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The effect of nitrogen and phosphorus on auxin and cytokinin production by mycorrhizal fungi*

INTRODUCTION

Mycorrhiza is a symbiotic association between fungal hyphae and roots of higher plants and is a common phenomenon in the plant kingdom. Up to 80 per cent of plants are believed to be in a symbiotic relationship with certain species of fungi.

Based on the interrelationship that exists between root cells and fungi, forest tree mycorrhizae are classified into two main types: ectomycorrhiza and endomycorrhiza.

Compared with the endomycorrhiza, the ectotrophic type has a much more limited distribution although among forest trees it is widespread and even common. Ectomycorrhiza is most characteristic for the families *Pinaceae, Fagaceae* and *Betulaceae*. Fungi which form ectomycorrhizae belong mainly to the *Basidiomycetes* and rarely to *Ascomycetes* and *Fungi Imperfecti*.

Physiologically, mycorrhizae represent a kind of symbiosis resulting in an increased uptake of nutrients from the soil, particularly in infertile ones. Hatch (1937) demonstrated that mycorrhizal white pine seedlings contained 86% more nitrogen, 230% more phosphorus and 75% more potassium than plants without mycorrhizae. Mycorrhizal fungi increase solubility of minerals and improve the uptake of nutrients for the host plant. Without mycorrhizae most plants, including important forest trees, would not survive in natural soil habitas, Therefore mycorrhizal fungi are known to influence the resistance of trees to frost, drought and high temperatures (Hatch 1937, Cromer 1935, Goss 1960, Lobanov 1960, Harley 1969, Marx and Bryan 1971, Theodorou and Bowen 1971, Žerdcov and Petrenko 1974, Theodorou 1978). Mycorrhizal roots are also less sensitive to such common pollutants as O_3, SO_2 and CH_4 (Carney et al. 1978, Sherwood and Klarman 1830).

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Mycorrhizal seedlings appear to be better adapted for growth on ecologically degradated soils after coal and copper strip mines (Marx and Artman 1979, Berry and Marx 1978). Zak (1964) suggested that ectotrophic mycorrhizal roots may be less susceptible than nonmycorrhizal ones to infection by root pathogens by: (i) providing a mechanical barrier to the pathogen in the form of the fungus mantle, (ii) secreting antibiotics which may inhibit or kill potential pathogens.

AUXIN AND CYTOKININ PRODUCTION BY MYCORRHIZAL FUNGI

Auxins. Nielsen (1928, 1932) first showed the presence of auxins in fungal cultures. Extracts of sporophores of *Boletus edulis*, a mycorrhizal fungus, as well as the media in which *Rhizopus suinus* and *Absidia ramosa* had grown, showed a positive *Avena* curvature test for auxin. The hormone in *R. suinus* was shown to be indoleacetic acid (IAA), (Thimann 1935). Since that time paper chromatography and the *Avena* coleoptile elongation or curvature tests have been used to demonstrate that liberation of auxins is a common feature among microorganisms. The production and importance of auxin in fungi have been reviewed by Gruen (1959). Moser (1959) tested 23 species of ectomycorrhizae-forming fungi for auxin production. He found that the majority of the fungi tested, produced IAA alone or together with IPA and/or IBA after adding tryptophan (2.041 g/l) to the nutrient solution. Ulrich (1960) has shown production of auxin by mycorrhizal species of *Boletus* (*Suillus*) and *Amanita* in the presence of tryptophan in the medium (1,0 to 30 mg/l), and also by some species of *Boletus* without this precursor. Moser (1959) showed production of auxin by mycorrhizal fungi in tryptophan deficient media but with a supplement of dl-alanine, l-asparagine and indole. Horak (1964) demonstrated the ability of fungi from genus *Phlegmacium* to metabolize IAA from anthranilic acid. Accorrding to him anthranilic acid is a basis for indole synthesis and the main metabolite in a pathway converting indole through tryptophan to IAA in the tested fungi. Gogala (1971) demonstrated the presence of auxin in the ectomycorrhizal fungus *Boletus edulis* var. *pinicolus*. Turowska et al. (1971) has also shown the presence of several indole compounds in fruit bodies of some mycorrhizal fungi. Tomaszewski (1974) demonstrated the production of auxin from tryptophan by mycorrhizal symbionts of Scots pine and also the ability of some fungi to synthesize auxin on a simple nutrient medium without tryptophan. Strzelczyk et al. (1977) obtained positive results following tests for auxin activity, with some mycorrhizal fungi isolated from mycorrhizae of Scots pine. Isolated fungi produced auxin without tryptophan but with the supplement of such precursors of auxin as anthranilic acid, indole or indole and serine.

Cytokinins. Documentary evidence on the occurrence of cytokinin in cultures of mycorrhizal fungi has been obtained later than for auxins. First Miller (1967) demonstrated that mycorrhizal fungi produced and liberated extracellular cytokinins. Using aseptic soybean tissue cultures, known to grow only in the presence of cytokinin, he obtained growth stimulation when pieces of these tissues were placed on agar remote from the mycelial inoculum of *Rhizopogon roseolus*. From a fungus culture solution Miller (1967) isolated in a crystaline form about 1 mg of the most abundant cytokinins — zeatin and the ribonucleotide of zeatin. Also a third cytokinin, probably zeatin ribonucleozide was present. Culturing cytokinin-requiring soybean callus tissue alongside the fungus or with the filtrate from the fungal culture on a medium lacking a cytokinin, Craft (1973) and Craft and Miller (1974) have demonstrated production of cytokinin by several mycorrhizal fungi, among them *Rhizopogon ochraceorubens* and *Suillus punctipes*. These cytokinins were identified as trans-zeatin and trans-ribosyl-zeatin. Employing similar methods as above Tomaszewski (1974) observed the production of cytokinins by several mycorrhizal symbionts of Scots pine. Miura and Miller (1969), Miura and Hall (1973) have demonstrated that N^6-/Δ^2isopentyl/adenosine is a key compound in the biosynthetic pathway of trans-ribosylzeatin in *Rhizopogon roseolus*. Laloue and Hall (1973) have reported that *R. roseolus* secretes into its culture medium the transfer RNA component. This compound was proposed to be the archetype of ureidopurines exhibiting cytokinin activity. Gogala (1971) reported that fruiting bodies, mycelium and also culture medium of *Boletus edulis* var. *pinicolus* contained one cytokinin, probably zeatin. Kampert and Strzelczyk (1978) found that eight out of nine fungi isolated from mycorrhizae of pine (*Pinus silvestris* L.) produced cytokinins. Most of the fungi synthesized compounds with Rf values identical or similar to zeatin, zeatin riboside or isopentyladenosine. Rudawska (1980) found variable amounts of cytokinins production by mycorrhizal fungal cultures supplemented with the root-powder from pine seedlings growing at different light intensities.

INFLUENCE OF MINERAL NUTRITION ON MYCORRHIZAE

The formation of mycorrhizae depends to a large extent on the environmental conditions which determine the physiological state of both symbionts, i.e. the fungus and the higher plant. Among the most important factors affecting the formation of mycorrhizae are the nutrition conditions in the soil.

Generally, mineral fertilizers do not facilitate mycorrhiza formation in forest trees. After Stahl postulated in 1900 that forest trees have

abundant mycorrhizae only in nutritionally poor soils, the effect of inorganic fertilizers on mycorrhizae formation was studied intensively. That high concentrations of mineral compounds in the soil arrest mycorrhizae formation and cause well-established mycorrhizal roots to become non-mycorrhizal has been reported by a number of workers (Melin 1923, Hatch 1937, Mc Comb 1943, Björkman 1942, Harley 1969). Similar findings were reported by Soviet researchers and described by Shemakhanova (1967).

Björkman (1942) observed that when he applied ammonium or nitrate to a forest soil, plant growth increased and the frequency of mycorrhiza diminished. Björkman concluded that N and P did not act in the soil directly but rather influenced the carbohydrate metabolism of the root. According to his carbohydrate theory the surplus of soluble sugars in the roots is a decisive factor for mycorrhiza formation. A high sufficiency of available nutrients, particularly nitrogen, stimulates protein synthesis in plant and thereby lowers the amount of available, soluble carbohydrates, which are required by the mycorrhizal fungi in the root. This hampers the development of fungi in the root. Handley and Sanders (1962) re-examined the investigations of Björkman and disagree with his suggestion. In their opinion, the increased concentration of easily soluble reducing substances occurring in roots of seedlings with prevalent mycorrhizae need not to be the cause but the result of the established symbiotic association due to an accumulation of reducing substances in the fungal mycelium. Similar findings were reported also by Meyer (1962, 1965) in an investigation with *Fagus silvatica* and by Schweers and Meyer (1970) in experiments with Scots pine seedlings. Lister et al. (1968) also grew seedlings in nitrogen and phosphorus regimes as were used by Björkman in 1942. The root systems were later removed and the content of glucose, fructose, sucrose was analysed. The highest amounts of radioactive glucose and fructose were detected in plants grown on moderate to very high phosphorus and nitrogen, where mycorrhizae formation was completely inhibited.

In rebuttal to his critics, Björkman (1970) again presented data supporting his carbohydrate hypothesis. Analyzing the level of carbohydrates in roots of Scots pine seedlings inoculated with mycorrhizal fungi and fertilized with N and P he found lower amounts of reducing sugars in roots treated with N and symbiosis with *Boletus subtomentosus* had little or no effect on the content of reducing sugars in mycorrhizal roots.

As we can see from the literature review presented above the mechanism of influence of mineral nutrition on mycorrhiza formation is not fully explained and requires much more detailed investigation. This problem seems to be of importance not only from a theoretical point of

view but also beacuse mineral fertilization has lately become a widespread practice both in nurseries and in old forests (Baule and Fricker 1973). There appears therefore many reports about unfavourable effects of fertilizers on mycorrhizae formation. Menge et al. (1977) showed it in study with *Pinus taeda*, Marais and Kotze (1978) with *Pinus patula*, Tetrault at al. (1978) on fertilized with urea of *Abies balsamea* stands. Ritter and Tölle (1978) demonstrated that in treated by nitrogen 35 and 110 year old stands of Scots pine significant reduction of mycorrhiza frequency and sporophore production were observed. Also Pachlewski et al. (1978) provides evidence that in laboratory conditions doses of nitrogen fertilizers used in forest nurseries fertilization are too high for the optimal growth of pure cultures of mycorrhizal fungi.

The studies of several investigators (Moser 1959, Slankis 1971, Tomaszewski and Wojciechowska 1974) try to explain the unfavourable effects of high mineral nutrition on mycorrhizae on the basis of several changes in growth substances production by mycorrhizal fungi in such nutritional condition. Of great interest are Moser's (1959) findings on the inhibition of auxin production by ectomycorrhizal fungi with increased dosages of inorganic or organic nitrogen. Tomaszewski and Wojciechowska (1974) have reported that isolates of *Suillus bovinus* produced IAA abundantly only at low doses of NH_4NO_3 and auxin production was totally inhibited at high doses of N, despite the luxurious growth of the mycelium.

The purpose of this study was to continue investigation which try to explain the effect of mineral nutrition on mycorhizae in connection with hormone production by mycorrhizal fungi. The effect of different levels of nitrogen and phosphorus on auxin and cytokinin production in pure culture of mycorrhizal fungi was studied.

MATERIAL

Cultures of mycorrhizal fungi. The following fungi were used in my studies: *Suillus bovinus*, *S. luteus*, *Amanita muscaria*, *Rhizopogon luteolus*. The fungi were grown in a sterilized liquid medium (basic medium) of composition described earlier (Rudawska 1980). A Roux bottle received 5 mycelium pieces (5 cm^2 totally) cut out from the mycelial stock culture on agar. Experiments were performed in darkness, at a temp. 23°C for a period of 30 days. The basic medium was supplemented depending on treatment with different amounts of ammonium tartrate, potassium nitrate or potassium phosphate monobasic in concentrations of N and P corresponding to 30, 300, or 3000 mg N or P per liter. Each variant of experiment was repeated 3 - 5 times. After the

termination of cultures the mycelium from the Roux bottles was filtered and dry weight has been determined. In the culture filtrate from each bottle the content of auxin and cytokinin was assayed.

METHODS

Auxin assay. Auxin was estimated in the culture filtrate using cold ether extraction according to Larsen (1955) and assayed in the standard *Avena* coleoptile curvature test (Larsen 1955).

Cytokinin assay. Cytokinin was extracted according to the modified (Friedrich et al. 1972) method of Biddington and Thomas (1973) described by Rudawska (1980). Miura and Miller (1969) test was used in order to determine cytokinin production by the fungi studied, employing the soybean callus tissue assay.

RESULTS

Ammonium nitrogen. The ability of tested fungi to utilize ammonium nitrogen was tested by growing the species on a basic solution with different doses of ammonium tartrate. The experiments showed that

Table 1

Mycelium dry weight of pure cultures of mycorrhizal fungi on different levels of ammonium nitrogen after 30 days of incubation in darkness at 23°C (The levels of N as mg/1 of the ammonium tartrate)

Levels of NH_4 nitrogen	Species			
	S. bovinus	*S. luteus*	*R. luteolus*	*A. muscaria*
0 N	79* a**	109 a	136 a	157 a
30 N	199 b	407 a	410 ab	348 ab
300 N	243 b	810 b	671 b	513 b
3000 N	75 a	323 a	227 a	510 bb

* mg of dry weight of mycelium per one culture (one Roux bottle)

** values followed by the same letter are not significantly different at $p=0.05$

Table 2

Mycelium dry weight of pure cultures of mycorrhizal fungi on different levels of nitrate nitrogen after 30 days of incubation in darkness at 23°C (The levels of N as mg/l of the potassium nitrate)

Levels of NO_3 nitrogen	Species			*A. muscaria*
	S. bovinus	*S. luteus*	*R. luteolus*	
0 N	101* a**	129 a	157 a	144 a
30 N	92 a	106 bd	267 bc	162 a
300 N	175 bc	116 bc	207 ac	124 ab
3000 N	126 ac	94 d	180 a	84 bc

* mg of dry weight of mycelium per one culture (one Roux bottle)

** values followed by the same letter are not significantly different at $p=0.05$

Table 3

Influence of different levels of ammonium nitrogen on the release of auxin by pure cultures of mycorrhizal fungi (The levels of N as mg/l of the ammonium tartrate). Filtrate from one culture (1 Roux bottle) was extracted after method of Larsen (1955) and assayed in the standard *Avena* coleoptile curvature test

Levels of NH_4 nitrogen	*Suillus bovinus*		*Suillus luteus*		*Rhizopogon luteolus*	
	ng/culture	µg/g dry mass	ng/culture	µg/g dry mass	ng/culture	µg/g dry mass
0 N	202* a**	2.6 a	608 a	5.6 a	56 a	0.4 a
30 N	9075 b	45.2 b	16900 b	41.5 b	58 a	0.1 a
300 N	344 a	1.4 a	1053 a	1.3 a	288 b	0.4 a
3000 N	171 a	2.3 a	813 a	2.5 a	163 a	0.7 a

* auxin as IAA equivalents

** values followed by the same letter are not significantly different at $p=0.05$

ammonium ions are a good source for all the tested fungi (Tab. 1). The growth of mycelium is stimulated up to the level of 300 mg N per liter and only the highest amount of N in the medium (3000 mg/l) was unfavourable for growth of the fungi. However, as may be seen in Table 3 and Fig. 1, the highest auxin and cytokinin activity for the two tested fungi *S. bovinus* and *S. luteus* was at the low level of N in the medium (30 mg N per liter), and is not correlated with an optimal growth of the mycelium. Increase of doses of nitrogen in the medium despite an excellent growth of the mycelium inhibited auxin and cytokinin production in cultures of the tested fungi.

Auxin and cytokinin level in the filtrate of the fungus *R. luteolus*, belonging to a different systematic group (*Agaricogastrales*) than the other tested fungi (*Agaricales*), is correlated with the growth of the mycelium though cytokinin production at the highest level of nitrogen (3000 mg/l) is also inhibited.

Nitrate nitrogen. The effects of nitrate nitrogen given as potassium nitrate on the growth of mycelium and the level of auxin and cytokinin in the cultures of tested fungi are shown in Table 2, 4 and Figure 2. In general, nitrate showed itself to be a considerably poorer nitrogen source than ammonium, in particular for *S. luteus*, *R. luteolus* and *A. muscaria*. Very low levels of auxin were observed in the presence of nitrate ions in the medium of the tested fungi and no cytokinin activity was shown except in fungus *R. luteolus*.

Phosphorus. Potassium phosphate monobasic was used for testing different levels of phosphorus on the growth of mycelium and auxin and cytokinin amounts in the medium of the studied fungi. Lack of potassium in the medium without phosphorus (O P) was replaced by an appropriate concentration of KCl (0,275 g/l). Table 5 shows that phosphorus even used at very high concentrations was not hampering the growth

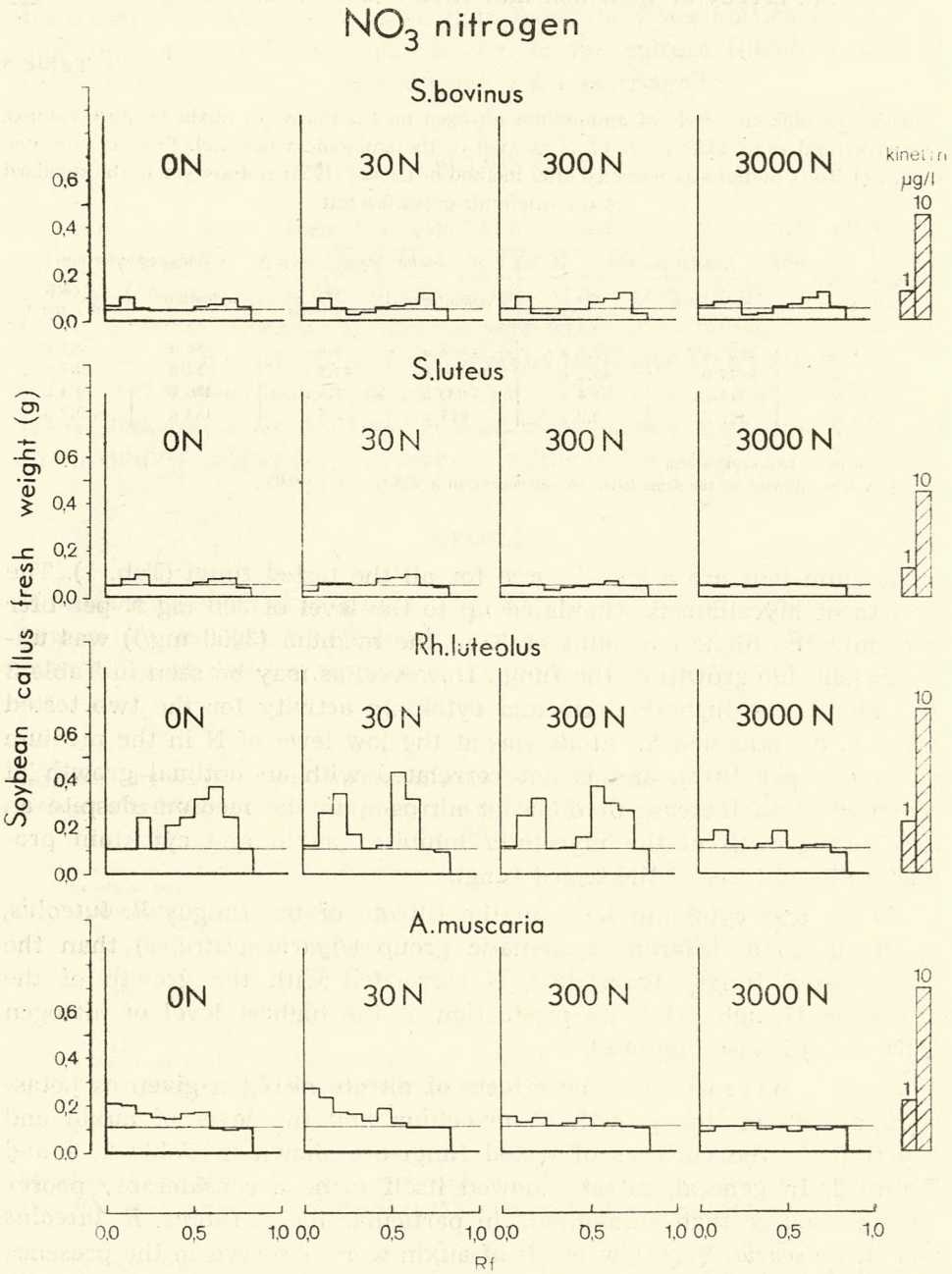

Fig. 1. Influence of different levels of ammonium nitrogen on the release of cytokinin by pure cultures of mycorrhizal fungi. (The levels of N as mg/l of the ammonium tartrate). Filtrate from one culture (1 Roux bottle) was extracted by the method of Biddington and Thomas (1973), streaked onto filter paper sheets and developed with water saturated with the sec-buthanol. The equal strips according to Rf value were cut and added directly into the medium for the growth of soybean callus tissue (Miura and Miller) 1969). The fresh weigth of one piece of callus tissue was measured after 28 days of growth

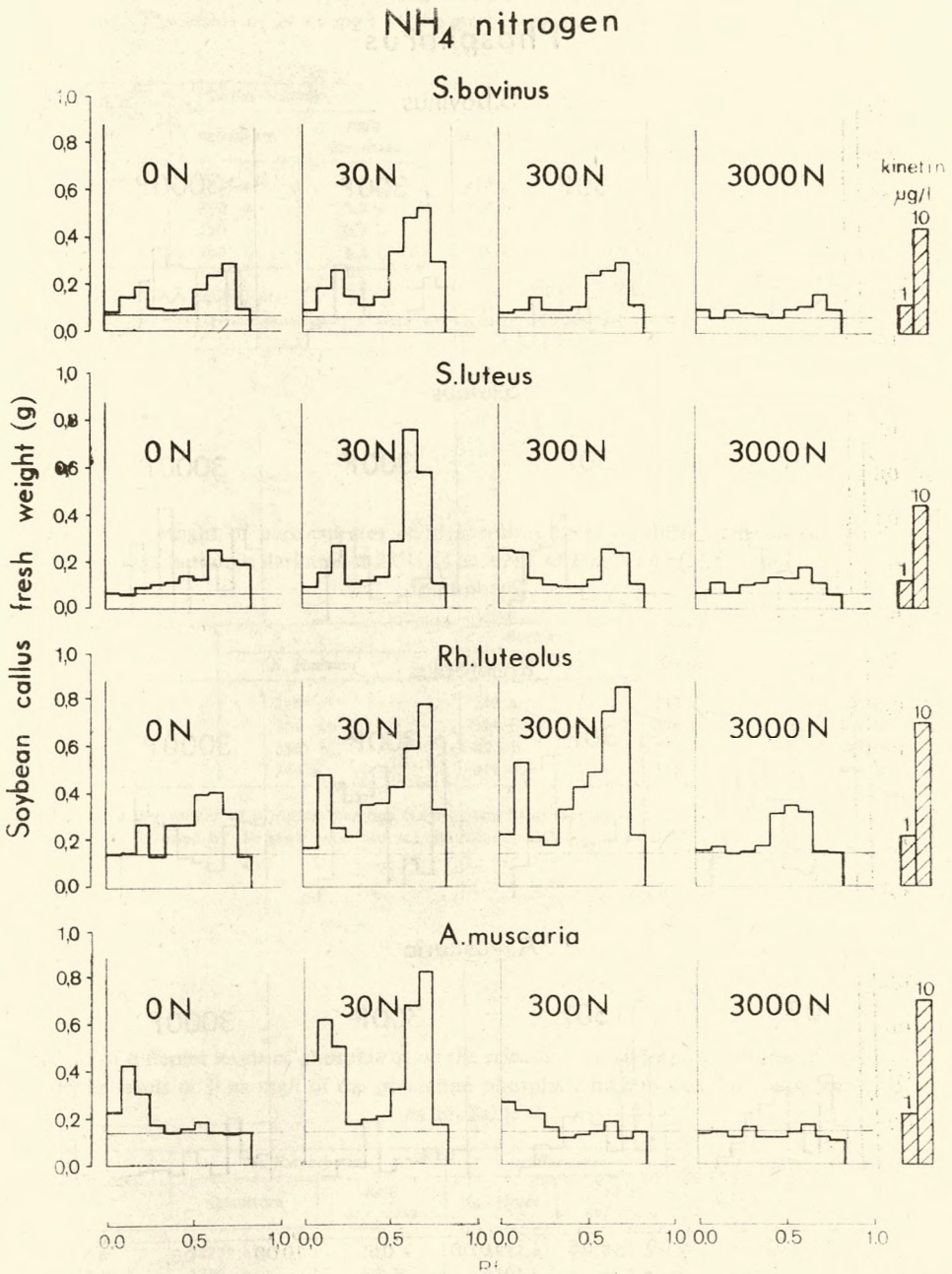

Fig. 2. Influence of different levels of nitrate nitrogen on the release of cytokinin by pure cultures of mycorrhizal fungi (The levels of N as mg/l of the potassium nitrate). The other explanations as in Fig. 1.

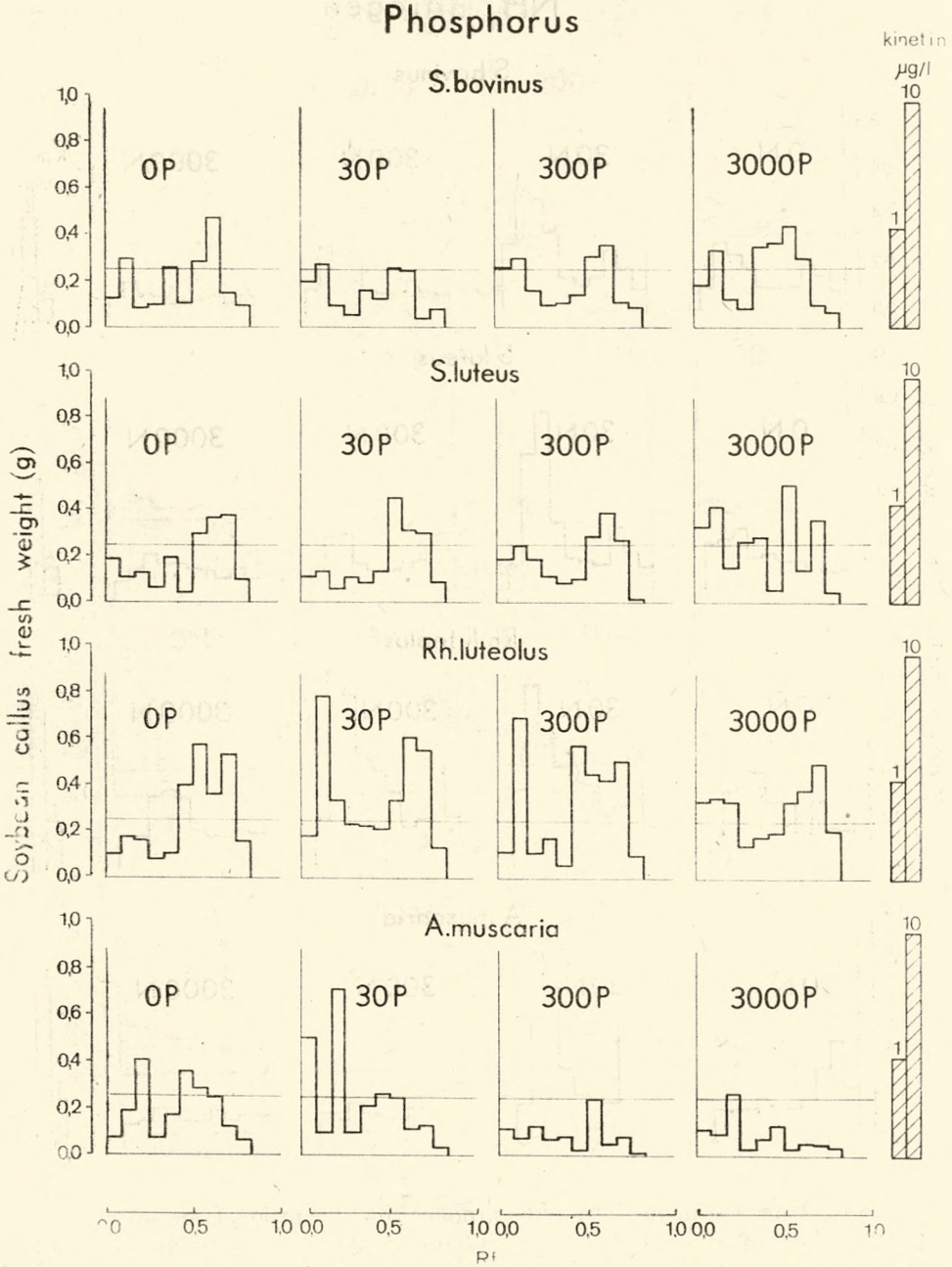

Fig. 3. Influence of different levels of phosphorus on the release of cytokinin by pure cultures of mycorrhizal fungi (The levels of P as mg/l of the potassium phosphate monobasic). The other explanations as in Fig. 1.

Table 4

Influence of different levels of nitrate nitrogen on the release of auxin by pure cultures of mycorrhizal fungi (The levels of N as mg/l of the potassium nitrate). The other explanations as in Table 3

Levels of NO_3 nitrogen	*Suillus bovinus*		*Suillus luteus*		*Rhizopogon luteolus*	
	ng/culture	µg/g dry mass	ng/culture	µg/g dry mass	ng/culture	µg/g dry mass
0 N	232* a**	2.3 a	658 a	5.1 a	65.0 a	0.4 ad
30 N	210 a	2.3 a	225 b	2.1 b	163.2 b	0.6 ab
300 N	150 b	0.9 b	113 b	0.9 b	63.8 a	0.3 c
3000 N	162 b	1.3 b	81 b	0.9 b	43.2 a	0.2 cd

* auxin as IAA equivalents

** values followed by the same letter are not significantly different at $p=0.05$

Table 5

Mycelium dry weight of pure cultures of mycorrhizal fungi on different levels of phosphorus after 30 day incubation in darkness at 23°C (The levels of P as mg/l of the monobasic potassium phosphate)

Levels of P	Species			
	S. bovinus	*S. luteus*	*R. luteolus*	*A. muscaria*
0 P	245* a**	249 a	312 a	406 a
30 P	306 ab	394 b	476 b	480 b
300 P	350 b	425 b	534 b	437 a
3000 P	349 b	418 b	516 b	444 ab

* mg of dry weight of mycelium per one culture (one Roux bottle)

** values followed by the same letter are not significantly different at $p=0.05$

Table 6

Influence of different levels of phosphorus on the release of auxin by pure cultures of mycorrhizal fungi (The levels of P as mg/l of the potassium phosphate monobasic). The other explanations as in Table 3

Levels of P	*Suillus bovinus*		*Suillus luteus*		*Rhizopogon luteolus*	
	ng/culture	µg/g dry mass	ng/culture	µg/g dry mass	ng/culture	µg/g dry mass
0 P	2877* ab**	1.17 a	21 777 a	87.3 a	290 a	0.9 a
30 P	1760 a	5.8 b	6 503 b	16.5 b	62 b	0.1 b
300 P	2109 a	6.0 bc	2 868 b	6.8 b	85 b	0.2 b
3000 P	3500 b	10.0 ac	963 b	2.4 b	32 b	0.1 b

* auxin as IAA equivalents.

** values followed by the same letter are not significantly different at $p=0.05$

of the mycelium and production of cytokinin (except *A. muscaria* Fig. 3) in cultures of the tested fungi. However higher auxin activity was observed in the medium without phosphorus (Tab. 6).

DISCUSSION

Although Björkman's carbohydrate theory on ectomycorrhiza formation was generally accepted for more than two decades, experimental data derived from more recent studies on forest trees reveal that the formation of this symbiosis appears to be far more complex.

Auxin and cytokinin produced by mycorrhizal fungi appear to be primarily involved in the process of mycorrhiza formation. These two hormones seem above all to be responsible for the formation of the characteristic mycorrhizal root structures. Thus all factors influencing growth of mycelium or release of auxin and cytokinin by them, might be expected to affect mycorrhiza development of the roots.

The result reported here indicate that growth of the mycelium and in the particular the auxin and cytokinin production in pure cultures of mycorrhizal fungi are influenced by the source and level of nitrogen in the medium. The highest auxin and cytokinin activity for two tested fungi *S. bovinus* and *S. luteus* was exhibited at a low level of ammonium nitrogen in the medium. Increased doses of nitrogen in the medium despite excellent growth of mycelium inhibited auxin and cytokinin production in cultures of the tested fungi. A similar relationship for the release of auxin by the fungus *S. bovinus* grown on NH_4NO_3 was found by Tomaszewski and Wojciechowska (1974). When nitrate was used as a nitrogen source for the culture of mycorrhizal fungi, auxin production was very low and no cytokinin activity was revealed (except for *R. luteolus*) in the filtrate of the tested fungi. It suggests that nitrogen can influence growth and hormone production of mycorrhizal fungi both in relation to the level and the form in which it is available to the fungi.

Carrodus (1966) found that excised beech mycorrhizae could readily absorb ammonium from ammonium chloride but had almost no ability to absorb nitrate. Lundeberg (1970) subsequently showed that many (though not all) of 27 mycorrhizal fungi could use nitrate as the sole source of nitrogen, nevertheless ammonium was in all cases a better source of nitrogen for the tested fungi. Trappe (1967) reported that two out of eight mycorrhizal fungi he tested possessed nitrate reductase and thus presumably had the ability to absorb and use nitrate. From presented data it follows that in some mycorrhizal fungi auxin and cytokinin production evidently decreases with increased supply of amn onium nitrogen in the medium. It leads to speculation that

in similar manner mycorrhizal fungi can behave in fertilized soil. Therefore, it is likely that the lowered release of hormones by mycorrhizal fungi in the case of excess mineral nutrients in the soil could diminish or even arrest mycorrhiza formation on roots. This can appear in all cases of dissemination of fertilizers in forests without sufficient recognition of site differentiation, from aeroplanes for example, or when seedlings are planted in a nursery established on agricultural soil.

Effect of phosphorus on the growth of mycelium and hormonal activity in pure cultures of tested fungi revealed, that phosphorus used even at extremely high concentration did not hamper the growth of mycelium, while nitrogen in similar concentration did. Probably this can be due to the high ability of mycorrhizal fungi to accumulate phosphorus as a nonmetabolic pool of orthophosphates (Harley 1963, Jennings 1964, Bowen 1973). Phosphorus also has no effect on the cytokinin release by the tested fungi. Auxin production by fungi *R. luteolus* and *S. luteus* decreased with increasing doses of phosphorus in the medium but was relatively high in a culture of *S. bovinus* grown at an elevated level of phosphorus. It seems therefore that the tested fungi differ in susceptibility of auxin production to various concentration of phosphorus. In the light of these facts it becomes clear why some reports mention negative effects of phosphorus fertilizers on mycorrhiza formation in some cases (Bakshi 1974, Mousain 1975).

The results presented above provide evidence for the interrelationship between the ability to liberate auxin and cytokinin by mycorrhizal fungi and the nitrogen and phosphorus levels in their media. This relationship, besides the level of sugars in the roots of host plant (Björkman 1970), could be the second very important factor regulating mycorrhizae formation in forest trees growing under elevated levels of fertilizer availability.

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SUMMARY

Attempts were made in order to determine the influence of different levels of nitrogen and phosphorus on the growth of mycelium and auxin and cytokinin production in pure cultures of mycorrhizal fungi. In the 4 investigated cultures of mycorrhizal fungi *Suillus bovinus, S. luteus, Rhizopogon luteolus* and *Amanita muscaria,* ammonium nitrogen was

better utilized than the nitrate ion. It was shown that high concentration of both nitrogen forms inhibited growth of mycelium. Highest auxin and cytokinin production was observed at lower doses of ammonium nitrogen and was inhibited by higher concentration while mycelium growth still increased. In the presence of the nitrate ion auxin production was low and lack of cytokinin synthesis was observed (except for *R. luteolus*). Phosphorus had no negative effect on the growth of mycelium and cytokinin production even at high concentrations.

The results demonstrate the interrelationship between the ability of auxin and cytokinin production by mycorrhizal fungi and nitrogen and phosphorus levels in their media. This relationship besides the level of sugars in the roots of the host plant could be the second very important factor regulating mycorrhizae formation in forest trees growing under elevated doses of fertilizer availability.

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Wpływ azotu i fosforu na zawartość auksyn i cytokinin w kulturach grzybów mikoryzowych

Streszczenie

Przeprowadzone badania wykazały, że w kulturach czterech badanych grzybów mikoryzowych: *Suillus bovinus, S. luteus, Rhizopogon luteolus* i *Amanita muscaria*, azot amonowy był znacznie lepiej wykorzystywany niż azotanowy, a wysokie stężenia obu form azotu hamowały wzrost grzybni. Najwyższy poziom auksyny i cytokininy stwierdzono przy niskiej dawce azotu amonowego w pożywce, wykazując jednocześnie niemal całkowity brak tych hormonów przy stężeniach wyższych mimo dalszego dobrego wzrostu masy grzybni. W obecności jonu azotanowego jako jedynego źródła azotu zawartość auksyny w filtratach była bardzo niska z wyjątkiem grzyba *R. luteolus*. Nie stwierdzono też aktywności cytokininowej. Fosfor nawet w stężeniach najwyższych nie wpływał ujemnie na wzrost grzybni i zawartość cytokinin w filtratach badanych grzybów.

Uzyskane wyniki wskazują na istnienie zależności pomiędzy wydzielaniem auksyny i cytokininy przez grzyby mikoryzowe a poziomem azotu i fosforu w pożywce. Zależność ta może być obok poziomu cukrów w korzeniach rośliny gospodarza ważnym czynnikiem regulującym tworzenie symbiozy mikoryzowej u drzew leśnych rosnących w warunkach obfitego nawożenia mineralnego.

Влияние азота и фосфора на содержание ауксинов и цитокининов в культурах микоризных грибов

Резюме

Преведенные исследования выявили, что в культуре четырех микоризных грибов *Suillus bovinus*, *S. luteus*, *Rhizopogon luteolus* и *Amanita muscaria* аммонийный азот был значительно лучше присваиваемым нежели нитратный, а высокие концентрации обеих форм азота тормозили рост грибницы. Самый большой уровень ауксинов и цитокининов был обнаружен при незначительных дозах аммонийного азота в питательной среде. При более высоких концентрациях, несмотря на хороший прирост массы грибницы, установлено почти полное отсутсвие этих гормонов. В присутствии нитратного иона в качестве единственного источника азота содержание ауксина в фильтратах было незначительное, за исключением гриба *R. luteolus*. Не обнаружено также активности цитокининов. Фосфор, даже в самых высоких концентрациях, не вызывал отрицательного воздействия на рост грибницы и содержание цитокининов в фильтратах исследуемых грибов.

Полученные результаты указывают на существование зависимости между выделением ауксинов и цитокининов микоризными грибами и уровнем азота и фосфора в питательной среде. Эта зависимость может быть, также как и уровень содержания сахаров в корнях растения хозяина, существенным фактором регулирующим возникновение микоризного симбиоза у лесных деревьев растущих в условиях обильного минерального питания.