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Effect of root aeration and form of nitrogen on photosynthetic productivity of Scots pine (*Pinus silvestris* L.)*

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Abstract

The response of 1-year old pine seedlings, grown in sand and water culture, to nutrition with nitrate or ammonium form of nitrogen, as well as to various aeration of the cultures was studied. Measurements of photosynthesis and respiration were carried out. Production of organic matter and its distribution to particular organs were determined.

Seedlings supplied with NH_4Cl were characterized by smaller contribution of root dry weight to the total weight of the plant. Poor aeration (heavy watering) of seedlings supplied with ammonium chloride caused a decrease in the rate of photosynthesis. Plants supplied with NH_4Cl did not show the typical decrease of photosynthetic rate at the end of the growing season.

INTRODUCTION

The problem of applicability of ammonium and nitrate salts as nitrogen sources was investigated for many years by numerous authors. It was not until the investigations of Prianishnikov (monography 1951) which showed that ammonium as well as nitrate form of nitrogen may have favourable effect on plant growth and development. However, the efficiency of uptaking one of the two nitrogen forms depends on many ecological factors. Soil aeration is one of these factors determining the response to nitrogen form. This fact was shown in earlier investigations (Shive, 1934; Arnon, 1937; Haas, 1937; Shive 1941; Gilbert and Shive, 1942; Gilbert and Shive, 1945; Gumiński, Czerwiński, Unger and Skrabka, 1957; Stabrowska, 1959; Poskuta, 1961; Stabrowska and Dziewulska, 1970; and Stabrowska and Paściak 1971). The above mentioned authors investigated the

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effect of root aeration on the uptake of nitrate and ammonium ions by crop plants. On the other hand there are no works which would sufficiently elucidate this problem as far as forest trees are concerned. Species grown in forestry are adapted to grow on poor and rather acid soils.

Forest soils are differentiated in water content and, as a result of this, also in their aeration. Hence, the response of forest species to different nitrogen nutrition under various conditions of soil aeration may be not quite the same as that of the formely investigated crop plants. Therefore, it seemed purposeful to study these relations for Scots pine (*Pinus silvestris* L.), one of the most important forest species.

MATERIAL AND METHODS

Part of investigations was carried out in sand culture with continuous inflow of the nutrient solution from the bottom (Fig. 1). The facility consists of several pots connected by plastic or rubber tubes to the bottle containing nutrient solution. There is sand in the pots, particles of which are 1.2—1.5 mm of diameter; in such sand capillary ascending is negligible and water level is the same as in the bottle. Differentiated aeration was achieved by using various levels of the nutrient solution in pots. Thus changes in the aeration of root environment were corelated with decreasing water content in the sand, what very well, imitated the situation under natural conditions. Investigations on the effect of one of the two factors separately seemed to be neither possible nor purposeful. In order to emphasize this close connection between aeration and soil water content, the

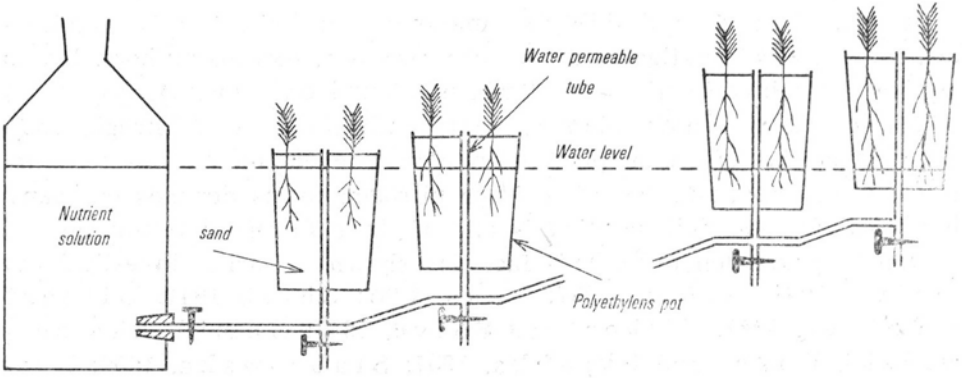

fig. 1

Fig. 1. Scheme of the sand culture with continuous inflow of the nutrient solution from the bottom

expressions: "decreasing aeration", and "increasing soil water content" were used in the whole paper interchangeably.

The experiments were carried out on pine seedlings (*Pinus silvestris* L.) during the first growing season. In the first experiment pots were placed on six various levels; the amount of nutrient solution was equivalent to 35, 50, 60, 75, and 100% of full water capacity. In the second experiment only three levels of aeration (watering) were used i.e. 30, 60, and 100% of full capacity.

The nutrient solution was prepared according to Ingestad (1962/63) for pine water culture. The control variant was supplied with basic nutrient solution containing nitrogen in the form of ammonium nitrate. The other variants were supplied with solutions containing either sodium nitrate or ammonium chloride, instead of ammonium nitrate, with equivalent amounts of nitrogen. The pH of each variant solution was adjusted to the value of about 5.0 using HCl. It was done, several times during the whole growing season.

The sand culture experiments were carried out in a greenhouse. Plants were kept outside during the days and were moved under the glass for the nights and during rainfalls.

Seeds were sown at the end of April. The amount of seedlings was reduced to 30 per pot, after germination. Plants were harvested at the beginning of November.

Measurements of photosynthesis and respiration rate were carried out on 3, 4, and 5 months old seedlings, with the use of manometric method. These measurements were carried out on detached needles in manometric vessels especially designed for this type of assimilatory organs. (Łotocki, Żelawski 1973). The concentration of carbon dioxide in gaseous phase was maintained at the level of 0.55 V % by use of carbonate buffer. Temperature, during the measurements, was maintained at 25°C, and light intensity was 20 Klx.

First experiment consisted of 18 variants — three types of nutrition, six levels of aeration (watering) whereas the second experiment consisted of 9 variants — three types of nutrition, three levels of aeration (watering). Final harvest consisted of 90 plants from each variant in first experiment and 170 plants from each variant in the second one. Dry weight of particular organs was determined at 105°C.

In the water culture experiment 1 l glass containers were used. Various root aeration was achieved by using different levels of the nutrient solutions. The containers were filled with solution to 1/2, 3/4 or full volume, in the well, moderately, and poorly aerated variant, respectively. There were 6 plants grown in each container. The nutrient solution was the same as in sand culture. It was renewed once a week. The pH value changed during such period not more than from 4.5 to 5.5.

The water culture experiment was carried out under laboratory conditions, with natural light from west exposed window and additional illumination added from mercury lamps with luminophor (LRFR — 400 W). Light intensity from these lamps was 8 Klx. Temperatures ranged between 10 and 26°C during the night and day periods, respectively. Seeds were sown at the begining of May. Plants were harvested at the end of November. There were 36 - 48 plants of each experimental variant sampled during the final harvest. There were also 9 variants in this experiment — three forms of nitrogen nutrition, and three levels of aeration (water content).

The variance analysis was carried out and t_μ was determined at $\alpha = 0.05$.

RESULTS

1. The main experiment in sand culture

Photosynthesis rates calculated per g of needles dry weight differed among the experimental variants particulary when their seasonal trends were considered (Fig. 2). The typical for conifers decrease of the photosynthesis rate towards the end of the growing season was clearly pronounced only in plants which received nitrogen in the form of natrium nitrate. The other two variants with ammonium nitrate or ammonium chloride showed either the tendency to increase slighty the rate of photosynthesis or at least to maintain it at the constant level. The highest rates were in the plants which were moderately watered (aerated) except the variant with ammonium chloride where the maximum values were reached at the lowest water level (the best aeration). In all variants of nutrition plants growing at

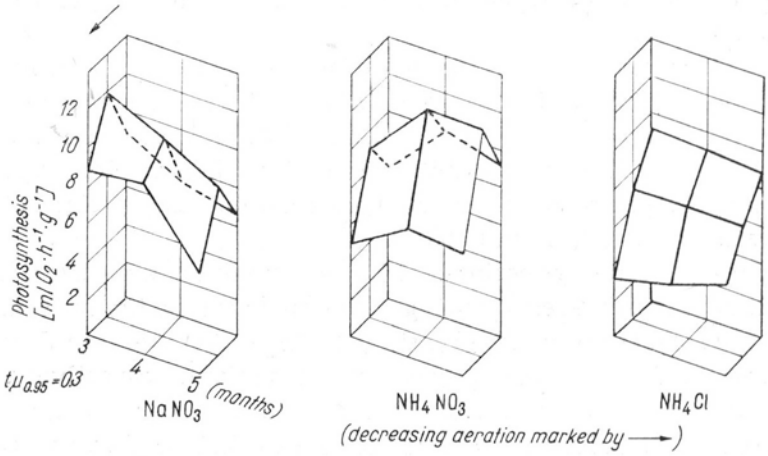

Fig. 2. Seasonal course of photosynthesis

excessive watering (poor aeration) exhibited the lowest rates of photosynthesis; the agove mentioned opposite seasonal trends in plants supplied with nitrate or ammonium forms of nutrition were best pronounced in these, standing in water, seedlings.

Respiration rates (Fig. 3) were less differentiated among the experimental variants but the pattern was very much the same as for photosynthesis rate: the clearly pronounced trend to decrease towards the end of the growing season in plants supplied with natrium nitrate form of nitrogen and more constant or even increasing values in the two other variants of nutrition. Most differentiated values of respiration were in plants supplied with ammonium chloride: the poorly aerated plants exhibiting the lowest and well aerated the highest rates of respiration, every period of examination.

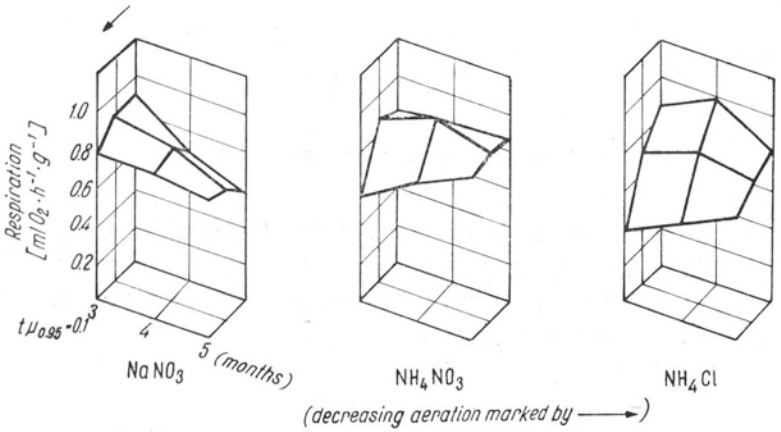

Fig. 3. Seasonal course of respiration

In plants harvested at the end of the growing season, after the apical buds had been formed, the highest dry matter accumulation were found in the variant supplied with nitrogen in a form of ammonium nitrate at the medium watering and aeration (Fig. 4). The lowest values was exhibited by plants receiving nitrogen in the form of ammonium chloride. In all nutrition variants dry matter decreased considerably towards the wettest (poorly aerated) experimental conditions. This trend was most distinctly pronounced in ammonium chloride series where maximum values, comparable with the control plants were only obtained under conditions of best aeration.

Not only the total growth but also the distribution of organic substance among particular organs of plants were highly affected both by nitrogen nutrition and soil aeration conditions (Fig. 5). A regular increase of needles and stems portion in the total dry weight of a plant and relative re-

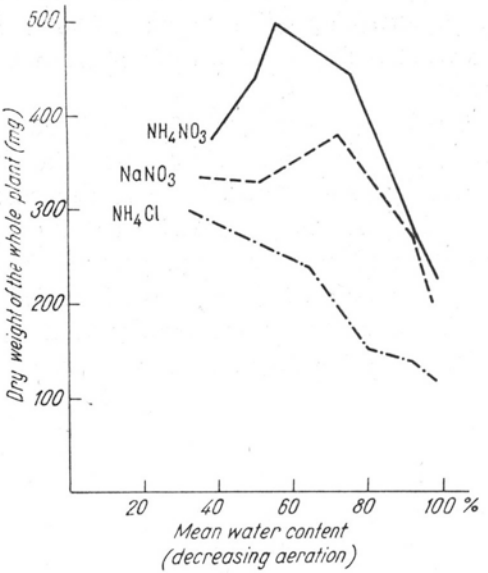

Fig. 4. Changes in dry matter of seedlings

duction of the root system is observed from favourable to stress conditions of aeration. This phenomenon takes place in all three variants of nutrition being similar at natrium nitrate and ammonium nitrate but different at ammonium chloride supply.

2. The verifying experiment in sand culture

The obtained results for photosynthesis and respiration rate were similar as in the previous experiment (Fig. 6 and 7). The percent contribution of particular organs dry matter is also similar (Fig. 8). The highest dry matter accumulation, at the end of the growing season, was found again

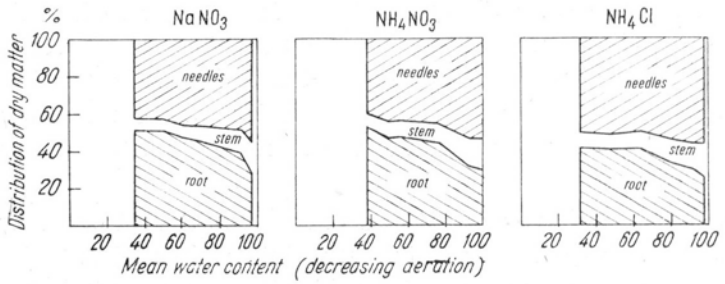

Fig. 5. Percent contribution of particular organs to the total dry weight of the plant

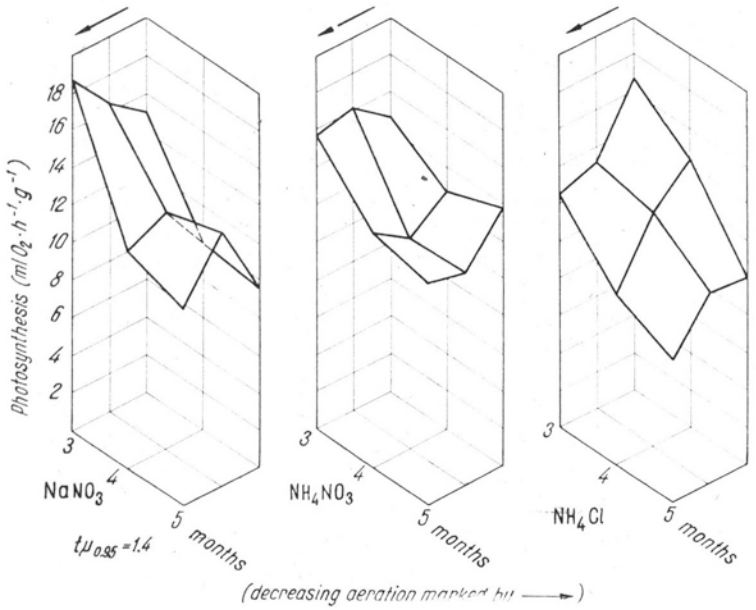

Fig. 6. Seasonal course of photosynthesis

in seedlings supplied with ammonium nitrate and grown under medium aeration (watering). However the distribution of dry matter in plants supplied with sodium nitrate or amonium chloride is somewhat different than in the main experiment. Seedlings supplied with ammonium chloride grown on sand under good aeration conditions (poor watering) showed higher

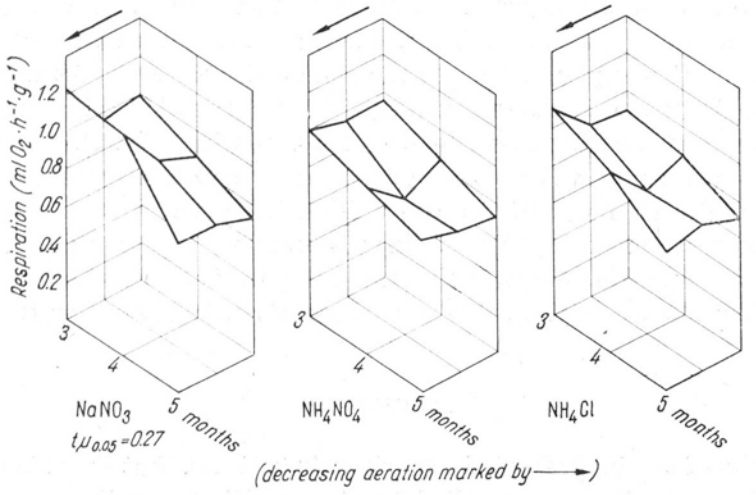

Fig. 7. Seasonal course of respiration

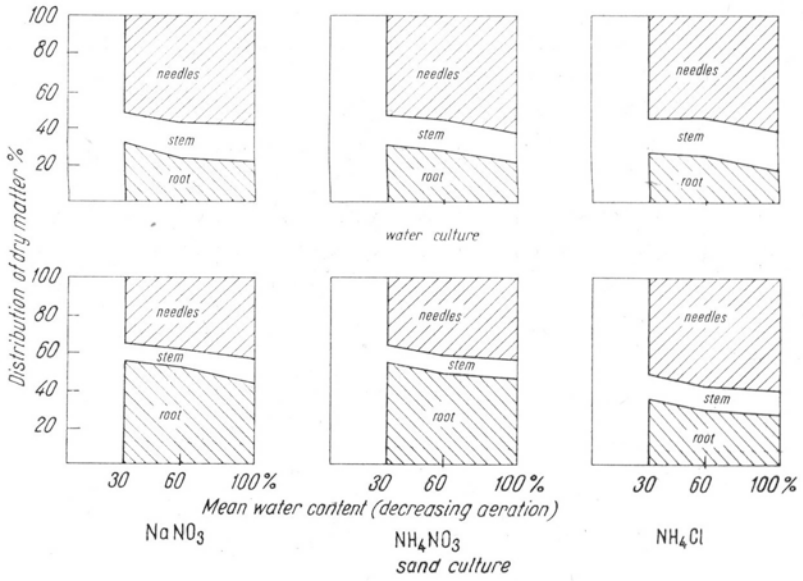

Fig. 8. Percent contribution of particular organs to the total dry weight of the plant

dry matter accumulation than those supplied with sodium nitrate, while seedlings grown under poor aeration conditions (heavy watering) showed a reversed response (Fig. 9).

3. The supplementary experiment in water culture

Dry matter of plants grown in water culture is not so strongly differentiated between particular experimental variants as is that in sand culture. The final dry matter of seedlings from water culture is generally 50% lower than that of seedlings grown in sand culture with continuous nutrient solution supply, although the age of plants at harvest was the same. Like in the previous experiments, plants supplied with ammonium nitrate showed the highest dry matter accumulation (Fig. 9). Whereas differences between plants grown under various aeration conditions (levels of watering) were not statistically significant. Percent contribution of root dry matter in total plant dry weight is smaller in plants supplied with ammonium chloride comparing to those supplied with sodium nitrate or ammonium nitrate (Fig. 8), like in the experiments in sand culture.

DISCUSSION

Results of all the presented experiments indicate, that there is an effect of the form of nitrogen, supplied to pine seedlings, on the formation of characteristic proportions between particular organs. Percent contribution

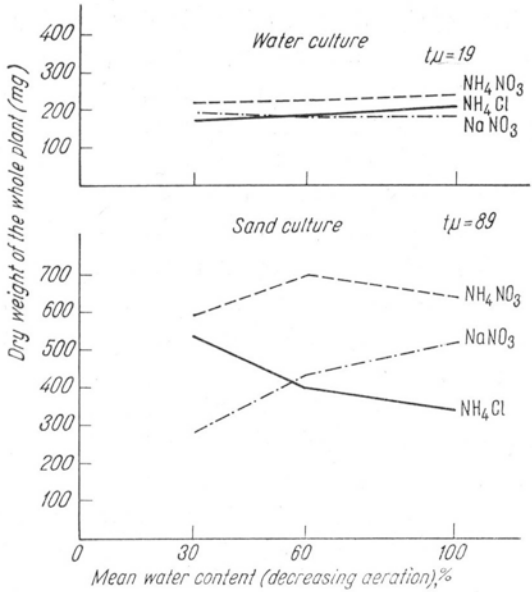

Fig. 9. Changes in dry matter of seedlings

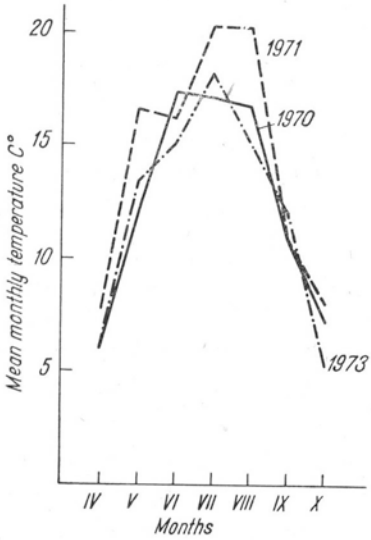

Fig. 10. Mean monthly temperatures

of root dry matter in the total dry weight of plants supplied with ammonium chloride is smaller than that of plants supplied with sodium nitrate or ammonium nitrate. This trend is found both in plants grown in sand and water cultures (Fig. 5 and 8). Earlier investigations, in which aeration (wa-

tering) was not differentiated showed a similar results (Łotocki and Żelawski, 1973). Other authors (Leyton, 1952 on spruce, Van Den Driessche 1971 on spruce and douglas fir, Christersson 1972 on pine, Zajączkowska, 1973 on pine) have also found that percent contribution of root dry weight in total plant weight is smaller on ammonium from than on nitrate from of nutrition.

Lehr (1942) found in his investigations on beet fertilization that higher sodium doses changed the proportions of organ dry weight in favour of the roots. Similar situation could have occured in our experiments: in the nitrate variant, where the nutrient solution contained 82 ppm of sodium more than in the other variants, the percent contribution of root weight in the total plants weight was the highest. However, on the other hand the highest contribution of roots in the total dry weight of seedlings supplied with sodium nitrate could be caused by the action of NO_3 and not by Na ions. Such an interpretation is supported by the results of Van Den Driessche (1971). He used nitrate nitrogen in the form of $Ca(NO_3)_2$ in his investigations on spruce and douglas fir and he observed that plants supplied with nitrate nitrogen were characterized by higher contribution of root weight than those supplied with ammonium or ammonium-nitrate form of nitrogen.

The root aeration (watering) factor influences, considerably, the photosynthetic rate of plants supplied with ammonium chloride (Fig. 2 and 6). Photosynthetic rate of these plants decreases markedly along with the decreasing amount of air (increasing amount of water) in the sand. Whereas the plants supplied with sodium nitrate and ammonium nitrate do not show such tendency. One can assume that the decrease in photosynthetic rate of plants supplied with ammonium chloride under conditions of poor aeration (heavy watering) is caused by the relatively weakest root formation of plants supplied with NH_4Cl. Probably the weakly developing roots of these plants can accumulate less photosynthates from needles than do the better developing roots of plants supplied with nitrates. If so, accumulation of photsynthates could take place in the needles of plants supplied with ammonium chloride, which could explain the decrease of photosynthetic rate, of these plants, caused by surplus photosynthetic product. However; such hypothesis would require investigation.

There was a strong decrease in photosynthetic rate towards the end of the growing season, in plants supplied with $NaNO_3$ (fig. 2 and 6). This tendency appeared both in the variants with good and poor aeration of roots. Plants from other nutritional variants showed the decreasing tendeny in photosynthesis towards the end of the growing season at a much smaller extent or none at all. A similar result was found in previous experiments (Łotocki, Żelawski, 1973). It seems that closer investigation on the

biochemical aspect may help explaining the causes of this decreasing tendency found in plants supplied with ammonium form of nitrogen.

In the present study the highest dry matter was obtained by plants supplied with ammonium nitrate (Fig. 4 and 9). The results of other authors working on different plants indicate that there exist a relation between the uptake of ammonium or nitrate ions by a plant and its stage of development. Jones and Skinner (1926), Naftel (1931), Sessions and Shive (1933), Chandler (1952), Durzan and Steward (1967), and Zajączkowska (1973), among others, have found that plants at younger growth stages utilize nitrogen mainly in the ammonium form, while older plants utilize nitrate nitrogen. Our results support this finding. Pine seedlings supplied with ammonium nitrate during the whole growing period could utilize this form of nitrogen which was assimilated better at a certain growth stage and as a result of it they reached the highest dry weight at the end of the growing season. Whereas plants supplied with sodium nitrate met apparent shortage of nitrogen for some time after germination. The final dry matter weight of these plants was lower than that of plants supplied with ammonium nitrate. Plants supplied with ammonium chloride met the apparent shortage of nitrogen at later growth stages i. e. when nitrate nitrogen was assimilated better. Again as a results of it they produced lower dry matter weight than did plants supplied with ammonium nitrate. Another factor limiting dry matter production of plants supplied with ammonium chloride may be the higher sensitivity to drought connected with relatively weaker growth of the root system of these plants. Such interpretation is supported by results of the first experiment carried out in 1971. The growing season of 1971 was warmer than those of other years of our experiments, thus favouring higher transpiration (Fig. 10). Comparing dry matter weight of seedlings supplied with ammonium chloride from both experiments on sand culture as well as from previous experiment (Łotocki and Żelawski, 1973) one can find that it was lowest in 1971. Under conditions favourable for higher transpiration the weaker developed root system of these plants was not able to supply the needles with sufficient amounts of water. Such situation lead to decreased gas exchange which then became the cause of decreased dry matter production.

Considering the effect of aeration (watering) of roots on the dry matter production by plants one can state that under conditions of poor aeration (heavy watering) of the sand seedlings supplied with $NaNO_3$ grow better than those supplied with NH_4Cl. May be, nitrates costitute an additional source of oxygen for plants grown on sand with small air content while ammonium salts do not give such possibility. Compensation of oxygen shortage, in root environment, by nitrates was found in earlier investigations on crop plants (Shive, 1934; Arnon, 1937; Haas, 1937; Shive, 1941; Gilbert and Shive, 1942, 1945; Gumiński et all., 1957; Posku-

t a, 1961). However, one should also consider the fact that chlorine from ammonium chloride may have a toxic effect on plants causing weaker growth of plants supplied with NH_4Cl (the nutrient solution in the ammonium variant contained 127 ppm of chlorine more than in other variants). Seedlings supplied with sodium nitrate could grow better not only because of additional source of oxygen, but also because they were not under the influence of toxic chlorine. However, if such an assumption is made one should expect the inhibiting effect of chlorine to occur regardless of the sand aeration conditions. Whereas, the second experiment shoved that, under condition of good aeration of the sand, seedlings supplied with ammonium chloride grew better than those supplied with sodium nitrate. While plants grown under conditions of poor aeration grew better when supplied with $NaNO_3$ than those with NH_4Cl. Considering these facts, it seems the hypothesis that sodium nitrate compensates the shortage of oxygen in poorly aerated sand to be more probable than the one relating to the toxic effect of chlorine.

Comparing the results obtained on pine grown in sand culture with continuous inflow of the nutrient solution from the bottom and those on pine grown on water culture it was found that seedlings grown in sand culture accumulated considerably more dry matter than did the seedlings grown in water culture (Fig. 9). Another marked fact was the considerably greater differentiation in seedling dry matter from sand culture than from water culture resulting from the application of various nitrogen forms and different levels of aeration (watering) of the roots. Finally the third item differentiating plants grown on sand culture from those grown on water culture was the proportion of organs. Seedlings grown on water culture developed a relatively smaller root than did seedlings grown in sand culture under similar conditions of nutrition and aeration. In spite of these differences it was found that both plants from sand and water culture showed similar tendency in dry matter production as well as in its distribution among particular organs. However, these tendencies were less marked in plants grown on water culture — resulting, most probably, from generally weaker growth of plants on water culture. It seems that the weaker growth of seedlings in water culture was caused by conditions too much different from natural.

The above considerations may allow to state that the proposed sand culture with the continuous inflow of nutrient solution from the bottom is more useful, for investigations on the effect of nutrition and aeration (watering) on plant growth, than the water culture. Such sand culture creates conditions, for plants, closer to natural, so the obtained results may give base to more practical conclusions. The presented results may suggest that, on poorly aerated soils, supplying pine with ammonium salts should avoided. However, such a conclusion requires support from field experiments.

CONCLUSIONS

1. Supplying Scots pine (*Pinus silvestris* L.), grown in sand culture, with ammonium chloride under conditions of poor aeration (heavy watering) of the roots, causes a decrease in percent proportion of root dry weight to that of the whole plant.

2. Poor aeration (heavy watering) of Scots pine roots supplied with ammonium chloride on sand culture caused a decrease in the rate of photosynthesis. Plants supplied with ammonium nitrate or sodium nitrate do not show any effect of aeration on their rate of photosynthesis.

3. Supplying Scots pine, grown in sand culture, with ammonium chloride caused the absence of the typical decrease in photosynthetic rate at the later stages of the growing season.

4. Under conditions of poor aeration (heavy watering) of Scots pine roots, grown in sand culture, nitrates may play the role of an additional oxygen source.

5. One may expect that supplying Scots pine with ammonium salts on poorly aerated soils can be unfavourable.

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Wpływ aeracji podłoża i formy żywienia azotowego na produktywność fotosyntezy siewek sosny zwyczajnej (Pinus silvestris L.).

Streszczenie

Przeprowadzono badania reakcji 1-rocznych siewek sosny zwyczanej, wyhodowanych w kulturze piaskowej i wodnej, na nawożenie azotem w formie azotanowej i amonowej, w różnych warunkach przewietrzania podłoża. Wykonano pomiary fotosyntezy, oddychania, określono produkcję substancji organicznej oraz jej dystrybucję do poszczególnych organów rośliny.

Siewki nawożone NH_4Cl charakteryzowały się zmniejszonym udziałem suchej masy korzenia w masie całej rośliny. Słaba aeracja (silne nawodnienie) korzeni siewek nawożonych chlorkiem amonu ogranicza intensywność fotosyntezy. U roślin nawożonych NH_4Cl stwierdzono brak typowego obniżania się intensywności fotosyntezy pod koniec okresu wegetacyjnego.