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Studies of root competition in a poor pine forest by supply of labelled nitrogen and phosphorus

by

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ABSTRACT

ODC 181.36—174.7 Pinus silvestris (485)

The phenomenon known as root competition in lichen pine forests has been studied by means of applying ammonium sulphate and potassium phosphate labelled with N^{15} and P^{32} respectively to a plot with a seed tree *(Pinus silvestris)* in the centre. Under the tree there was a typical competition zone. Both *Calluna vulgaris* and *Vaccinium vitis idaea* proved to be at least as efficient absorbers of nutrients as the pine plants in the natural regeneration under the seed tree. In the vegetation immediately outside the fertilized area only traces of the added nutrients could be found.

An analysis of the root distribution revealed that the suppressed pine plants in the competition zone had their roots spread chiefly in the deeper layers while the root system of the older tree dominated the upper layers where the supply of nutrients available to vegetation is largest. At a distance of 5—7 m from the tree, where its competition began to decrease, the small plants were found to have a considerably more superficial root system than what they had nearer to the tree.

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Studies of root competition in a poor pine forest by supply of labelled nitrogen and phosphorus

The phenomenon known as "root competition" on poor forest sites began to attract the interest of experts many years ago and has since been the subject of several biological studies. It is still an open question why the apparent effects of root competition vary so much in different cases. The phenomenon is most conspicuous on dry and extremely poor sites especially in the North Swedish lichen pine heath forests where in fact most of the research in this field has been made.

The first man in Sweden to make a more thorough investigation of the problem of root competition was *Hesselman*. He elucidated various aspects, especially on what is known as the "extreme" lichen pine heaths in upper Norrland, in several papers (*Hesselman* 1910, 1917, cf. *Wretlind* 1931, *Romell* 1938, *Björkman* 1945, *Romell* and *Malmström* 1945). On such biotopes regeneration usually takes place under the older trees whereas the small plants in the open areas between the trees never grow up. *Hesselman* believed that this regeneration pattern was caused primarily by a richer supply of easily available nitrogen in the humus layer deriving from the fall of litter under the trees. On the other hand *Hesselman* discovered that the water supply could not be of decisive significance since the water content of the mineral soil where the roots are generally to be found was consistently higher in the gaps than under the trees.

More common than lichen pine heaths with regeneration developing under the trees is the opposite, viz. that vigorous plants grow only in the wider gaps while the trees, particularly in thinned-out stands are surrounded by a competition zone or sterile belt. This type of regeneration occurs practically on all forest lands but is most common on nutrient poor or dry sites where occasionally a small number of trees, for instance a few left-over seed trees are capable of preventing regeneration in wide surrounding belts. Such fields have also been subject to thorough research, particularly in Finland (e.g. by *Aaltonen* 1920, 1926) and in the U.S.A. (e.g. by *Waever* 1919, *Clements et al.* 1929, *Stevens* 1931, *Toumey* and *Korstian* 1937). The origin of the competition zones is in such cases generally attributed to root competition from the older trees.

Thanks to the isotope technique it is nowadays possible to make a closer study of this problem which is of great significance for our understanding of the biology of the forest and for silviculture as a whole.

In 1967 *Björkman, Lundeberg* and *Nömmik* showed that when N^{15}-labelled ammonium sulphate and calcium nitrate was added to about 15-year-old *Pinus silvestris* L. trees approximately 10 % of the added nitrogen had been absorbed by the trees after one growing season (May—October). Between 10 and 20 % had been absorbed by the ground vegetation (*Calluna vulgaris* [L.] Hull, *Vaccinium vitis idaea* L. and mosses) while approximately 60 % could be recovered in the ground, mainly in bound form. Between 10 and 20 % of the added N^{15} could not be traced and was assumed to have been lost by leaching.

In an effort to illustrate the competition situation on sediment grounds of the lichen pine forest type another experiment was conducted, also this time using isotope technique.

Materials and methods

The experiment was carried out on a sediment soil of the lichen pine forest type approximately twelve km north of Hamrånge in the province of Hälsingland, Central Sweden. The ground vegetation consisted of the characteristic lichen pine forest growth of *Calluna vulgaris* and *Vaccinium vitis idaea* in the field layer and species of *Cladonia (C. rangiferina* [L.] Web., *C. silvatica* L. and *C. alpestris* [L.] Rabenh.*)* in the ground layer. The tree layer consisted of *Pinus silvestris,* age about 70 years.

The soil profile was a typical iron podzol. Data on pH and nitrogen content in Table 1.

In a clear-felled area (cut about 20 years ago) where seed trees had been left a circular experimental plot was prepared with one tree in the centre. This tree stood inside the cleared area though not far from the

Table 1. Nitrogen and pH characteristics of the soil profile.

Horizon	Depth cm	pH_{H_2O}	Total N %	Inorganic N Ammonium ppm	Nitrate ppm
A_0—A_1	0— 3	4,0	0,322	9,7	11,6
A_2	— 8	4,3	0,030	2,7	4,1
B	—20	4,9	0,028	1,4	0,5
C	20—40	5,1	0,011	1,1	3,4
	40—60	5,2	0,011	1,1	3,2
	60—80	5,2	0,007	0,8	1,8

Fig. 1. A view over experimental plot with the seed tree to the left and adjacent forest to the right and behind the tree.

adjacent stand. Around the seed tree and outwards towards the clear-felled area a typical "sterile zone" with suppressed pine plants of various ages had developed owing to the competition from the tree. On the other hand some plants of the same age had grown vigorously in the absence of such competition at a distance of 6—8 m from the seed tree on the experimental plot towards the adjacent stand (Fig. 1 and 2). The experimental plot which had a radius of 4 m was treated with nitrogen on 10 July 1965. The applied fertilizer consisted of 301 g ammonium sulphate with 2.95 atomic-% N^{15}-excess which corresponds to 60 kg N per hectare. On 23 September 1965, 14 October 1966 and 24 October 1967 samples were collected from pine plants and other vegetation inside the experimental plot and from pine plants inside the zones 0—2 and 2—4 m outside the plot. All the different types of samples were combined to a composite sample which with one replication was analysed for total N by the Kjeldahl macro-digestion procedure and for nitrogen isotope ratio after *Rittenberg's* (1946) method with a Consolidated Nier isotope mass spectrometer (Model 21—202). The samples taken from the pine plants consisted of needles from the top whorl, those from *Calluna vulgaris* were annual shoots and those from

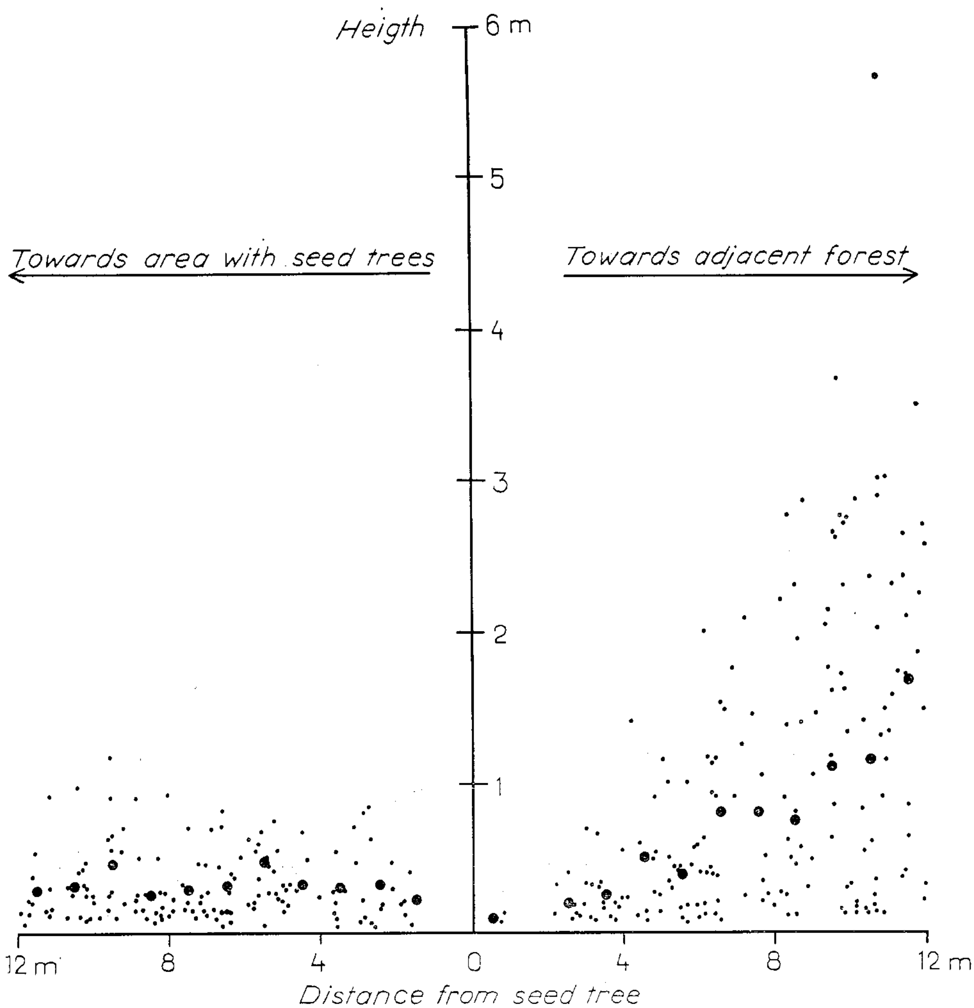

Fig. 2. Natural regeneration on and in immediate vicinity of experimental plot with a 70-year-old pine tree (*Pinus silvestris* L.) in centre. Small points indicate height of individual plants and their distance from seed tree. Large points show average plant height in each 1-metre zone counted from the tree.

Vaccinium vitis idaea were leaves. In June 1969 another collection was made of 2-year needles from the third whorl on eight pine plants inside and outside the plot. These samples were each analysed separately.

The section of the experimental plot which faces the adjacent stand was also treated with P^{32}-labelled ortophosphate. This was done on 8 June 1966. On one hundred points, evenly distributed over the semi-circular area, lichen was removed wherever it occurred whereupon

10 ml 0.81 molar potassium phosphate solution with an activity of 1.25 mCi was applied to each point. The amount applied to the experimental plot corresponded to 10 kg/hectare. The points of application were covered with so much sand (a couple of handfulls) that a battery-powered GM-counter failed to respond. On 27 July of the same year samples were collected from the existing vegetation on and outside the plot. Their activity was measured on the following day, after they had been transferred to ashes (450° C), with a Tracerlab Autoscaler (SC-51) with Tracerlab Geiger tube TGG-2.

Results

The results of the N^{15} and P^{32} determinations are collocated in Tables 2 and 3. As regards nitrogen (expressed as atomic-% N^{15}-excess in total N) the same range of values was received for samples collected on the plot, irrespective of plant species, both in the year of fertilization (1965) and the year after. Even in 1967 the content remained on the same level in *Vaccinium vitis idaea* and *Calluna vulgaris* while it had gone down by approximately 40 % in the pine plants, a N^{15}-content which they also held in 1969 (plants No. 15, 16 and 17 in Table 3). This result indicates a) that both *V. vitis idaea* and *C. vulgaris* had at least equally good chances as the pine plants in the natural regeneration under the tree to compete about the applied fertilizer, and b) that the added nitrogen remained in the system in significant amounts and had not been lost by leaching away in the four-year period from the time of fertilization to the last sample taking.

The return of the phosphate fertilization was somewhat different from that of the nitrogen treatment with considerably higher P^{32} activity recordings from both *V. vitis idaea* and *C. vulgaris* than what had been received from the pine plants. It is uncertain whether this discrepancy was real or due to the possibility that the point by point application of phosphate was an unsatisfactory method.

Even if the above-mentioned results were not quite unexpected this was certainly the case with those received from the analyses of plant material collected in the immediate vicinity of the fertilized area (zones 0—2 and 2—4 m from the boundary of the plot). The N^{15} content of the pine plants here reached only 1—2 % of that of the plants on the plot. This phenomenon was even more pronounced as regards the P^{32} activity and applied to *V. vitis idaea* and *C. vulgaris* as well. In order to endeavour to find an explanation of this pronounced difference a root examination was performed in two stages. In the first the distribution of the roots of the pine plants was examined in a segment of con-

Table 2. Total N, N^{15}-excess and P^{32}-activity in different parts of the vegetation on and outside a plot fertilized with $(N^{15}H_4)_2SO_4$ in July 1965 and with $KH_2P^{32}O_4$ in June 1966.

Localisation	Analysed material	SEPT 1965		JULY 1966	OCT 1966		OCT 1967	
		N_{tot} %	N^{15}-excess atomic-%	P^{32} CPM /g dw	N_{tot} %	N^{15}-excess atomic-%	N_{tot} %	N^{15}-excess atomic-%
On the plot	*Pinus silvestris* current needles from seedlings	1.45	0.742	917	1.08	0.703	1.15	0.438
	Calluna vulgaris current shoots	0.85	0.783	6600	1.06	0.874	0.90	0.712
	Vaccinium vitis idaea leaves	1.13	0.761	4383	1.10	0.798	0.87	0.844
0—2 m from the plot	*Pinus silvestris* current needles from seedlings	1.35	0.013	4				
	Calluna vulgaris current shoots			15				
	Vaccinium vitis idaea leaves			9				
2—4 m from the plot	*Pinus silvestris* current needles from seedlings	1.35	0.007	3				
	Calluna vulgaris current shoots			10				
	Vaccinium vitis idaea leaves			0				

centric circles with a radius of 5 and 7 m with a 60° angle and the seed tree as central point. Inside this segment were nine plants (Nos. 1—9 on Fig. 3). The mapping which also included the roots of the seed tree was performed to a depth of 20 cm, which means that practically all the plant roots and approximately 80 % of the roots of the seed tree inside the segment in question were accounted for (*Kalela* 1949). For practical reasons, and because the main interest concerned the spread of the horizontal root system, that alone was mapped. In the course of the investigation, which included mapping of all the long laterals ("roots generally originating from the root-collar region which show great and prolonged growth in length, and which often have few branches", *Sutton* 1969) and also secondary roots down to approximately one mm diameter, it was perfectly evident that the root system was mainly orientated horizontally. The vertical roots of the plants

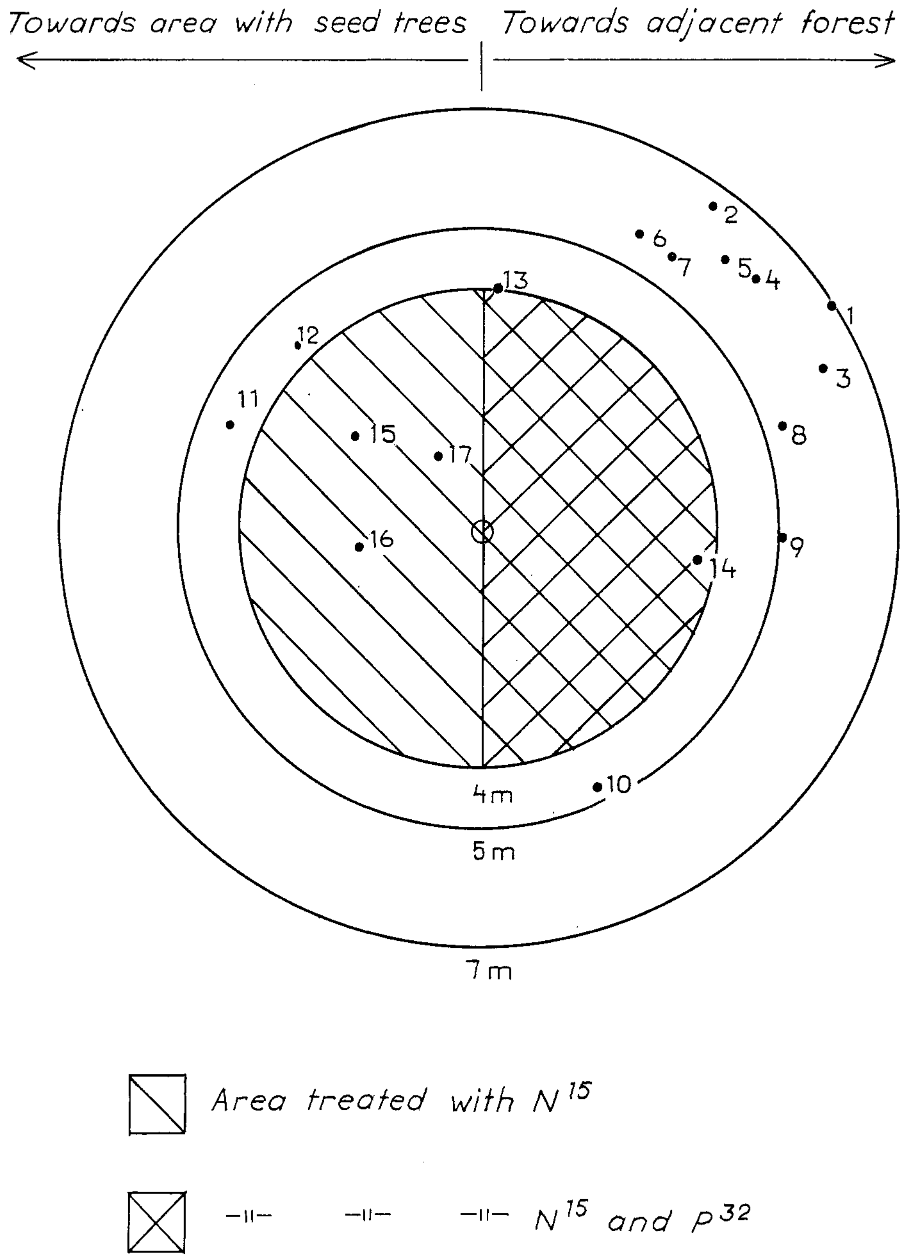

Fig. 3. Sketch of experimental plot. Points indicate positions of pine plants the roots of which were mapped. The ring in centre indicates position of the seed tree.

Table 3. Data about the horizontal root system by pine plants in a natural regeneration under a seed tree. The tree constituted the center of a circular plot (radius = 4 m) which was fertilized with $(N^{15}H_4)_2SO_4$ in July 1965. The N^{15}-excess in the 2-year needles by the plants closest to the tree is given.

Plant	Horizontal roots								
No	Height	Distance from seed tree	Total length	Percentual distribution					N^{15}-excess in 2-year needles, June 1969,
				in soil horizons			in plane		
							outside fertilized plot	inside fertilized plot	
	m	m	m	A_0—A_1	A_2	B			atomic-%
1	1.4	6.9	11.5	69	26	5	100	0	—
2	0.5	6.5	7.7	39	48	13	100	0	—
3	1.3	6.2	13.6	49	41	6	100	0	—
4	0.8	6.1	3.6	66	10	24	100	0	—
5	1.0	6.0	7.6	47	16	37	100	0	—
6	0.3	5.5	3.6	23	68	9	100	0	—
7	0.3	5.4	3.4	30	26	44	100	0	—
8	0.8	5.2	5.4	52	10	38	100	0	—
9	2.0	5.0	24.2	24	68	8	92	8	—
Seed tree, 5—7 m from stem:				3	76	21			
10	0.7	4.7	14.1	36	35	29	100	0	0.023
11	1.2	4.5	16.7	35	20	45	89	11	0.039
12	1.5	4.3	19.1	18	42	40	93	7	0.026
13	1.2	4.0	9.0	20	32	48	53	47	0.237
14	1.3	3.6	14.4	58	27	15	57	43	0.247
15	1.0	2.6	7.2	23	28	49	4	96	0.472
16	1.4	2.0	10.6	6	26	68	0	100	0.475
17	1.1	1.5	15.3	7	27	66	0	100	0.313

were as a rule only "sinkers", i.e. secondary roots growing vertically from the long laterals (*Sutton* 1969). These sinkers, of which there were on the average two for each m of long lateral, were relatively short and had as a rule their tips buried in the B-horizon layer or the upper layer of the C-horizon. Besides these vertically growing sinkers half the plants were equipped with tap-roots. Roots growing in an oblique vertical direction forming an angle of between 20° and 70° to the ground level were found only rarely (cf. *Köstler et al.* 1968, page 118).

The mapping revealed (Table 3, plants 1—9) that only one of the examined pine plants had a small part (8 %) of its root system inside the fertilized plot, although the plant stood as close as 1.0 m from the plot and in spite of the fact that the long laterals and the thicker secondary roots had a total length of more than 24 m. Even if this result as such constituted an acceptable explanation why such small quantities of fertilizer had been utilized by the plants in the immediate

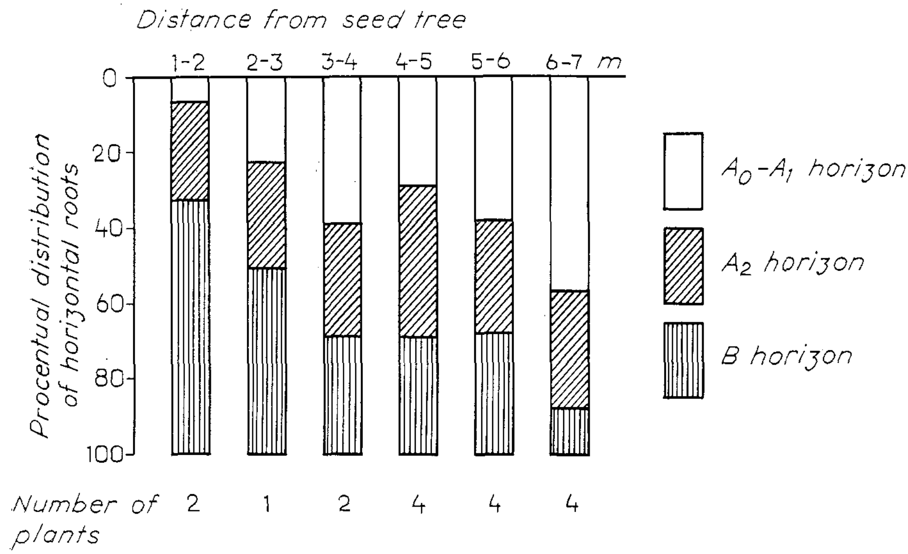

Fig. 4. Distribution in different soil layers of horizontal roots of pine plants in natural regeneration under a seed tree.

vicinity of the fertilized plot a supplementary root investigation was made involving four plants inside the plot (Nos. 14—17 in Fig. 3), a fifth plant on the boundary of the plot (No. 13) and three plants outside but within a distance of 0.7 m from it (Nos. 10—12). This root investigation was preceeded by an individual determination of the N^{15}-excess in total N in the two-year-old needles of the plants. As is shown in Table 3 the N^{15}-excess was entirely dependent on the spread of the horizontal root system inside and outside the plot. An analysis of the orientation of the roots on the horizontal plane showed that one third of the longitudinal growth had resulted in an approaching of the roots towards the centre of the experimental plot. The remaining two thirds had resulted in a removing from the centre. This was one of the reasons why none or only a small portion (max. 11 %) of the root systems of the three plants which stood 0.3—0.7 m from the plot could be found within the plot. No such root orientation trend could be discovered in the plants of the previous root investigation, possibly because the root density created by the seed tree in this region (5—7 m from the seed tree) was considerably less than in the one closer to the tree. It should be mentioned in this connection that the bulk of the root mass was concentrated within a radius of 7 m from the centre of the tree even if the seed tree in the concentric circle segment subject

Table 4. Localisation to different soil horizons of basal and apical part of long laterals and secondary roots (diam. > 1 mm) by pine plants — No. 1—17 in fig. 2 and table 3.

		Percentual number of roots ending in			
	horizon	A_0—A_1	A_2	B	Sum
Percentual number of roots originating in	A_0—A_1	17	10	10	37
	A_2	5	20	8	33
	B	2	2	26	30
	Sum	24	32	44	100

to investigation had one or two runners extending further than 7 m from the tree (cf. *Laitakari* 1927). Furthermore the root density was manifestly lower between the sixth and the seventh m than in the area 1 m nearer to the tree.

The root inventory further provided as a by-product some other worth-while information. There was for instance a clear indication that the proportional distribution of the horizontal root system in the different soil horizons was dependent on the plant's distance from the seed tree in the investigated area (Fig. 4). Thus in the immediate vicinity of the big tree the bulk of the plant's horizontal root system was found in the B-horizon layer, but as the distance increased the proportion in this soil horizon decreased with a corresponding increase in the humus layer. The proportion in the bleached horizon was on the whole unchanged in the area 7 m from the tree.

It was also remarkable how efficiently the big tree had claimed the bleached horizon in the investigated ring segment 5—7 m away from the tree (Table 3). In this area 3 % of the roots were located in the humus layer, no less than 76 % in the bleached horizon and 21 % in the B-horizon, while the corresponding values for the plants in the segment referred to was 44, 35 and 21 % respectively. The last mentioned figure is thus identical with that of the tree.

It has been mentioned before that the plant root growth was clearly oriented either in the horizontal or vertical direction and that only exceptionally it had an oblique downward direction. In an effort to throw some light on this the collected material was revised to the extent that the beginning and end of every mapped root (301 in all) were determined as to soil horizon. This process revealed that 63 % of the roots had their tips in the same horizon as they had started in while 9 % had sought their way to a higher horizon and 28 % to a lower one (Table 4). Even if thus the majority of the roots retained their original position in the vertical plane there was a tendency that in changing horizons a root would rather proceed downwards than upwards. This type of positional change developed gradually—never by leaps—provided there were no thick transversal roots, stones etc. blocking the way.

Summary and discussion

Though competition about nutrients and water is a fundamental feature in all plant communities its expressions are nowhere more conspicuous than on poor and dry soils. The observations made here a contribution towards a better understanding of some hitherto unexplained expressions of root competition on coarse sediment soils where it manifests itself distinctly and has been most exhaustively studied, in Sweden particularly by *Hesselman* and *Wretlind.*

One highly characteristic feature is the more or less perfectly circular "competition zones" in lichen pine forests around individual big trees which have been spared at the final felling of a stand as seed trees. In this investigation it has been found that the roots of an older tree completely dominate the upper soil layers inside an area 5—7 m from the stem. This means that the tree, thanks to the density of its root system in its nearest surroundings, dominates the layers where the nutritionally most important substance, nitrogen, occurs most abundantly in available form. This provides an explanation of the regularity of the competition zone. The reason why small pine plants—competition being most effective between individuals of the same species—are strongly reduced in growth in the competition zone appears to be that from here they have access only on a very limited scale to the nitrogen of the upper layers. They have to rely mainly on the lower layers where available nitrogen is more rare. This is in fact where their roots have chiefly been found to spread. Furthermore the roots of these plants are usually directed outwards from the tree. At a distance of 5—7 m from the stem where the density of roots of the older tree is much less than in the real competition zone the roots of the small pines have a better chance of occupying the upper soil layers with increased growth as a result. The competition from the tree is thus decreasing here.

The addition of nitrogen and phosphorus to the humus layer of the barren flat ground on which the experimental plot was situated revealed that there was hardly any lateral movement of the added nutrients at all. A very great difference was noted in the N^{15} and P^{32} content in needles from small plants in the fertilized area and in needles from plants even immediately outside the fertilized area.

From the practical point of view the experiment confirms the old experience that production and reproduction cannot occur simultaneously in an acceptable manner in nutrient-deficient—and especially nitrogen-deficient—areas. By allowing seed trees to remain too long or by sparing groups of trees in cutting operations on such sites one will provide opportunities for a root competition implying dominance by the larger or more favoured trees over simultaneously developing smaller trees which for some reason have been retarded and over new plants. This leads to the pattern of stratification and gap formation in stands of this type which has been a common feature in Swedish forestry for many years although it implies unsatisfactory utilization of the productive capacity of forest soil.

Through other experiments conducted over an extended period other expressions of root competition on nutrient-deficient sites have been studied—particularly in connection with very large clear-fellings and also with investigations of sparse residual stands or residual stands after dimension felling (cf. *Björkman* 1951). A comprehensive report on these experiments will be presented later.

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Sammanfattning

Den s. k. rotkonkurrensen på tallhedar har studerats genom tillsättning av ammoniumsulfat och kaliumfosfat märkt med N^{15} resp. P^{32} till en yta med ett fröträd *(Pinus silvestris)* i centrum. Trädet hade en utpräglad konkurrenszon under sig. Både *Calluna vulgaris* och *Vaccinium vitis idaea* visade sig vara minst lika effektiva näringsupptagare som tallplantorna i den naturliga föryngringen under fröträdet. Blott spår av tillsatt näring kunde återfinnas i vegetationen omedelbart utanför den gödslade ytan.

En rotanalys visade att de undertryckta tallplantorna inom konkurrenszonen hade sina rötter utbredda företrädesvis i djupare markskikt, medan det äldre trädet med sitt rotsystem behärskade överliggande skikt, där den för vegetationen tillgängliga näringen är störst. På 5—7 m avstånd från trädet, där konkurrensen från detta tenderade till att avta, befanns småplantorna äga ett betydligt ytligare rotsystem än närmare trädet.

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