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Effect of grass competition on the growth and mineral nutrition of spruce *Picea abies* Karst.

INTRODUCTION

It has been frequently reported that various grasses represent serious competition for spruce (Belkov 1960, Zlobin 1962, Fober and Giertych 1968) as well as other tree species (Richardson 1953, Knapp 1959, Baron 1962, Jakušaj 1968). In a study with labelled phosphorus Pobedov (1963) was able to show that while some weeds close to the point of ^{32}P application did not pick it up grass plants from as far as 25 cm were able to absorb it. Grass competition was shown to increase the shoot/root ratio in pine seedlings (Belkov 1960).

The competition effects operate of course both ways. Karpov (1959, 1960) has shown that nutrient content of ground vegetation under canopy of spruce and birch stands is affected by competition from mature trees. He believes that the frequent lack of ground vegetation under spruce stands is caused by competition for nitrogen. This could well be so. Spruce seedlings in spite of their sensitivity to grass competition grew better on a clear felling in luxuriant grass than in the parent stand or even on its edge (Horvat Marolt 1967). Thus an established spruce stand represents strong competition even for its own natural regeneration.

Fertilization has been known to favour weeds at the expense of the tree species in several studies. Fertilization of *Pinus taeda* seedlings with nitrogen, phosphorus or potassium fertilizers in various combinations resulted in the stimulation of Bermuda grass that smothered the pines (McClurkin 1961). Berg (1958) has found that on giving higher concentrations of complete fertilizer grass has smothered *Picea abies* natural regeneration. In a *Larix decidua* seed orchard fertilization was shown to favour nutrient uptake by grasses at the expense of the larches (Faulkner 1966). In a *Pinus silvestris* seed orchard removal of grass was found to favour flowering (Nilson 1955) as does fertilization (Faulkner 1966). On heaths, hoeing (Rommell and Malmström 1944 - 1945) and shading of heather (Leyton 1955) was found to improve mineral status in the needles of *Pinus silvestris* and *Picea sitchensis* respectively, though as the authors pointed out this was caused by removal of competition as well as by provision of a mulching effect by the decomposing ground vegetation.

There are indications that some grasses or other weeds exude toxic substances that hinder the growth of tree seedlings. Sensitivity to such exudates was shown in germinating pine seeds (M a t v e e n and T i m o f e e v 1964) and in apple and oak seedlings (R u b i n at al. 1952).

Competition should be strongest between organisms having identical requirements. In fact it has been shown that in forest communities a natural thinning leads to diversity of species due to intraspecific competition (P i e l o u 1966). Some trees grow better in mixture with other species than in pure stands (M a j a c k i j 1963). In a tropical rain forest, where conditions are optimum for vegetation, two specimens of the same species rarely grow in close proximity. Where conditions are more demanding, as in the North Temperate zone, plant communities are often almost monospecific. This implies that one species was successful in competing with all others and taking dominion of a site. S a k a i et al. (1968) have shown that even on the intraspecific level competition between *Cryptomeria japonica* trees of the same genotype (from vegetative propagation) is weaker than between trees of seedling origin. Thus in spite of having identical requirements related individuals favoured one another at the expense of others. This indicates that some form of cooperation is operating on an intraspecific level. Root grafting so common among forest trees (B o r m a n n 1961) could be an explanation here (S a u n i e r and W a g l e 1965).

As regards grass communities G r e g o r and W a t s o n (1954) point out that once a habitat has been filled to capacity the population in occupation becomes insulated against immigration. In other words grasses dominate areas by being first to capture them and by being able to survive in compact monospecific communities (turfs) impermeable to other species.

Silvicultural practices often bring transplants of forest trees into direct contact with grasses and other weeds. If the weeds are not placed under control the tree seedlings will die. The mechanism of competition for mineral nutrients was the subject of a series of experiments reported in this paper.

MATERIALS AND METHODS

Spruce seedlings of Polish origin have been raised on sand cultures in the greenhouse, with or without grass (*Poa annua* L.) in the pots. Details have been reported before (F o b e r and G i e r t y c h 1968). The experimental variables were competition (number of grass plants per pot) and the supply of mineral nutrients.

Three major experimental series have been conducted with slight modifications.

In the first one three levels of competition were employed (zero, 5 and 20 grass plants) and four levels of nitrogen supply (ON, 1/4N, 1/2N and 1N) the last one being the full medium. The competition from grass appeared to be very severe and the difference between the effect of 5 and 20 grass plants was almost negligible.

In the second series, in which phosphorus nutrition was the main variable, again at four levels of supply (OP, 1/4P, 1/2P and 1P) it was decided to employ less intense competition, namely zero, 1 and 5 grass plants per pot. The introduction of the „1 grass plant" variant proved useful but the absence of an extreme level of competition for comparison proved a disappointment.

Thus in the third series it was decided to have four competition levels (zero, 1, 5 and 20 grass plants per pot) and to reduce the macronutrient supply variable to three levels (0, 1/4 and 1). In this case jointly the three metallic macronutrients (K, Mg and Ca) have been employed. Since each element was at three concentrations there were in all 3×3×3=27 nutrient solutions (table 1): 1K1Mg1Ca; 1K1Mg1/4Ca; 1K1MgOCa; 1K 1/4Mg1Ca; 1K1/4Mg1/4Ca; 1K1/4MgOCa; 1KOMg1Ca; 1KOMg1/4Ca; 1KO MgOCa; 1/4K1Mg1Ca; 1/4K1Mg1/4Ca; 1/4K1MgOCa; 1/4K1/4Mg1Ca; 1/4K1/4Mg1/4Ca; 1/4K1/4MgOCa; 1/4KOMg1Ca; 1/4KOMg1/4Ca; 1/4KO MgOCa; OK1Mg1Ca; OK1Mg1/4Ca; OK1MgOCa; OK1/4Mg1Ca; OK1/4 Mg1/4Ca; OK1/4MgOCa; OKOMg1Ca; OKOMg1/4Ca; OKOMgOCa.

In the first and second series spruce seedlings of 20 different provenances have been employed. However since competition effects tended to obliterate provenance differences it was decided to eliminate the provenance aspect from the study of competition in the third series and therefore spruce seedlings of only one provenance (Rycerka) were used.

Each series was appropriately replicated and randomized. The results were analysed statistically. Significant results are signalized in table 2.

The performance of the seedlings, which grew in the three series for slightly different periods of time and under somewhat different weather conditions (in three consecutive years) was uneven and therefore the results are not directly comparable, however the trends in response to the experimental variables can be compared. It is these that are primarily dealt with in this paper.

The measurements made on the spruce seedlings covered such characters as height, presence of resting buds and side shoots, dry weight of leaves, stems and roots, and the internal concentrations of the macroelements under investigation.

Nitrogen concentration was estimated by the Kieldahl method (Pi-

Table 1

Composition of the nutrient solutions used in the third experimental series. Besides the salts mentioned in the table the solutions contain 2.142 ml of 1 molar NH_4NO_3, 0.630 ml of 1 molar NaH_2PO_4, 6.425 ml of 1 molar HNO_3, 240.06 mg NaOH, 1.9 ml of 0.01 molar $FeSO_4$ and 1 ml of microelemental solution, all per one liter of the nutrient solution

Sol. No.	Signature			Ml. per 1 liter of solution			
	Ca	Mg	K	$CaSO_4$ 0.01 M	$MgSO_4$ 1 M	K_2SO_4 0.5 M	Na_2SO_4 1 M
1	1	1	1	26.20	0.524	2.494	–
2	1	1	1/4	26.20	0.524	0.624	1.147
3	1	1	0	26.20	0.524	–	1.530
4	1	1/4	1	26.20	0.131	2.494	0.333
5	1	1/4	1/4	26.20	0.131	0.624	1.480
6	1	1/4	0	26.20	0.131	–	1.863
7	1	0	1	26.20	–	2.494	0.444
8	1	0	1/4	26.20	–	0.624	1.591
9	1	0	0	26.20	–	–	1.974
10	1/4	1	1	6.55	0.524	2.494	0.188
11	1/4	1	1/4	6.55	0.524	0.624	1.335
12	1/4	1	0	6.55	0.524	–	1.718
13	1/4	1/4	1	6.55	0.131	2.494	0.521
14	1/4	1/4	1/4	6.55	0.131	0.624	1.668
15	1/4	1/4	0	6.55	0.131	–	2.051
16	1/4	0	1	6.55	–	2.494	0.632
17	1/4	0	1/4	6.55	–	0.624	1.779
18	1/4	0	0	6.55	–	–	2.162
19	0	1	1	–	0.524	2.494	0.251
20	0	1	1/4	–	0.524	0.624	1.398
21	0	1	0	–	0.524	–	1.782
22	0	1/4	1	–	0.131	2.494	0.584
23	0	1/4	1/4	–	0.131	0.624	1.731
24	0	1/4	0	–	0.131	–	2.114
25	0	0	1	–	–	2.494	0.695
26	0	0	1/4	–	–	0.624	1.842
27	0	0	0	–	–	–	2.225

per 1957), phosphorus by the Kuttner and Lichtenstein method (Fink 1963) and the metallic elements by the flame photometric method (Humphries 1956). A Zeiss spectrophotometer (Spekol) and flame photometer (Flaphokol) have been employed for the determination of phosphorus and the metallic elements respectively.

Three supplementary experiments were made: 1. One consisted of supplying isotopically labelled phosphorus to a spruce and grass culture growing on a phosphorus deficient medium and following the resultant absorbtion of the element by the two competing plant species. Results of this experiment have been reported elsewhere (Fober and Giertych 1970). Here they will be only recapitulated to integrate them with other results of this competition study.

2. The second supplementary experiment consisted of raising spruce seedlings in sand cultures on a full nutrient medium and watering them with distilled water or with washings from grass roots. The washings have been obtained by growing grass on a water culture with full nu-

Table 2

Results of variance analyses

Source of variation	Characters													
	Ht.	Dry wt.				No. of buds	% of seedl. with term. buds	No. of laterals	Length of laterals	N%	P%	K%	Mg%	Ca%
		Total	Lvs.	Stems	Roots									
Competition	**	**	**	**	**	**	**	**	**	**				
N level	**	**	**	**	**	–	**	**	**	**				
Comp. × N	**	**	**	**	**	**	**	**	**	**				
Competition	**	**	**	**	**	**	–	**	**		**			
P level	**	**	**	**	**	–	–	*	**		**			
Comp. × P	**	**	**	**	–	**	–	**	**		**			
Competition	**	**	**	**	**	**	*	**	**			**	**	**
K level	–	–	–	–	–	–	*	–	–			**	**	–
Mg level	–	*	–	–	*	**	*	**				**	**	**
Ca level	–	–	–	–	–	–	–	–	–			*	–	**
Comp. × K	–	–	–	*	*	*	*	–	*			**	**	–
Comp. × Mg	**	**	**	**	**	**	–	*	**			*	**	–
Comp. × Ca	–	*	*	*	*	–	–	–	–			–	*	–
K × Mg	–	–	*	–	–	–	*	–	*			–	*	–
K × Ca	–	–	*	–	–	–	–	–	–			–	–	–
Mg × Ca	–	–	–	–	–	–	–	–	–			–	**	–
Comp. × K × Mg	–	*	–	–	*	–	–	–	–			–	*	–
Comp. × K × Ca	–	–	–	–	–	–	–	–	–			–	**	–
Comp. × Mg × Ca	–	–	*	*	–	–	–	–	–			*	–	*
K × Mg × Ca	–	–	–	–	–	–	*	–	–			–	*	–
Comp. × K × Mg × Ca	–	–	–	–	–	–	–	–	–			–	**	–

** significant at 0.01 level, * significant at 0.05 level, – not significant.

trient supply and then after rinsing the roots with distilled water by allowing it to grow for a further 10 days only on distilled water. This water was then used for the watering of the spruce seedlings. The aim of this experiment was to test the toxicity to spruce of grass root exudates.

3. The third experiment consisted of growing spruce seedlings of various provenance in competition with grass and after 9.5 months treating the plants with 10 ml per pot of herbicide solutions at concentrations that have been first tested to be lethal to grass and bearable to spruce seedlings (Pielik, containing 85% solution of sodium salt of 2,4-D- at 100 g/l and 50 g/l, Antyperz 38, containing 38% of sodium salt of TCA at 250 g/l and 100 g/l and a water control). After further 6 weeks of growth the spruce seedlings were cropped dried and weighed.

RESULTS

Table 2 summarizes the results of the major three experimental series. It indicates which sources of experimental variation have induced significant responses in the development of the studied characters.

GROWTH

Growth measured as seedling height, the dry weight of leaves, stems and roots and the total length of side shoots was in all instances affected very significantly by the competition from grass. Increase in the number of grass plants growing together with spruce has always resulted in the growth of spruce being inhibited (fig. 1). This is hardly surprising.

An increase in supply of individual macronutrients resulted in an increase of growth, this however is true only in the absence of competition (fig. 1). When this effect is very great as for example in response

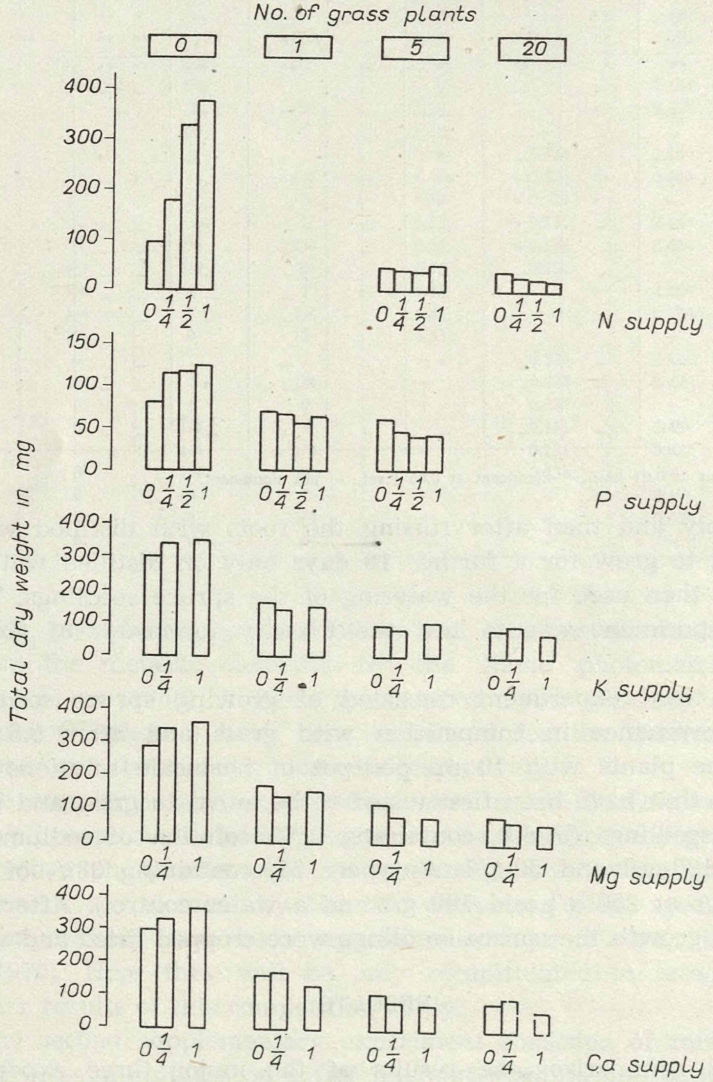


Fig. 1. Dry weight of spruce seedlings as affected by grass competition and supply of mineral nutrients

to different levels of nitrogen or phosphorus supply it dominates the opposite or nil effects observed in the presence of competition and results in a significant positive response over the whole series (table 2). However in the presence of competition the trend is obviously reverse (fig. 1), namely an increase in the supply of nutrients (with the possible exception of potassium) results in a reduction of growth. This observation is of importance as is shown by significant interactions between competition and level of nutrient supply for most of the growth characters (table 2). Variation in the fresh weight does not differ from that of the

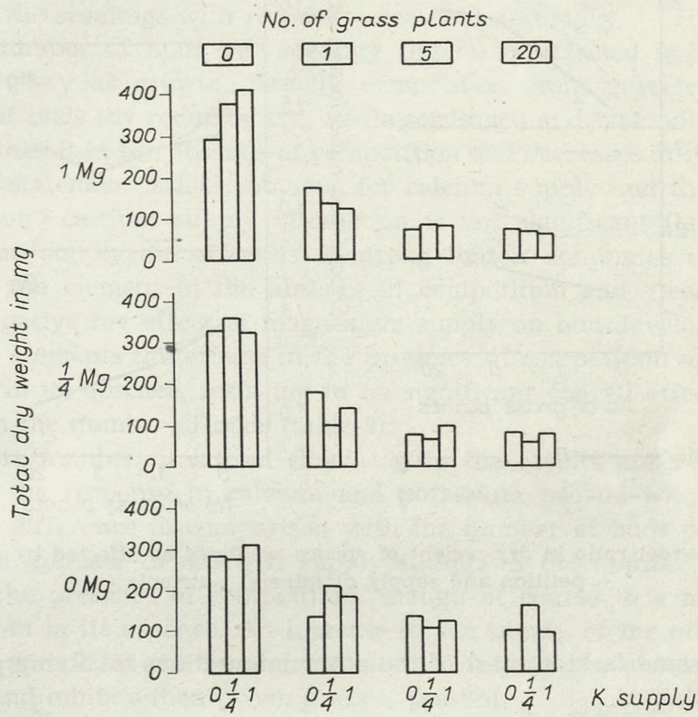


Fig. 2. Dry weight of spruce seedlings as affected by grass competition supply of potassium and supply of magnesium

dry weight. There is about 70% of water in fresh seedlings and the deviation from this average is no more than 1 or 2% for the different experimental variables (calculated only for the third series – K, Mg, Ca nutrition).

Height is the single growth character that is unaffected rather than reduced by an increase in mineral supply in the presence of competition.

The significant third order interaction between the effects of competition, level of magnesium supply and level of potassium supply on dry weight was found to have been caused by the fact that the growth response of spruce seedlings to increase in potassium supply is normal (i.e. positive in the absence of competition and negative in its presence) only when full magnesium supply is available (fig. 2). When magnesium is limiting the response to potassium is erratic.

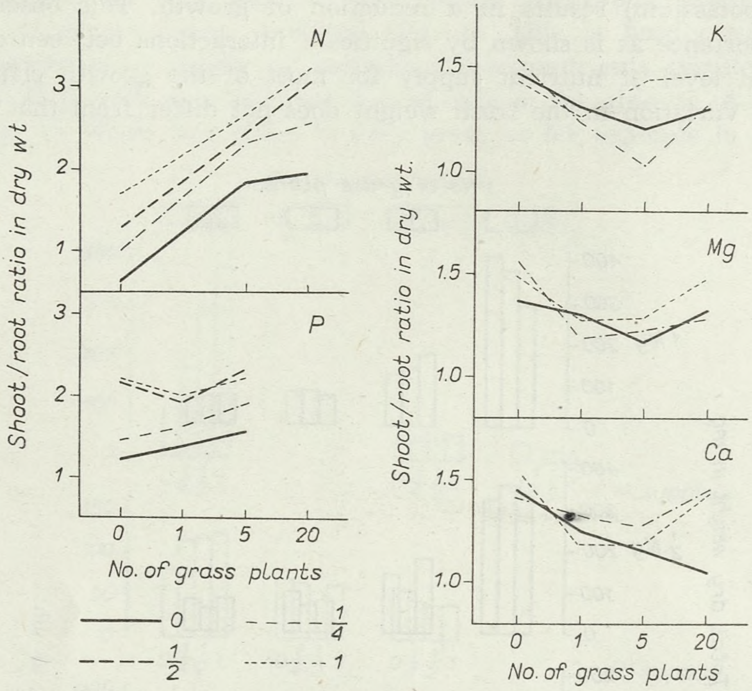


Fig. 3. Shoot/root ratio in dry weight of spruce seedlings as affected by grass competition and supply of mineral nutrients

In the same fashion most of the other interactions involving potassium can be explained.

The significant interaction between the effect of competition, level of magnesium supply and level of calcium supply was caused by the fact that in the absence of calcium one grass plant provided insufficient competition to induce a growth decline in spruce in response to increased magnesium supply. At other levels of competition or calcium supply the response to magnesium supply was normal, in the sense discussed above.

As has been pointed out in an earlier paper (G i e r t y c h 1969) competition results in an increase of the aerial plant part relative to root weight at all levels of nitrogen or phosphorus supply (fig. 3). This has been confirmed for the metallic macronutrients at high competition intensities. However weak competition first reduces the shoot/root ratio in dry weight, and it is only when 20 grass plants are present that spruce roots significantly decline in relative size (fig. 3). This inhibitive effect of competition on roots is least obvious when any of the macronutrients is absent in the culture medium and non existant when calcium is lacking.

DEVELOPMENT OF BUDS AND LATERALS

The presence or absence of dormant terminal buds, as well as the overall number of buds on a seedling or the number of lateral shoots, are developmental characters that could be informative about the condition of the seedlings with respect to seasonal dormancy.

The number of buds per seedling (fig. 4) is affected in very much the same way as growth, namely competition from grass reduces the number of buds (by reducing the whole seedlings) and macronutrient supply increases it in the absence of competition and decreases in its presence. This last statement is least obvious for calcium supply and therefore the competition×calcium supply interaction is not significant (table 2). For magnesium supply the effect is so strong that it dominates the positive effect of the element in the absence of competition and gives a significantly negative net effect of magnesium supply on bud development. For the other elements the effects in the presence of competition are nullified by those in its absence, resulting in no significant overall effects of their supply on the number of buds (table 2).

For the number of lateral shoots again the results are very similar, although the response to calcium and potassium proved not significant. The only difference in comparison with the number of buds per seedling is that an increase in nitrogen supply stimulates the number of laterals even in the presence of competition, though of course to a much lesser degree than in its absence. An increase in the supply of the other macro-elements stimulates the number of laterals only in the absence of competition and inhibits them when grass is present.

Thus it can be said that the development of buds and laterals is affected by competition and mineral nutrition parallel with vegetative growth.

The development of the terminal bud responds to the experimental variables very differently (fig. 5). To start with, only in the first experimental series (nitrogen nutrition) some of the spruce seedlings (those without grass) were actively growing at the time the experiment was terminated. As a result the number of seedlings with a formed terminal bud was much lower in the variant without competition for this series (fig. 5). In the third series (K, Mg and Ca nutrition) competition had an opposite effect — it reduced the percentage of seedlings with resting terminal buds. The differences between series reflect undoubtedly differences in the state of seasonal development of the seedlings. In the first one the effect of competition was to delay onset of growth, while in the third to delay growth cessation. In the second series (phosphorus nutrition) practically all seedlings were in a state of rest as regards growth in height and therefore had terminal buds. Thus there was no significant (table 2) differentiation with respect to this character.

Increased nitrogen supply lowered the percentage of seedlings with terminal buds, or in other words stimulated growth of the stem apex.

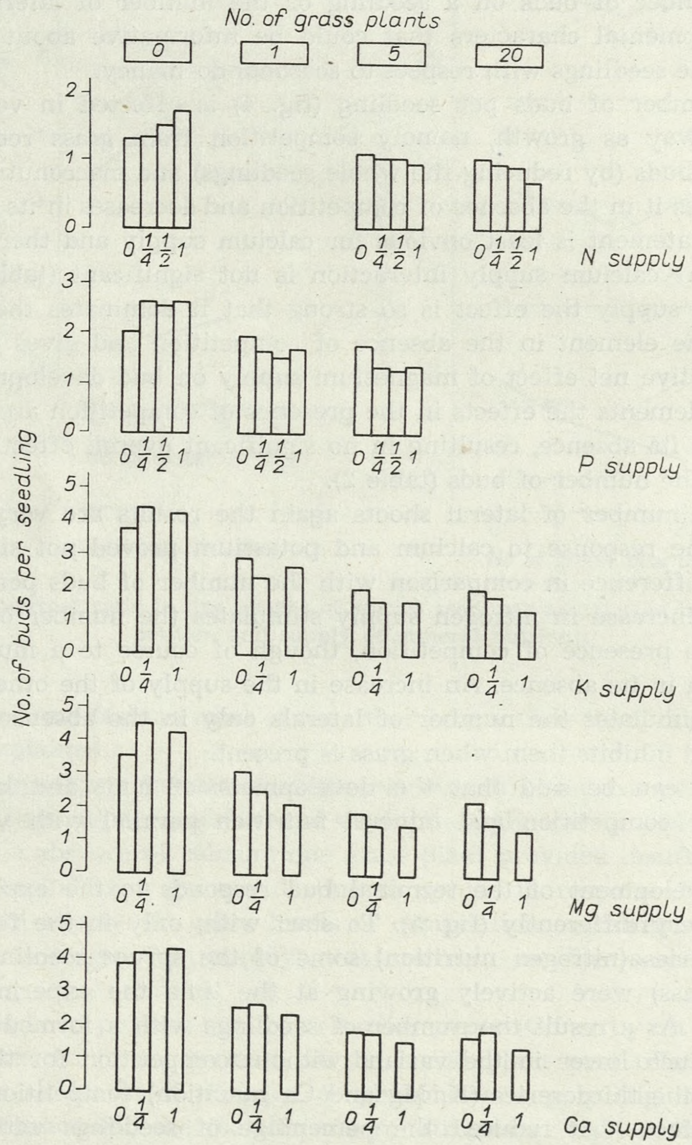


Fig. 4. Number of buds per seedling as affected by grass competition and supply of mineral nutrients

This was most pronounced in the absence of competition, but also true in its presence (fig. 5).

Potassium and magnesium had an opposite effect. Increase in their supply increased the number of seedlings with terminal buds and this effect was most distinct in the presence of competition (fig. 5). Calcium supply had no significant effect on this character (table 2), but as is indicated by the significant K×Mg×Ca interaction the effects of K and Mg referred to above are best observable in the presence of full Ca supply.

In the presence of full K supply the effect of Mg is least clear and vice versa (K×Mg interaction).

One would expect the percentage of seedlings with terminal buds

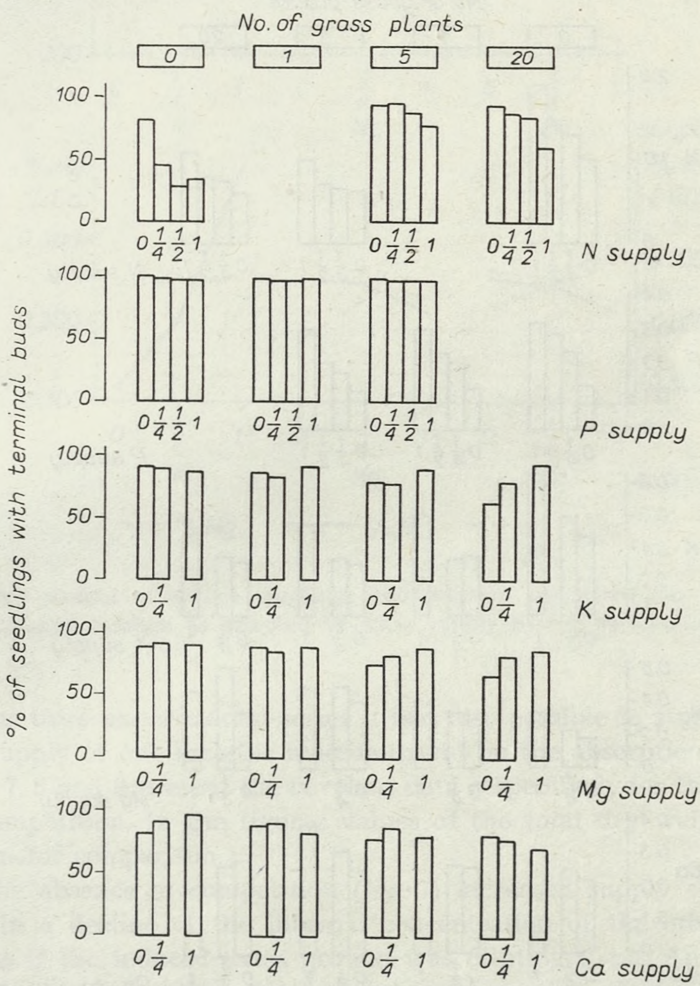


Fig. 5. Percent of seedlings with terminal buds as affected by grass competition and supply of mineral nutrients

to be affected by the experimental variables inversely as growth. This is true or almost so for K and Mg supply and for N supply in the absence of competition. However an increase in N supply in the presence of competition inhibits dry weight as well as the development of terminal buds (figs 1 and 5).

INTERNAL MINERAL CONCENTRATION

Figure 6 summarizes the main results of mineral analyses made on the seedlings. As is indicated in table 1 the supply of each element had an effect on the concentration of this element in the seedlings. Increased supply leads to increased internal concentration (fig. 6).

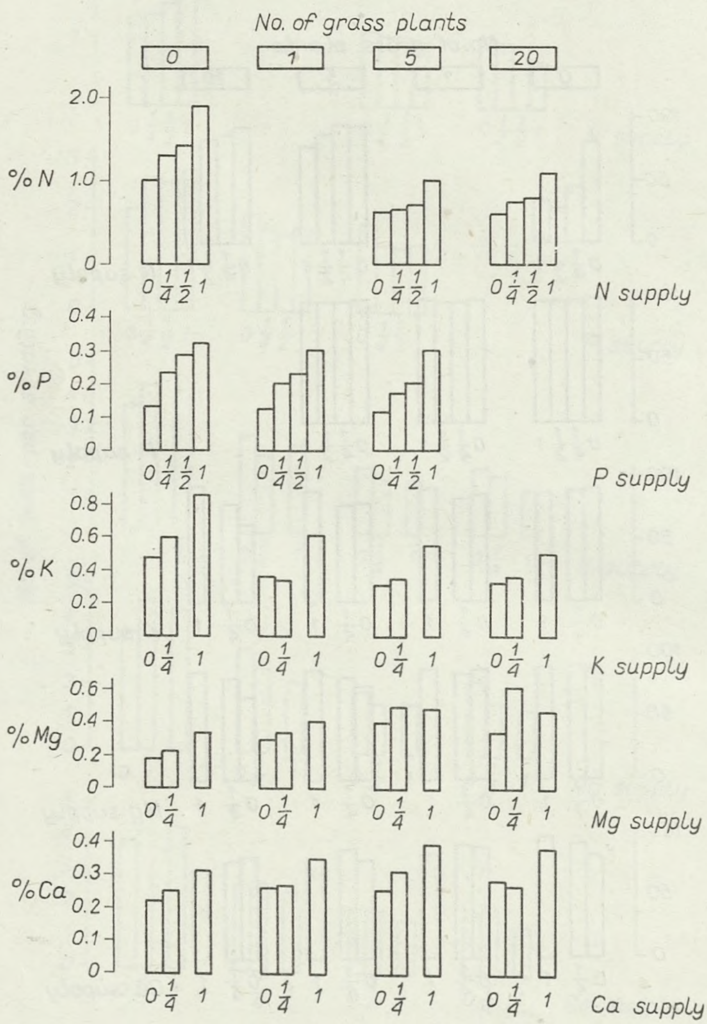


Fig. 6. Internal concentration of mineral elements in spruce seedlings as affected by their supply and competition from grass

Competition from grass significantly increases the internal concentration of magnesium and calcium, and decreases that of nitrogen, potassium and to a lesser extent phosphorus (fig. 6).

The effect of increasing mineral supply on its internal concentration is either accentuated (P) or reduced (N, K, Mg) by the presence of grass competition.

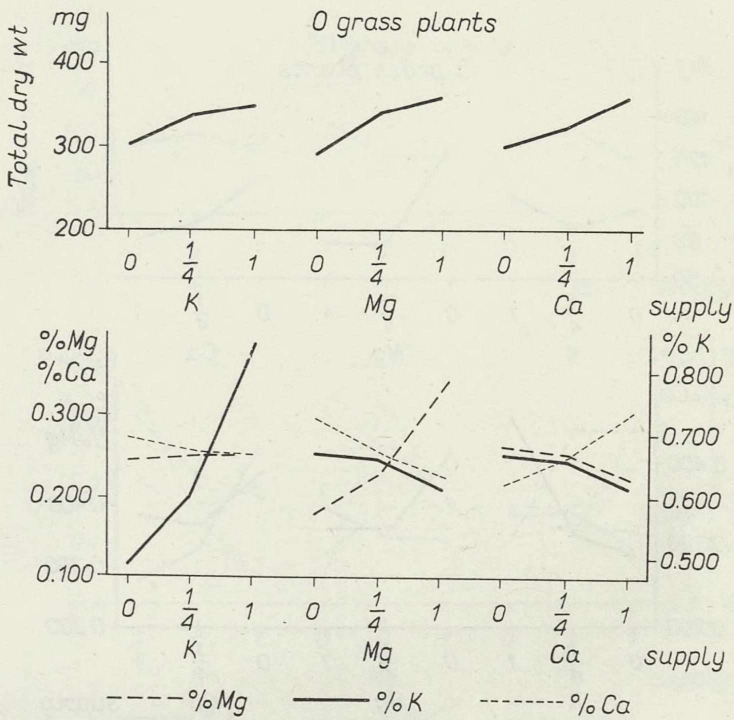


Fig. 7. Dry weight of spruce seedlings and internal concentrations of potassium, magnesium and calcium as affected by their supply in the absence of competition

In the third experimental series it was also possible to study the effect of the supply of one metallic macronutrient on the absorption of another. Figures 7, 8 and 9 present the revelant data respectively for three levels of grass competition. In the figures values of the total dry weight are also drawn in for comparison.

In the absence of competition (fig. 7) increased supply of Ca or Mg results in a decline of the internal concentration of the other two elements as if the induced extra growth was diluting them. An increase in K supply does not affect the internal concentration of Mg or Ca. Thus when K supply is limiting growth no luxury uptake of Mg and Ca takes place.

In the presence of competition (figs. 8 and 9) the effects become much more complex. The internal concentration of K, apart from the fact that it is increased by richer supply of the element, follows fairly closely the pattern of seedling dry weight. In the presence of competition, factors stimulating growth stimulate also K absorption. Exactly the opposite can be said for Mg⁰/₀ and Ca⁰/₀ (figs. 8 and 9). Here growth appears to be diluting the internal concentrations of these elements.

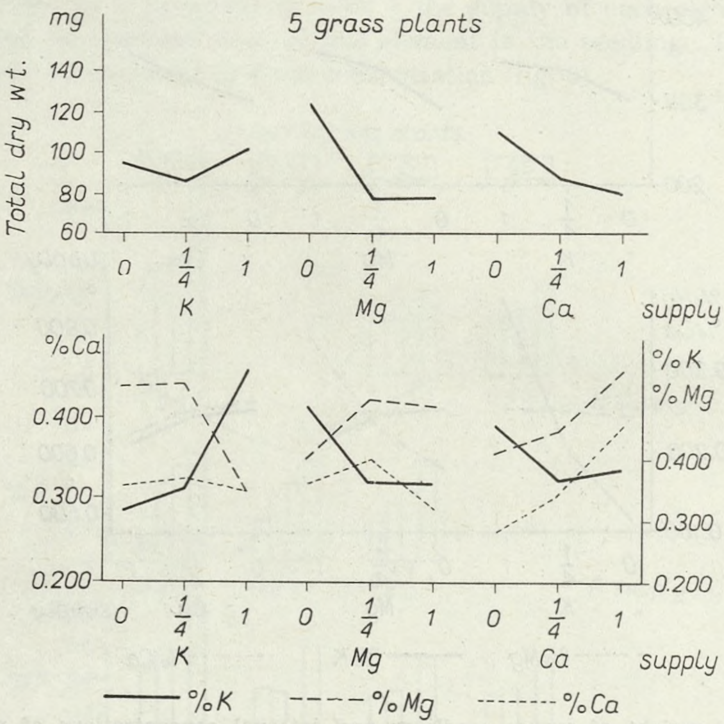


Fig. 8. Dry weight of spruce seedlings and internal concentrations of potassium, magnesium and calcium as affected by their supply in the presence of competition from 5 grass plants

Some of the other interactions involving only the supply of two or even three metallic macroelements will be discussed in greater detail at a later date. Where competition is involved its influence can be explained by the fact it can either accentuate or obliterate the overall effect of mineral supply levels. Thus for example (fig. 10) an increase of both calcium and potassium supply will tend to decrease the internal concentration of magnesium in the seedlings, however the effect of Ca is best seen in the absence of competition while the effect of potassium in its presence (Competition×K×Ca interaction — table 2, fig. 10).

RATE OF ^{32}P ABSORPTION

Results of the experiment on absorption of ^{32}P by grass and spruce seedlings growing together in pots for a prolonged period in conditions of phosphorus deficiency have been presented elsewhere (F o b e r and G i e r t y c h 1970). Here it may be relevant to recapitulate the main observations.

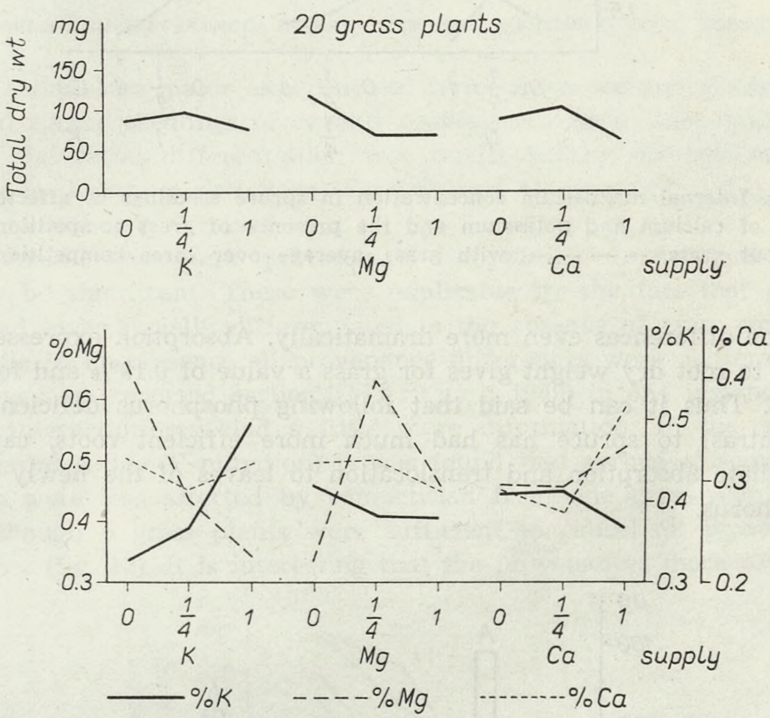


Fig. 9. Dry weight of spruce seedlings and internal concentrations of potassium, magnesium and calcium as affected by their supply in the presence of competition from 20 grass plants

Visually grass appeared to have suffered the phosphorus deficiency much more than spruce. In dry weight it represented only 27% of biomass in a pot. The main results of ^{32}P absorption are presented in fig. 11 from which it is obvious that grass was able to absorb much more of the supplied phosphorus than spruce and that it did so on the first day after. application. Furthermore grass has immediately transported bulk of newly absorbed phosphorus to the leaves while in spruce even after 7 days most of what was absorbed remained in the roots. In view of the considerably greater total dry weight of spruce than of grass, these results expressed as internal concentration of labelled phosphorus under-

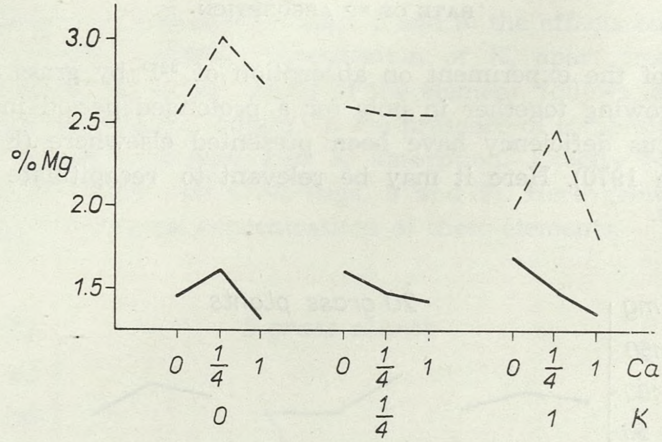


Fig. 10. Internal magnesium concentration in spruce seedlings as affected by the supply of calcium and potassium and the presence of grass competition ——— without grass, — — — — with grass, average over three competition levels

line the differences even more dramatically. Absorption expressed in relation to root dry weight gives for grass a value of 0.19% and for spruce 0.02%. Thus it can be said that following phosphorus deficiency grass in contrast to spruce has had much more efficient roots, capable of immediate absorption and translocation to leaves of the newly supplied phosphorus.

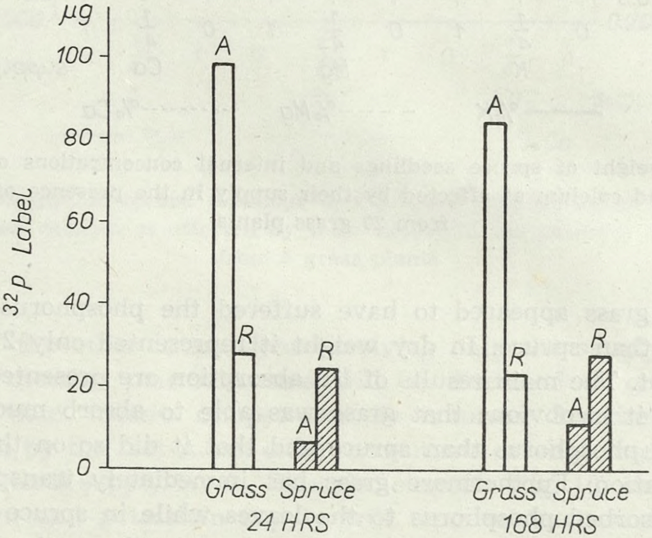


Fig. 11. Presence of labelled phosphorus in spruce seedlings and grass growing together in the aerial parts (*A*) and in the roots (*R*) after 24 and 168 hours of absorption

EFFECT OF GRASS ROOT EXUDATES

The second supplementary experiment described in materials and methods has given a definitively negative result. There were absolutely no differences between the spruce seedlings watered with distilled water and those watered with the washings from grass roots. Thus in the washings there was no substance toxic to spruce seedlings.

PROVENANCE DIFFERENCES IN RESPONSE TO COMPETITION FROM GRASS

In the first two major experimental series (nitrogen and phosphorus nutrition) spruce seedlings of several provenances have been employed. Most of the racial differentiation was unaffected by competition and therefore is discussed elsewhere (F o b e r and G i e r t y c h 1971). Here only two points will be raised.

For several characters provenance×competition interactions were found to be significant. These were explicable by the fact that spruce was found to be racially differentiated in the absence of grass competition, while in its presence all provenance differences were obliterated.

As has been reported earlier (G i e r t y c h 1969) in one instance this type of interaction revealed a little more information. In the second experimental series (P nutrition) it was found that spruce of some provenances were less affected by competition from one grass plant than others, though 5 grass plants were sufficient to cancel all provenance differences (fig. 12). It is interesting that the provenances more resistant

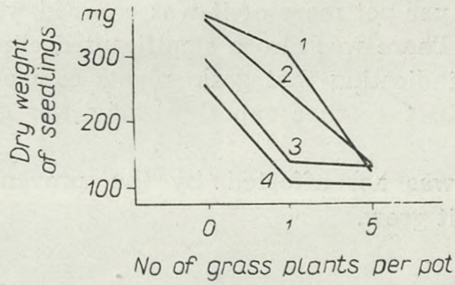


Fig. 12. Interaction between provenances and levels of competition (0, 1 or 5 grass plants per pot) in the dry weight of spruce seedlings. Provenances 1, 2, 3 and 4 are respectively Stronie Śląskie, Iława, Białowieża and Dolina Chochołowska. Shapes of the curves for all other provenances are intermediate between those for 2 and 3

to competition come from regions where the history of forest management is old (Sudety Mts., Pomerania, Silesia) while those most susceptible come from the most primeval forests (High Tatras, Białowieża, Augustów).

GROWTH OF SPRUCE AND GRASS FOLLOWING HERBICIDE TREATMENT

The supplementary experiment on spruce provenance differentiation following growth with grass and herbicide treatment has yielded little new information. The four herbicide treatments were lethal to grass, but after some time proved also to be inhibitory to the growth of spruce. Only after antyperz at 100 g/l did the spruce seedlings maintain the same fresh and dry weight as in the controls. However they still did not benefit from the herbicidal death of the grass. In all cases the herbicides lowered the percentage of dry weight (increased water content of spruce seedlings). The experimental results confirm that spruce seedlings of various provenance differ in fresh and dry weight and that grass competition is inhibitive. Also there was a significant interaction between the competition and herbicide variables, which was explicable by the observation that spruce seedlings weakened by competition from grass were more sensitive to the herbicides than those growing without grass. However there were no interactions between provenances and herbicides or competition. Since the search for these interactions was the object of this experiment the results have to be considered as negative.

GROWTH OF GRASS

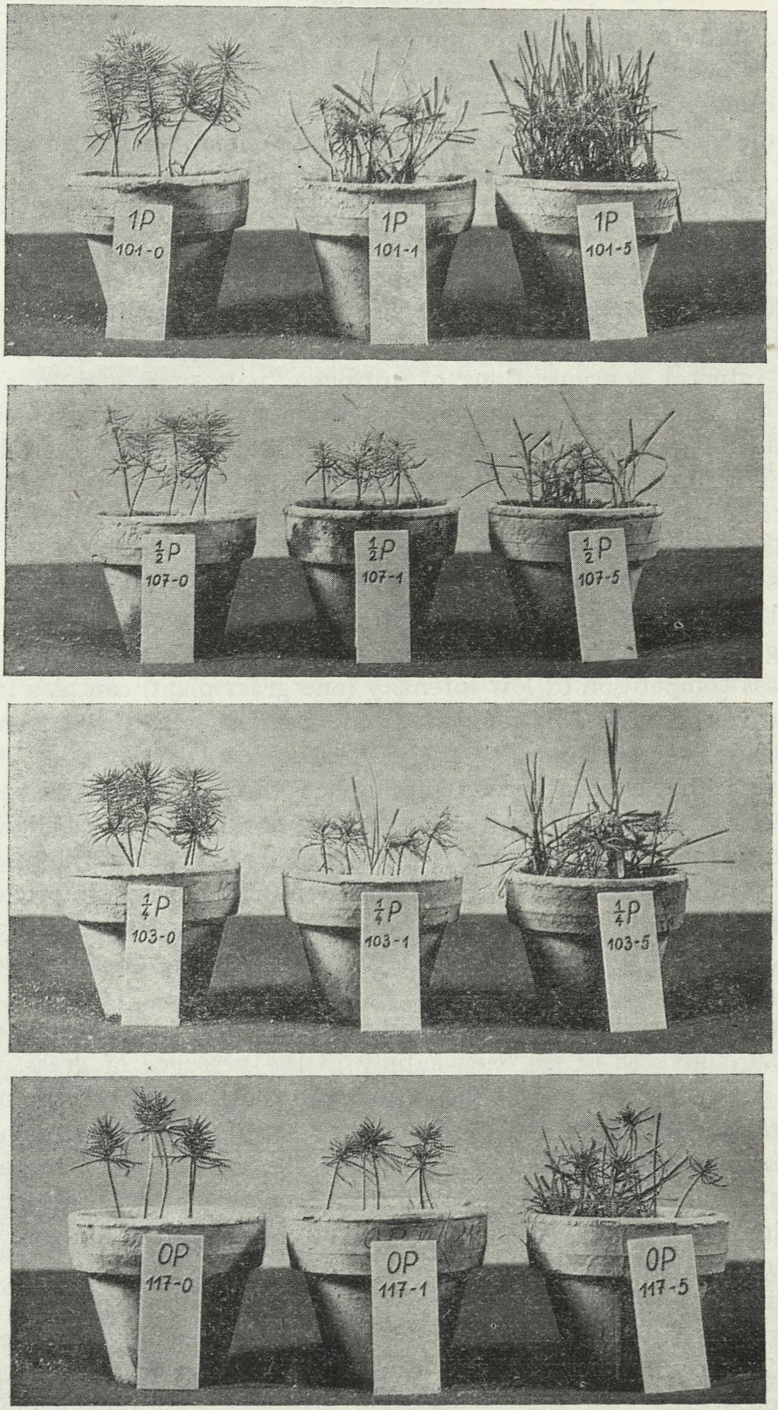
Finally a word is needed about the growth of grass in our conditions. For example an increase in the supply of nitrogen significantly stimulated grass growth and increased its nitrogen concentration (table 3). When more grass was sown per pot more of it was cropped, yet not in proportion to seed number. There was also a significant decline in internal nitrogen concentration indicating that grass plants competed for nutrients between themselves. In the other experimental series grass behaved similarily (fig. 13).

Growth of grass was not affected by the provenance of spruce seedlings with which it grew.

Table 3

The influence of nutrition level and sowing density on nitrogen content and growth of grass in pot cultures with spruce

Averages per pot	Level of nitrogen supply				No of grass seeds sown per pot	
	ON	1/4N	1/2N	1N	5	20
Fresh wt.g	.61	.73	.86	1.08	.56	1.15
Dry wt.g	.09	.11	.14	.15	.08	.17
N%	3.9	4.2	4.5	5.0	4.6	4.1



phot. I. Kuberacka

Fig. 13. Spruce seedlings growing together with various amounts of grass under various levels of phosphorus supply

DISCUSSION

This study of grass competition effects on the physiological responses of spruce seems to indicate that at least two quite distinct mechanisms of the competition phenomenon are operative.

In the first place one can mention the competition for mineral nutrients. This is what we normally mean when we speak of plant competition and the existance of such competition was not surprising. We propose to refer to it as privative competition since it leads to a situation where plants are deprived of essential foodstuffs. In our material, we were able to show that presence of grass in pots led to an inhibition of the growth of spruce seedlings accompanied by a reduction in the internal concentrations of nitrogen, potassium and to a lesser extent phosphorus. Thus shortage of these elements could have been the cause of growth inhibition. This effect was observable at all levels of nutrient supply (fig. 1). It is also true that privative competition affects grass itself by lowering its percentage mineral content and average size per grass plant (table 3, fig. 13).

It is well known (Ingestad 1959) that shortage of nitrogen and phosphorus leads to an increase in the relative root size in spruce seedlings. This was confirmed in this study (fig. 3) and it was found that grass competition of low intensity (one grass plant) can also increase the relative root size. This could well have been effected through competition for mineral nutrients.

There is however a second mechanism through which grass exerts an inhibitive effect on the growth of spruce seedlings. It was shown that in the presence of grass there is a reduction of spruce seedling growth (fig. 1) parallel with the level of mineral nutrition being improved, not only in terms of supply per pot but also for spruce specifically as is evidenced by an enhenced internal concentration of the macroelements (fig. 6).

This second competition mechanism has not influenced seedling height. An increase of nitrogen supply in the presence of grass, though reducing seedling dry weight did not reduce their height nor the number of lateral shoots. Since the percentage of seedlings with terminal buds is inversely correlated with N% (compare fig. 5 and fig. 6), the activity of the stem apex appears to be determined by the internal nitrogen concentration and therefore affected by privative competition but not by the second competition mechanism.

At higher levels of competition intensity the top/root ratio in spruce seedlings increases (fig. 3) as it did in the pine seedlings of Belkov (1960). This could not have been caused by shortage of mineral supply. It is noteworthy that this competition effect is least observable when the level of mineral, particularily calcium, supply is low (fig. 3) and therefore grass is weak.

The above observations suggest that this second competition effect is operative below the soil surface. Above the soil spruce development is normal, at least as regards height growth, development of laterals and activity of the terminal meristem. Competition for CO_2 is unlikely, particularily since in a tussock of grass respiration of dying leaves should be high. Competition for light was eliminated by the practice of cutting grass to the level of the spruce seedlings in order to expose them.

Thus the second competition mechanism is to be sought in the interaction between roots of grass and spruce. Competition for mineral nutrients was excluded — since none of the macroelements was limiting. The parallelism between internal K⁰/₀ and growth demonstrated in figs. 8 and 9 could suggest that potassium was limiting, however its concentration did increase with an increase in supply in the presence of competition (fig. 6) while growth was inhibited (fig. 2). Thus the parallelism between K⁰/₀ and growth is likely to be due to growth affecting K absorption and not vice versa.

Micronutrients have been regularily supplied in ample quantities for both grass and spruce and thus were unlikely to have been limiting.

Water was supplied regularily in such quantities, as were necessary to keep the pots moist.

Soil aeration is generally considered to be sufficient in sand cultures with an outlet for the water that is supplied daily. Such flushing of the cultures should have provided sufficient oxygen even though distilled water was used.

Washings from grass roots were found to be indifferent to the growth of spruce. Toxic exudates would have been soluble in water if they were to be physiologically active and therefore the inertness of the washings from grass roots suggests that this type of antagonism did not operate in our material.

The only other environmental requirement for which spruce and grass might have been competing is space, and in the absence of any other explanations we would suggest that the second mechanism of competition involves mechanical interference of grass roots with the growth of spruce roots. We propose to call it restrictive competition.

The next point to consider is wheather this study has thrown any light one the question why grass is more successful than spruce when the two species are in competition. The study on the absorption of isotopically labelled phosphorus has shown that grass is quicker to respond to phosphorus supply by immediate absorption and transport of the element to the aerial plant part. Grass roots are more efficient phosphorus absorbing organs. These observations can explain privative competition wherby grass deprives spruce of mineral nutrients.

It is also reasonable to conclude that this greater ability of grass to benefit from available nutrients determines the potential for grass growth, and that intense growth is a necessary precondition for restrictive competition to become operative. When the level of mineral supply is low grass is weak (table 3) and the competition effect in reducing relative size of spruce roots is least obvious (fig. 3).

If as suggested competition for soil space ensues, rate of root growth as well as the physical pressure roots must exert on each other will be of importance. Since obviously spruce roots cannot grow through the roots of grass, nor vice versa, the plant first able to occupy the available space between sand particles will win in restrictive competition. Root tips that are stronger in shifting sand particles and other roots will have and advantage. Since rate of root growth as well as the turgor within root tip cells will benefit from more efficient absorption of mineral nutrients, it is very likely that both the competition mechanisms depend on the same physiological characteristic of grass.

The domination of an ecosystem by grass species depends on the ability of these plants to form tussocks or turf, while spruce dominates communities by shading. Spruce in order to shade has to grow above other vegetation and has to form a canopy by joining crowns. Grass in order to turf a soil has to fill all spaces with rootlets. To succeed spruce must shade grass before the latter turfs the soil.

The search for racial differentiation in the ability of spruce to compete with grass was singularily unsuccessful. The only observation permitting such differentiation to be suspected (fig. 12) indicated that spruces from regions long under silviculture had more inherent resistance to grass than those from primaeval forests. This observation only serves to remind us that grass competition is a man-made problem. In natural spruce stands wherever a gap forms it is soon dominated by a dense community of spruce seedlings. Grass seldom participates, and therefore ability to compete with it is not needed.

When a clear felling is made the ground is exposed to light which favours growth of grass and other weeds. Furthermore the spacing of planted seedling stock is very wide compared with natural regeneration and therefore the closing of a canopy and root grafting come late — at a time when the process of soil turfing by grass might have begun. Hence silviculture has introduced the weed problem and possibly initiated the evolution in spruce of competitive ability against weeds.

The practical conclusion is obvious. Spruce seedlings have no inherent defence against grass. Thus effective weed control must accompany all phases of artificial spruce regeneration. Since soil fertilization increases competition effects, it may cause damage to spruce seedlings unless they are really free from weeds.

SUMMARY

Spruce (*Picea abies* Karst.) seedlings have been grown in pot cultures together with various amounts of grass *Poa annua* L. The levels of mineral macroelements in the supplied nutrient solutions were diversified. Growth, development and absorption of the mineral nutrients by spruce seedlings were studied. It was found that grass competition has had a very negative effect on the growth and development of spruce seedlings, particularily when mineral nutrition was optimum. Grass deprives spruce seedlings of nutrients (privative competition) and turfs the soil in the pot, leaving no space for the growth of spruce roots (restrictive competition). Efficient root system and rapidity of absorption and translocation to aerial parts of mineral nutrients, following their application, permits grass to succeed in privative competition which in turn leads to better growth of grass and success in restrictive competition.

As a result of privative competition spruce seedlings have lower internal concentrations of nitrogen, potassium and phosphorus and proportionately lower shoot/root ratios. Restrictive competition leads to opposite symptoms in spruce. Internal mineral concentration is increased, since growth restriction is not paralleled by limitation in mineral absorption and since the competition is intensified by increase in mineral supply. Shoot/root ratios are increased since the growth restriction affects primarily the roots. Antagonism through toxic root exudates was not found to be involved in the interactions between spruce and grass roots. Spruce lacks inherent adaptation to competition with grass and therefore artificial control of weeds must accompany all phases of spruce seedling growth, particularily when soil is rich or fertilizers are applied.

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HENRYK FOBER I MACIEJ GIERTYCH

Wpływ konkurencji trawy na wzrost i żywienie mineralne świerka (Picea abies Karst.)

Streszczenie

Siewki świerka (*Picea abies*) różnych proweniencji były hodowane w doniczkach razem z różnymi ilościami trawy *Poa annua* L. Poziom makroelementów w dostarczanej pożywce mineralnej był zróżnicowany. Badano wzrost i rozwój siewek, jak też zawartość w nich soli mineralnych. Stwierdzono, że konkurencja trawy miała bardzo negatywny wpływ na wzrost i rozwój siewek świerka, szczególnie przy wysokim poziomie żywienia mineralnego. Trawa bowiem pozbawia siewki świerka pokarmów (konkurencja pozbawiająca) oraz zadarnia glebę w doniczce nie pozostawiając miejsca na wzrost korzeni świerka (konkurencja wypierająca). Wydajny system korzeniowy oraz szybkość pobierania i transportowania soli mineralnych do części nadziemnej pozwala trawie na zwycięstwo w konkurencji pozbawiającej, co z kolei prowadzi do lepszego wzrostu trawy i konkurencji wypierającej. Siewki świerka w rezultacie konkurencji pozbawiającej mają niższe stężenie azotu, potasu i fosforu oraz proporcjonalnie mniejszy stosunek części nadziemnej do korzenia. Konkurencja wypierająca prowadzi do odwrotnych symptomów. Stężenie soli mineralnych w siewkach świerka jest zwiększone, ponieważ ograniczenie wzrostu jest większe niż ograniczenie pobierania soli i ponieważ intensywność tej konkurencji wzrasta w wyniku poprawy żywienia mineralnego. Stosunek części nadziemnej do korzenia wzrasta, gdyż przede wszystkim ograniczony jest wzrost korzeni. Antagonizm poprzez toksyczne wydzieliny korzeniowe nie występuje w interakcjach korzeni świerka i trawy. Świerk nie posiada wrodzonej odporności na konkurencję z trawą i dlatego kontrola zachwaszczenia jest konieczna, szczególnie gdy gleba jest bogata lub stosuje się nawożenie mineralne.

ХЕНРЫК ФОБЕР И МАЦЕЙ ГЕРТЫХ

Влияние конкуренции травянистых растений на рост и минеральное питание Picea abies Karst.

Резюме

Сеянцы ели различного происхождения выращивались в цветочных горшках вместе с разными количествами мятлика (*Poa annua* L.). Концентрация микроэлементов в питательном растворе во всех горшках была одинаковой. Исследовались рост и развитие сеянцев, а также содержание в них минеральных солей. Установлено, что конкуренция травяного покрова отрицательно сказывалась на росте и развитии сеянцев ели, особенно при высоком уровне минерального питания. Злаки отбирали у сеянцев питательные вещества (конкуренция мешающая) и, задерняя почву в горшке, не давали расти корням (конкуренция вытесняющая). Мощная корневая система и быстрота всасывания и перемещения минеральных солей в надземные части растения позволяют злакам побеждать в конкуренции мешкающей, что в свою очередь приводит к их более интенсивному росту и, соответственно, повышает шансы в конкуренции вытесняющей. В результате конкуренции мешающей у сеянцев ели понижается концентрация азота, калия и фосфора и пропорционально уменьшается отношение надземной части растения к подземной. Конкуренция вытесняющая вызывает противоположные изменения. Концентрация минеральных солей у сеянцев ели в этих условиях увеличивается, так как ограничение роста растений опережает уменьшение поступления минеральных солей, а интенсивность конкуренции усиливается по мере улучшения минерального питания. Отношение надземной части к подземной увеличивается, поскольку в первую очередь тормозится рост корневой системы. Во взаимоотношениях корней ели и злаков не наблюдаются явления антагонизма, обусловленные корневыми выделениями. Ель не обладает врождённой способностью выдерживать конкуренцию с травяным покровом, и поэтому необходимо искусственное регулирование степени зарастания последним, особенно при богатой почве или при применении минерального удобрения.