblemet belyst ved studier av vekstrytme og klima Medd. Norske Skogforsøkov Vol. 19(5), No. 71, 1964, p. 499-656.
- [4] Fowler, D. P., Natural Self-Fertilization in Three Jack Pines and Its Implications in Seed Orchard Management — For. Sci. Vol. 11(1), 1965, p. 55-58.
- [5] Fröhlich, H. J., Sonderherkünfte und Forstpflanzenzüchtung dargestellt am Beispiel der Fichte — Mitt. Hess. Landes forstverwaltung Vol. 4, 1966, p. 36-56.
- [6] Fröhlich, H. J., Untersuchungen über Benadelungsverhältnisse verschiedener Fichten Provenienzen – Abstr. in Silv. Genet. Vol. 9(5), 1960, p. 138.
- [7] Gathy, P., Recherches Belges sur la variabilité génetique des espéces forestières Silv. Genet. Vol. 6, 1957, p. 32-38.
- [8] Gathy, P., L'origine des graines d'epicéa commun (Picea abies Karst.) Bull. Soc. Roy. For. de Belgique. Nov. 1960a, p. 1–16.
- [9] Gathy, P., L'expérience internationale sur l'origine des graines d'epicéa (*Picea abies* Karst), Resultats en Belgique. Stat. de Rech. Eaux et Forêst, Groenedaal-Hoeilaart, Belg. Trav., Ser. B, No. 24, 1960b.
- [10] Gerhold, H. D., Seasonal Variation of Chloroplast Pigments and Nutrient Elements in the Needles of Geographic Races of Scotch Pine - Silv. Genet. Vol. 8, 1959, p. 113-123.
- [11] Giertych, M., Farrar, J. L., A Provenance Study of Jack Pine Seedlings Silv. Genet. Vol. 11(4), 1962, p. 111–114.
- [12] Holst, M., Growth of Norway Spruce (*Picea abies* (L.) Karst). Provenances in Eastern North America. (FAO) FORGEN 63/1; 3/3, 1963.
- [13] HORTICULTURAL COLOUR CHART, The British Colour Council, The Royal Horticultural Society, 1938.
- [14] Ingestad, T., Studies on the Nutrition of Forest Tree Seedlings. II. Mineral Nutrition of Spruce — Physiol. Plant. Vol. 12, 1959, p. 568-593.
- [15] Kral, F., Untersuchungen über den Nährstoffhaushalt von auf gleichem Standort erwachsenen Fichtenjungpflanzen in Abhängigkeit von ihrer Wuchsenergie und Herkunft-Cbl. ges. Forstw. Vol. 78(1), 1961, p. 18-38.
- [16] Langlet, O., Studier över tallens fysiologiska variabilitet och dess samband med klimated. Ett bidrag till kännedomen om tallens ekotyper. Medd. Stat. Skogsförsöksanstaet. Vol. 29, 1936/37, p. 219–470.
- [17] Langlet, O., Polsk gram för Sverige Skogen No. 5, 1959.
- [18] Langlet, O., Mellaneuropeiska granprovenienser i avenskt skogsbruk. K. Skogs o. Lantb. Akad. Tidskr. Stockh. Vol. 99(5/6), 1960, p. 259–329.
- [19] Langlet, O., Practical Results of Current Problems in Provenance Research in Sweden. (FAO) FORGEN 63/1; 3/1, 1963.
- [20] Langner, W., Eine Mendelspaltung bei Aurea-Formen von Picea abies (L.) Karst. als Mittel zur Klärung der Befruchtungsverhältnisse im Walde – Z. Forstgenetik Vol. 2, 1953, p. 49–51.
- [21] Mergen, F., Worrall, J., Effect of Environment and Seed Source on Mineral Content of Jack Pine Seedlings – For. Sci. Vol. 11(4); 1965, p. 393–400.
- [22] Nanson, A., Données complémentaires au sujet de l'expérience internationale sur l'origine des graines d'epicéa en Belgique — Sta. Rech. Eaux. et Forêts, Groenendaal-Hoeilaart, Belgique Travaux, Ser. B. No. 28, 1964.
- [23] Piper, C. S., "Analiza gleby i roślin" (Analysis of Soil and Plants), PWN, Warszawa 1957.
- [24] Rubner, K., Ergebnisse eines heute 20-jährigen Fichtenherkunftsversuches Silv. Genet. Vol. 6, 1957, p. 65-74.

- [25] Sarvas, R., Investigations on the Flowering and Seed Crop of Pinus silvestris Commun. Inst. For. Fenn. Vol. 53(4), 1962, p. 1–198.
- [26] Schönbach, H., Ergebnisse eines heute 20-jährigen Fichtenprovenienzversuches. Silv. Genet. Vol. 6, 1957, p. 74-91.
- [27] Slabaugh, P. E., Rudolf, P. O., The Influence of Seed Source on the Development of Scotch Pine and Norway Spruce Planted in Lower Michigan (Fifteen-Year Results). Pap. Mich. Acad. Sci. 42; p. 41-52, F. A. 19, 1958, No. 4060, 1956.
- [28] Steinbeck, K., Variations in the Foliar Mineral Content of Five Widely Separated Seedlots of Scotch Pine — Quart. Bull. Mich. Agric. Exp. Sta. Vol. 48(1), 1965, p. 94-100.
- [29] Troeger, F. R., Die Fichten-Provenienz-Versuche in Württemberg Allg. Forstzeitsch. Vol. 13(9), 1958, p. 109–114.
- [30] Tyszkiewicz, S., "Nasiennictwo leśne z zarysem selekcji drzew". (Sylviculture Seed Production with an Outline of Tree Selection), PWRiL, Warszawa 1952.
- [31] Vincent, G., Vincent, J., Ergebnisse des Internationalen Fichtenprovenienzversuches Silv. Genet. Vol. 13, 1964, p. 141–146.
- [32] Vinš, B., Report on the State and Preliminary Evaluation of Czechoslovak Provenence Trial Plots of Norway Spruce in the International Series from the Year 1938. (FAO) FORGEN 63/1, 3/6, 1963.

Translated by W. Kulerski

SUMMARY

The response of spruce *Picea abies* (L.) Karst. seedlings from 20 different localities in Poland to various levels of nitrogen supply and different degrees of competition from grass (*Poa annua* L.) has been studied under greenhouse conditions. Considerable racial variation with respect to many characters has been demonstrated. Spruce populations which have been included in the international provenance experiments and are known for their good performance in the experiments have demonstrated their superiority in dry matter attained also in our studies. Some new populations, so far not tested in provenance experiments also appear to be no worse than the famous ones from the foreign experiments, and probably most of the spruce populations in Poland could be considered as good. An exception is provided by slow growing populations from the Tatras and the Bieszczady Mts.

Among the provenances from southern Poland the concentration of nitrogen in the seedlings is positively correlated with the elevation of the site of origin, while seedlings height and dry weight are correlated inversely with altitude. Weight of seeds and their nitrogen content in mg are inversely correlated with the latitude of the site of origin.

When comparing provenances the better growing seedlings were characterized by a lower level of nitrogen, but they can be considered as more economic utilizers of the nitrogen they have absorbed, and also they had a greater weight ratio of the aerial plant part to roots (relatively greater photosynthetic apparatus). On the other hand, the amount of nitrogen absorbed by a unit dry weight of the roots was greater for the populations with weaker seedlings. Spruces which had large and efficient root systems as well as poor growth came from the high mountain regions with extremal site conditions, while the spruces with a large photosynthetic apparatus, a high total dry weight and an efficient mechanism for nitrogen utilization came from regions where vegetation conditions are very good. The concentration of nitrogen in the seeds is positively correlated with the weight of seedlings. Thus spruces with a low nitrogen concentration in the vegetative tissues have relatively abundantly supplied their seeds with nitrogen.

With respect to many characters there exist provenance differences. However it was not possible to correlate any of these characters with data available about the sites of origin.

The number of grass plants in a pot (5 or 20) is of little significance since in any case the grass clump develops exploiting the full capacity of the pot. For this reason spruce growing in the two levels of competion did not differ significantly. Also with respect to most spruce characters the effect of grass competition was to obliterate any differences between provenances.

Increase of nitrogen in the medium leads to intensification of competition through an increase in the growth of grass, which has a negative effect on spruce, whose weight, particularly that of roots, is lowered.

http://rcin.org.pl