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# Genetic reactivity of Norway spruce *Picea abies* (L.) Karst. to soil fertility

**Abstract:** Seedlings of various provenances and progenies were greenhouse grown in sand cultures with different levels of nitrogen, phosphorus, potassium, calcium and magnesium. The first experiment tested 20 provenances and the next studied 45–50 half-sib families of 9–10 provenances to establish the interaction between *Picea abies* genotypes and nutrition levels. Spruces of various origins differed in their nutrient requirements. In particular, seedlings from Wisła and Istebna grew better at smaller phosphorus levels. The genotype × environment interactions were significant for numerous traits when seedlings were grown at different levels of nitrogen, phosphorus and calcium, and for a few traits for potassium. The proportion of variance explained by interaction was small. Generally, the interactions were significant for a greater number of traits at progeny level than at provenance level. The results suggest that it is possible to select genotypes which are suitable for specific site conditions and genotypes which are stable over a wide range of nutrition levels.

**Additional key words:** edaphotypes, provenance, half-sib families, genotype × nutrition level

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## Introduction

Beside climatic conditions and water supply, also mineral nutrition is very important to plant growth and productivity. The developmental potential of plants is determined by all these environmental variables and additionally by genetic factors. If the varied genetic background of trees within a given species is affected by environmental conditions, we can distinguish so-called soil races (edaphotypes, edaphic ecotypes). Generally, ecotypes are distinguished on the basis of their response to the environment but it is not always easy to identify them on the basis of morphological features.

The observed phenotypic variation is associated with the conditions of a given habitat, as inherited features cannot be separated from environmental effects. Thus, the issue of soil races is not purely genetic. Only the testing of various edaphotypes in uniform conditions may reveal the genetic character of the variation. Hence, numerous comparative experiments test plant material of the same species but from various local populations. Such experiments, established in various environmental conditions, make it possible to determine the contribution of the interaction of genotype with the environment. In the field, we can estimate the interaction of provenance with location. There are many reports on the statistical significance of such interactions for various features (Wright 1973; Gullberg and Vegerfors 1987; Li and McKeand 1989; Woolaston et al. 1991). A number of studies concern various species, but only few deal with Norway spruce (Ekberg et al. 1982; Kleinschmit 1985; Bentzer et al. 1988; Krupski et al. 1996; Karlsson et al. 2001; Sonesson et al. 2002).

In the field, individual environmental factors cannot be separated from one another, e.g. climatic factors from edaphic ones. Among the various edaphic factors, nutrient levels are particularly noteworthy. However, experiments involving them can be conducted under controlled conditions in a greenhouse where it is possible to treat plants with varied rates of the elements studied. Our research focused on one of the experimental factors, namely the interrelations between genotypes and nutrition levels.

## Material and methods

The provenance and progeny variation of Norway spruce (*Picea abies* (L.) Karst.) seedlings raised under conditions differing in the level of mineral nutrition was tested in a series of experiments. The seeds used in these studies had been collected in presumably indigenous stands from northeastern Poland, central Poland and the mountain region of southern Poland. Young spruces were grown in sand cultures in orthogonally designed greenhouse experiments. The first experiment (Fober and Giertych 1970) tested 20 provenances (Table 1), and the next series investigated 45–50 half-sib families of 9–10 provenances (Table 2). During the first growing season, the seedlings were treated with different levels of nitrogen, phosphorus, potassium, calcium or magnesium in mineral solutions. Every day, the seedlings were supplied with destilled water, and twice weekly, with a mineral solution having optimal concentrations of all elements except that under study which was applied at four levels, i.e. 0, 1/4, 1/2 and 1, or 0, 25, 50 and 100%, of the maximum value, respectively. The maximum level represented the concentration of nutrients in the pots which is required by the trees for optimum growth as established by Ingestad (1959).

The experiment was terminated at the end of the first growing season. At that time, growth measurements including seedling height, root length, fresh and dry weight were carried out and developmental observations regarding the number and length of laterals, number of buds and dry-to-fresh weight ratio were made. The results were subjected to variance analysis. In the provenance-progeny series of experiments, hierarchical variance analysis was performed and the contribution of interaction to the total variation (V%) was calculated.

The present paper concerns only one source of variance, i.e. the interaction between provenances or progenies within provenances and the levels of the individual nutrients supplied. Information on the genotype × mineral nutrition performance, as suggested by Giertych (1984), was based on the regression coefficient (b) of Finlay and Wilkinson (1963) and the variance of the deviation from the regression ($V_d$) of Eberhart and Russell (1966). The regression coefficient “b” is an inverse measure of “phenotypic stability”. When $b < 1$, the genotypes are stable, and when $b > 1$, they are interactive. Regression analysis (r) was made of the $\log_{10}$ of seedling height for prove-

Table 1. Origin of seeds used in the provenance experiment, the dry weight of seedlings (means over all levels of phosphorus in the media) and its response to the phosphorus level in the medium: maximum dry weight of seedlings at a low (A), medium (B) and maximum (C) level of phosphorus (see Fig. 1)

| Locality | Latitude and longitude | Dry weight of seedling (mg) | Type of response |
|---|---|---|---|
| Rycerka (comp. 51 l) | 49°32' 19°00' | 150.5 | C |
| Wisła (comp. 82 d) | 49°37' 18°56' | 129.5 | B |
| Istebna (comp. 17 g) | 49°33' 18°52' | 126.9 | B |
| Gorce | 49°31' 20°07' | 122.4 | C |
| Brody | 51°42' 14°53' | 121.9 | C |
| Augustów | 53°54' 23°11' | 118.1 | B |
| Nowe Ramuki | 53°39' 20°34' | 112.5 | A |
| Wetlina | 49°08' 22°30' | 111.3 | A |
| Iława | 53°39' 19°34' | 110.8 | B |
| Konstancjewo | 53°11' 19°08' | 110.0 | B |
| Bliżyn | 51°05' 20°42' | 106.7 | C |
| Kowary | 50°48' 15°52' | 106.0 | B |
| Międzyrzec | 52°03' 22°57' | 105.5 | C |
| Zwierzyniec | 52°43' 23°47' | 103.1 | C |
| Myszyniec | 53°22' 21°09' | 100.7 | C |
| Stronie Śląskie | 50°18' 16°55' | 98.7 | C |
| Gołdap | 54°20' 22°24' | 95.9 | A |
| Suwałki | 53°59' 23°07' | 91.6 | A |
| Białowieża | 52°40' 23°47' | 90.1 | C |
| Dolina Chochołowska | 49°13' 19°48' | 77.8 | A |
| Average | | 109.5 | |

Table 2. Origin of seeds used in the provenance-family trials

| Provenance | Latitude and longitude | Experimental series |
|---|---|---|
| Supraśl | 53°15' 23°20' | N, P, K, Ca |
| Szczebra | 53°55' 22°55' | N, P, K, Ca |
| Zwierzyniec | 52°40' 23°45' | N, P, K, Ca |
| Radom | 51°27' 20°55' | N, P |
| Łagów | 50°46' 21°00' | N, P |
| Miechów | 50°22' 19°44' | N, P, K, Ca, Mg |
| Wieluń | 51°20' 18°23' | N, P, K, Ca, Mg |
| Ujsoły | 49°26' 18°59' | N, P, K, Ca, Mg |
| Węgierska Górka | 49°34' 19°10' | N, P, K, Ca, Mg |
| Wisła (comp. 1 a) | 49°31' 18°54' | N, P, K, Ca, Mg |
| Gołdap | 54°18' 22°25' | Mg |
| Borki | 54°10' 22°10' | Mg |
| Maskulińskie | 53°40' 21°30' | Mg |
| Skarżysko Kamienna | 51°05' 20°49' | Mg |
| Skarżysko Kamienna | 51°03' 20°43' | Ca |

nance or progeny on the $\log_{10}$ of mean height for trial. High "r" values indicate that the logarythmic transformations assured excellent linearity.

## Results

In a series of five provenance-family experiments, spruce seedlings were treated with nutrition solutions containing varied levels of nitrogen, phosphorus, potassium, calcium and magnesium (four levels of each were used). Due to the lack of seeds, in successive experiments some provenances or families were replaced with others. Table 2 shows the list of provenances used in each experimental series.

The design of these experiments required the use of hierarchical variance analysis which made it possible to evaluate progeny variation within the Polish provenances of Norway spruce and to compare it with provenance variation. For all the traits studied also the interaction between genotype and mineral nutrition was assessed.

Hierarchical variance analysis showed that provenances and progenies within provenances differ significantly in numerous traits. The provenance variation was less obvious for growth traits only. There were significant interactions between genotype and mineral nutrition (Table 3, 4 and 5). They involved various traits, depending on the kind of nutrient, and were most frequent in the case of nitrogen, phosphorus and calcium (Table 3 and 4). The provenance × potassium supply interaction was significant for two characters of seedling dry weight only (Table 4). There were no significant interactions with varied magnesium nutrition (Table 5).

The contribution of interaction to the total variation was small. The maximum value was 6.4% at provenance level for the length of laterals in the nitrogen experiment, and 12.4% at progeny level for the percentage of seedlings with apical buds in the phosphorus experiment (Table 3). In general, the interactions at progeny level were significant for a greater number of traits than at provenance level, and the proportion of variance explained by interaction was greater for developmental than for growth traits.

Table 6 presents an assessment of the provenance × nitrogen supply interaction for seedling height. The Beskid provenances, i.e. Ujsoły, Węgierska Górka and Wisła, and two other from northeastern Poland, Zwierzyniec and Szczebra, have low values of the regression coefficient "b" and therefore high stability, and exhibit good adaptability on many sites differing in nitrogen availability. All other provenances from this list, such as Wieluń, Miechów, Łagów, Radom and Supraśl, with a high "b" value, are sensitive to environmental change and able to profit from higher levels of nitrogen. Table 7 shows stable progenies, fairly independent of varying nutritional conditions (progenies No 740, 2123, 2133 and 2147), and the most interactive ones, adapted to the highest level of nitrogen fertiliser (progenies No 1390, 1405, 1421 and 2141).

## Discussion

The most important observation is that significant genotype × environment (GE) interactions occur both at provenance level and progeny-within-provenance level. It follows from earlier studies that GE interactions can be induced by phosphorus levels more than by those of other macroelements (Fober and Giertych 1970; Burdon and Harris 1973; Shelbourne 1973; Jahromi et al. 1976; Wanyancha and Morgenstern 1987a; Fober 1990; Zhou et al. 2000). Fewer works provide information about significant

Table 3. Variance analysis (F-test) and the contribution of interaction to the total variation (V%). Experiments with differing levels of nitrogen (N) and phosphorus (P)

| Trait | Source of variation | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Prov. × N | | Rp × N | | Prov. × P | | Rp × P | |
| | F | V% | F | V% | F | V% | F | V% |
| Height of seedling | ** | 3.1 | ** | 5.2 | ** | 3.6 | ** | 6.7 |
| Length of root | * | 4.4 | – | 0 | – | 2.7 | – | 0 |
| Number of laterals | ** | 6.1 | ** | 10.1 | – | 3.5 | * | 7.7 |
| Length of laterals | * | 6.4 | – | 3.6 | – | 3.5 | – | 1.8 |
| Fresh weight of seedling | ** | 3.9 | ** | 4.4 | | | | |
| Fresh weight of aerial part | ** | 3.6 | ** | 5.4 | ** | 3.7 | ** | 7.2 |
| Fresh weight of root | ** | 4.7 | – | 2.4 | – | 1.3 | – | 2.1 |
| Dry weight of seedling | * | 2.6 | ** | 4.3 | | | | |
| Dry weight of aerial part | ** | 2.7 | ** | 5.4 | | | | |
| Dry weight of needle | ** | 2.8 | ** | 5.2 | * | 2.8 | ** | 6.0 |
| Dry weight of shoot | * | 2.6 | ** | 5.7 | * | 3.3 | ** | 6.3 |
| Dry weight of root | – | 0.9 | – | 0 | – | 1.6 | – | 0 |
| % dry weight of seedling | – | 0.7 | ** | 4.3 | – | 0.3 | * | 4.3 |
| Number of buds | * | 4.6 | ** | 9.1 | | | | |
| % seedlings with apical bud | | | | | – | 0 | * | 12.4 |

– nonsignificant, * significant at 0.05, ** significant at 0.01, Prov. – provenance, Rp – progeny within provenance

Table 4. Variance analysis (F-test) and the contribution of interaction to the total variation (V%). Experiments with differing levels of potassium (K) and calcium (Ca)

| Trait | Source of variation | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Prov. × K | | Rp × K | | Prov. × Ca | | Rp × Ca | |
| | F | V% | F | V% | F | V% | F | V% |
| Height of seedling | – | 0.5 | – | 0 | – | 0 | – | 0.1 |
| Dry weight of seedling | * | 0.8 | – | 0.4 | * | 0.9 | ** | 1.6 |
| Dry weight of aerial part | * | 0.9 | – | 0.3 | * | 0.1 | * | 1.6 |
| Dry weight of needle | – | 0 | – | 0 | – | 0.6 | * | 1.2 |
| Dry weight of root | – | 0.2 | – | 0.9 | * | 1.7 | * | 2.1 |

See Table 3 for the description of symbols

Table 5. Variance analysis (F-test) and the contribution of interaction to the total variation (V%). Experiments with differing levels of magnesium (Mg)

| Trait | Source of variation | | | |
|---|---|---|---|---|
| | Prov. × Mg | | Rp × Mg | |
| | F | V% | F | V% |
| Height of seedling | – | 0.1 | – | 1.2 |
| Length of root | – | 0 | – | 0 |
| Number of laterals | – | 2.2 | – | 0 |
| Length of lateral | – | 1.7 | – | 5.7 |
| Dry weight of seedling | – | 2.7 | – | 0 |
| Dry weight of aerial part | – | 2.3 | – | 0 |
| Dry weight of needle | – | 0 | – | 3.2 |
| Dry weight of root | – | 1.9 | – | 1.6 |

See Table 3 for the description of symbols

interactions between genotype and the level of nitrogen fertiliser. In an experiment with 40 full-sib families of *Picea mariana*, Mullin (1985) observed such interactions for seedling height growth, root collar diameter, top and root weight. Wanyancha and Morgenstern (1987b) established varied responses of half-sib families of *Larix laricina* grown under differing nitrogen availability. Both experiments mentioned used three nitrogen levels. Two ecotypes of loblolly pine, investigated by Wu et al. (2000), differed in the response of root system volume to nitrogen regime, as indicated by a significant ecotype × treatment interaction.

In the present paper the genotype × nutrition interactions were investigated in half-sib Norway spruce families grown at varying nutrient levels. These interactions were statistically significant for numerous traits of seedlings grown at differing levels

Table 6. Mean height of seedlings and the parameters describing the provenance × nitrogen level interaction

| Provenance | Height of seedling (mm) | b | Vd × $10^2$ | r |
|---|---|---|---|---|
| Supraśl | 69 | 1.039 | 0.1 | 0.998 |
| Szczebra | 68 | 0.893 | 0.9 | 0.970 |
| Zwierzyniec | 74 | 0.844 | 0.1 | 0.997 |
| Radom | 70 | 1.047 | 0.5 | 0.988 |
| Łagów | 88 | 1.048 | 0.0 | 0.999 |
| Miechów | 90 | 1.133 | 0.1 | 0.997 |
| Wieluń | 95 | 1.208 | 0.2 | 0.996 |
| Ujsoły | 58 | 0.737 | 0.5 | 0.975 |
| Węgierska Górka | 69 | 0.932 | 0.1 | 0.997 |
| Wisła | 73 | 0.926 | 0.3 | 0.992 |

b – Finlay-Wilkinson coefficient, Vd – Eberhart-Russell coefficient, r – correlation coefficient

full-sib families grown on moist and dry sites, in which the authors cited observed family × environment interactions in growth. Norway spruce clone trials conducted at locations ranging from western Denmark to central Sweden showed GE interactions for growth increment (Karlsson et al. 2001). The main cause of those interactions was probably the damage caused by late spring frost. Climatic conditions may alter the ranking of genotypes in breeding programmes and thus decrease the genetic gain (Sonesson and Eriksson 2000).

Field trials can confirm genotype × location interactions which involve climatic and edaphic conditions. Because they are difficult to separate, interactions that seem very strong in greenhouse tests are much less evident in field trials, even when the environments are extensively modified by fertilisers (Matheson and Cotterill 1990). Testing in varied edaphic conditions is a method for identifying proge-

Table 7. Mean height of seedlings and the parameters describing the progeny-within-provenance × nitrogen level interaction

| Provenance | Progeny number | Height of seedling (mm) | b | Vd × 102 | r |
|---|---|---|---|---|---|
| Szczebra | 740 | 60 | 0.513 | 0.0 | 0.996 |
| Łagów | 1390 | 95 | 1.177 | 0.5 | 0.990 |
| Miechów | 1405 | 88 | 1.235 | 0.1 | 0.999 |
| Wieluń | 1421 | 87 | 1.195 | 0.6 | 0.990 |
| Ujsoły | 2123 | 58 | 0.494 | 0.9 | 0.910 |
| Węgierska Górka | 2133 | 67 | 0.720 | 0.7 | 0.967 |
| Wisła | 2141 | 91 | 1.238 | 0.7 | 0.988 |
| Wisła | 2147 | 53 | 0.461 | 0.7 | 0.921 |

See Table 6 for the description of symbols

of nitrogen and phosphorus, and also for some traits for potassium and calcium. In all cases the amount of variation explained by interaction was greater at progeny level than at provenance level, which agrees with the results obtained in another experiment (Hodge and Dvorak 1999).

GE interactions normally disturb tree-breeding programmes. In contrast to agriculture, where interactive genotypes are sought to enable efficient utilisation of mineral fertilisers, in forestry stable genotypes appear more useful, especially in view of unpredictable factors that can operate here, such as harsh climatic conditions (e.g. late spring frost, adverse soil and air temperature) or unfavourable water regimes of soil, which are beyond our control. A study of the open-pollinated families of Scots pine revealed a significant family × temperature interaction for the growth traits of young seedlings (Sonesson and Eriksson 2000). Yearly and seasonal water relations appear to contribute to the genetic variation in growth (Major and Johnsen 2001). This was demonstrated by an experiment with black spruce trees from nies with regard to their adaptability to specific conditions. McKeand et al. (2000), who investigated the response of loblolly pine genotypes to poor and rich nutrient regimes, confirmed a significant provenance × treatment interaction for stem volume. Provenances from the Atlantic Coastal Plain exhibited a greater responsiveness to nutrient amendments than a Texas provenance. Karki et al. (2000) showed also a high GE interaction for all measured traits of 33 families of *Picea sitchensis* saplings growing on fertile farm-field sites and on poor forest sites. Linhart et al. (2001) informed about significant GE interactions for the accumulation of some mineral elements, such as aluminium, boron, copper, molybdenum, sodium, phosphor, titanium and zinc, in the phloem of ponderosa pine trees planted at two locations.

The results from the experimental series presented in this paper showed that young Norway spruce seedlings reached their maximum height growth and weight at various nutrition levels. Very interesting populations are those from the Beskid region, such as Rycerka, Wisła and Istebna, which are most pro-

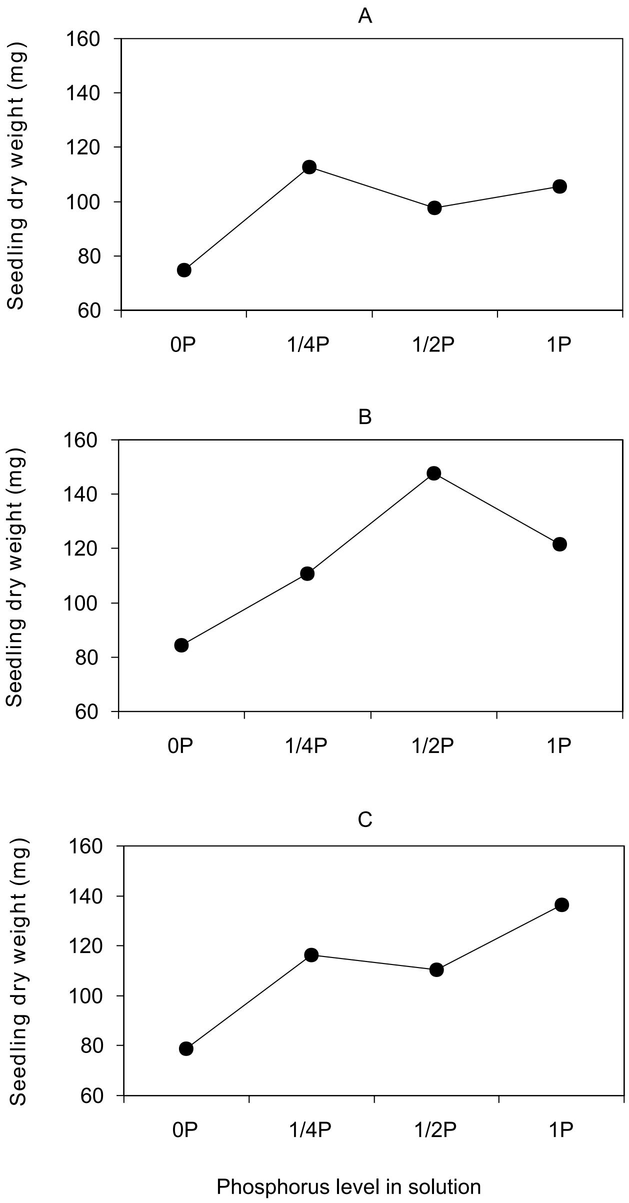


Fig. 1. Various types of response of the dry weight of seedlings to the differing phosphorus levels in the medium (on the basis of mean values for provenance groups): maximum dry weight of seedlings at a low (A), medium (B) and high (C) phosphorus level (see Table 1)

ductive in the juvenile stage but differ in nutrient requirements. Seedlings of Wisła and Istebna provenances grew better at a lower concentration of phosphorus than those of Rycerka which needed a higher phosphorus level in the solution.

Seedlings from Dolina Chochołowska, from northern Poland (Białowieża, Suwałki, Gołdap) and from Kotlina Kłodzka (Stronie Śląskie and Kowary) had the smallest dry weight (Table 1).

The reaction of provenances to the level of phosphorus varied significantly (see Fig. 1) (Fober and Giertych 1970). One group of provenances, Nowe Ramuki, Gołdap and Suwałki from northeastern Poland and Wetlina and Dolina Chochołowska from the Carpathians, reached the maximum dry weight of seedlings when grown under poor phosphorus nutrition (1/4 P) (Fig. 1 A). These are weak-growing populations. Seedlings of some provenances reached the maximum dry weight at a medium phosphorus level (1/2 P) (Fig. 1 B). Here belong provenances with well-growing seedlings, such as those from Wisła, Istebna and Augustów, as well as provenances with seedlings exhibiting slower growth, such as Iława, Konstancjewo and Kowary. The third group includes the largest number of provenances. In these the dry weight of seedlings attained the maximum value at the highest phosphorus supply (1 P) (Fig. 1 C). This group embraces the best provenance Rycerka and the provenances with seedlings of lowest growth energy.

The requirements of Norway spruce seedlings of various provenances or families can differ significantly, and the optimal nutrition for one race may be harmful for another. For nurseries and highly productive plantations the interactions between genotypes and nutrition levels should not be ignored. The results obtained suggest that it is possible to select genotypes which are suitable for specific site conditions as well as those that are stable over a wide range of nutrition levels. Both in view of environmental protection and economic aspect, the rationalisation of mineral fertilisation is necessary and beneficial in forest management.

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