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**Effect of treating Scots pine (*Pinus sylvestris* L.)
seedlings with phytohormones on the growth of
the root system and on the peroxidase and IAA
oxidase enzyme activity in roots***

Abstract

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The treatment of pine seedlings with growth substances changed root growth and peroxidase IAA oxidase activity in enzyme preparations of roots. The effect of the growth substances on the pine roots depends on the concentration of the growth substances and on the age of seedlings. A relatively short period of treatment (2 weeks) induced a very high total enzyme activity but a longer treatment caused a progressive decrease of this activity. The data from this work do not indicate any simple relationship between the activity of peroxidase and IAA oxidase and the growth of pine roots, but they indicate a relationship between the appearance or disappearance of one of isoperoxidase bands and the growth of roots, especially their elongation.

Additional key words: Phytohormones interaction, root elongation, isoperoxidase bands.

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INTRODUCTION

Peroxidase (donor: H_2O_2 oxidoreductase, 1.11.1.7) is a nonspecific enzyme known to oxidize such substrates as phenols, aromatic amines, cytochrom c and indole-3-acetic acid (IAA). The first studies on peroxidase (PO) activity were made more than 100 years ago and they have been lately reviewed by Gaspar et al. (1982).

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According to the literature some isoperoxidases are able to oxidize IAA in the presence or in the absence of H_2O_2 (Lee, 1974, Srivastava and Van Huystee, 1977, Lee and Pilet, 1977, Stonier et al., 1979, Klisurska and Dencheva, 1983, Kieliszewska-Rokicka, 1980, 1985). However, Sequeira and Mineo (1966) and van der Mast (1969) isolated enzyme preparations able to oxidize IAA without H_2O_2 but showing no peroxidase activity.

PO and IAA oxidase activity are thought to be connected with IAA metabolism and regulation of plant growth. Plant hormones, like IAA, GA₃ and kinetin may change the activity and isoenzyme patterns of PO (Mc Cune and Galston, 1959, Ockerse et al., 1966, Galston et al., 1968, Birecka and Galston, 1970, Lee 1971 a, b, Meudt and Stecher, 1972, Gaspar et al. 1973). Some authors found that in plant treated with hormones a correlation exists between the activity of PO or IAA oxidase and the rate of tissue culture growth (Gaspar and Xhanflaine, 1967, Lee, 1971 a, b, Wolter and Gordon, 1975).

In the present paper the relationship between the growth of Scots pine roots and the PO and IAA oxidase activity and the isoperoxidase pattern are discussed.

MATERIAL AND METHODS

Plant material. Seeds of Scots pine (*Pinus sylvestris* L.) were sown in perlite acidified with 0.1 N phosphoric acid to pH 7 and subjected to a 16 hrs photoperiod. After 2 weeks the seedlings were treated with growth substance solutions, separately or in combination, every other day. Once a week the seedlings were fertilized with a nutrient solution (Laiho, 1970). The roots were analysed.

Enzyme preparations. Enzymes were washed out from acetone powder with a 0.2 M phosphate buffer, pH 6. Acetone powder were obtained from roots or from embryo axes as described in a previous paper (Kieliszewska-Rokicka, 1980). Extracts were centrifuged at 10,000 g, the supernatants were dialysed against 0.01 M phosphate buffer pH 6 and then used as the enzyme preparations.

Determination of protein content. The method of Potty (1969) was used with albumin of bovine blood serum as the standard.

Enzyme assays. For the determination of the IAA oxidase activity the decomposition of IAA by the enzyme preparation was investigated by the method of Shinshi and Noguchi (1975) using the Salkowski reagent (Gordon and Weber, 1951). IAA oxidase activity was defined as μg of IAA oxidized by 10 μg of protein during 1 hour. PO activity was determined according to the method of Quoirin et al. (1974) with modifications (Kieliszewska-Rokicka, 1980). The activity of PO was defined as ΔOD_{480nm} per 1 mg of protein per 1 minute.

Isoenzyme separation. Isoperoxidases were separated by polyacrylamide disc electrophoresis method in an anionic system (Davis, 1964) and in a cationic system (Reisfeld et al., 1962). Comparable amounts of protein were applied onto gel columns.

Isoenzyme staining. PO isoenzymes were stained by the method described by Safonov et al. (1969) with benzidine as a substrate. The reaction was performed for 15 minutes at room temperature. After staining the gel columns were scanned in a Vitatron MPS densitometer.

RESULTS

ISOPEROXIDASE PATTERN IN EMBRYONIC AXES FROM SEEDS TREATED FOR 5 DAYS WITH IAA AND KINETIN

Pine seeds were placed in Petri dishes on blotting-paper with IAA or kinetin solutions in concentrations: IAA 10^{-6} M, 10^{-5} M, 10^{-4} M, and kinetin 10^{-4} and 10^{-5} M. Seeds imbibed with water only were the control. Petri dishes with seeds were put in a refrigerator. Figure 1 shows isoenzyme patterns and densitometer scanning of peroxidase after electrophoresis of extracts from embryo axes on acrylamide gel. Qualitative and quantitative differences between isoperoxidase patterns were observed. The presence of IAA 10^{-6} M and 10^{-5} M increased the activity of particular PO bands. The higher concentrations of IAA 10^{-4} M and kinetin 10^{-5} M inhibited completely the activity of two PO bands (B and E) and kinetin 10^{-6} inhibited PO band B.

EFFECT OF GROWTH SUBSTANCES ON SCOTS PINE SEEDLINGS

a. Growth of seedling roots and peroxidase and IAA oxidase activity after 5 weeks of treatment with IAA, 2,4-D, kinetin, ABA and GA₃

Two weeks old pine seedlings growing on perlite (pH 7) were treated with growth substance solutions (IAA 10^{-5} M, 2,4-D 10^{-5} M, kinetin 10^{-6} M,

Table 1

Changes of peroxidase and IAA oxidase activity in pine roots after 2 and 5 weeks of treatment of pine seedlings with growth substances. Results were expressed as percentage of the control

Treatment	Time of incubation			
	2 weeks		5 weeks	
	PO	IAA oxidase	PO	IAA oxidase
Control	100	100	100	100
Kinetin 10^{-6} M	251	116	159	111
ABA 10^{-6} M	161	110	213	114
IAA 10^{-5} M	180	108	133	132
2,4-D 10^{-5} M	380	117	124	120
GA ₃ 5×10^{-6} M	217	114	164	121

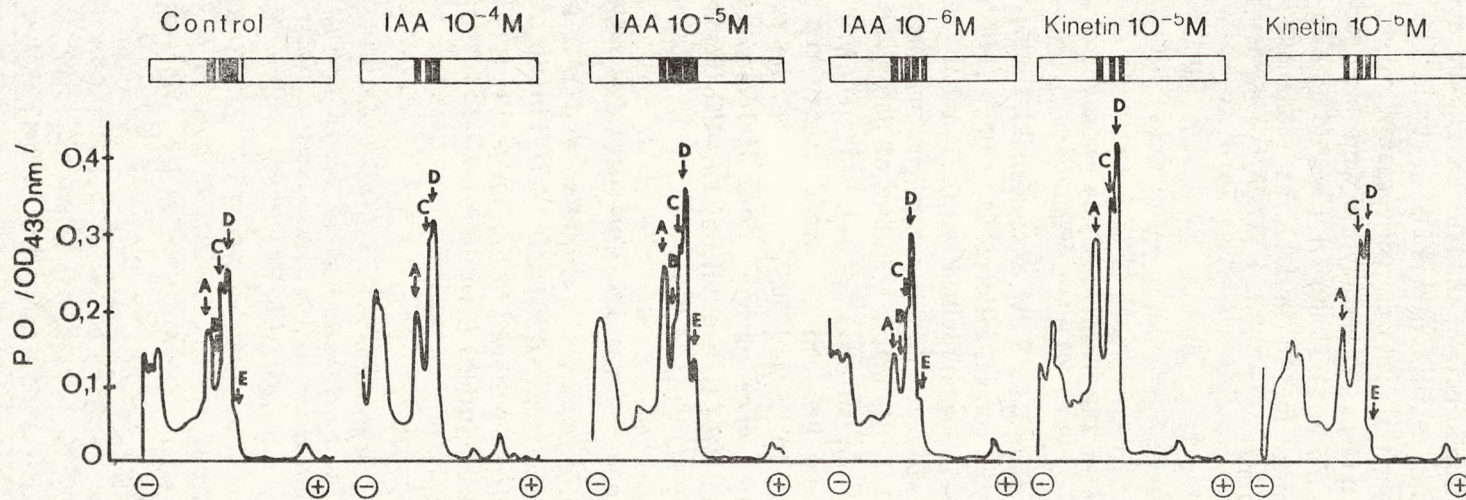


Fig. 1. Isoenzyme patterns and densitometer scanning of peroxidase in embryonic axes from Scots pine seeds treated for 5 days with IAA and kinetin. Polyacrylamide gel electrophoresis was carried out in an anionic system at pH 8.3

ABA 10^{-6} M, GA₃ 5×10^{-6} M) as was mentioned in Methods. Table 1 shows the changes of PO and IAA oxidase activity in roots after 2 and 5 weeks of treatment calculated per unit of protein. Two weeks as well as five weeks of treatment of seedlings with growth substances induced PO and IAA oxidase activity in roots compared with the untreated control. After 2 weeks of treatment the total PO activity increased substantially (160 - 380% of the control), but there were no qualitative changes in isoenzyme patterns, except after treatment with 2,4-D (Fig. 2A). However, after 5 weeks of treatment the total PO activity was markedly lower: 124 - 213% of that of the control (Table 1). The presence of growth substances over 5 weeks caused qualitative changes in isoenzyme patterns (Fig. 2B). IAA, 2,4-D and kinetin inhibited completely some PO bands in the anionic system while in the cationic system new bands appeared. ABA and GA₃ affected only the intensity of some peroxidase bands.

Table 2

Differences in the growth of roots of pine seedlings treated with growth substances for 5 weeks (mean value from 10 seedlings). Results were expressed as percentage of control

Treatment	Length of root system	Dry weight
Control	100	100
Kinetin 10^{-6} M	135	181
ABA 10^{-6} M	171	131
IAA 10^{-5} M	125	136
2,4-D 10^{-5} M	152	124
GA ₃ 5×10^{-6} M	154	127

Table 2 presents differences in the growth of roots of pine seedlings treated with growth substances for 5 weeks. Growth substances markedly stimulated growth (i.e. elongation and dry weight) of roots as compared with the untreated control.

b. Growth of seedlings roots and peroxidase and IAA oxidase activity after 16 weeks of treatment with IAA, kinetin and GA₃, separately and in combination

The treatment of pine seedlings for 16 weeks with IAA, kinetin and GA₃ or their combinations (as indicates Table 3) decreased the total activity of PO and IAA oxidase in comparison with the untreated control, except the case of the IAA 10^{-5} M, kinetin 5×10^{-7} M and GA₃ 5×10^{-6} M (variants No. 2, 3, 5). However, growth substances enhanced the activity of particular isoperoxidases compared to that of the control (Fig. 3). Only one qualitative difference between isoperoxidase patterns

Table 3

Influence of growth substances on the growth of pine roots and on the activity of peroxidase and IAA oxidase in root preparations. Pine seedlings were treated for 16 weeks with growth substance solutions separately or in mixtures. Results are expressed as percentage of control

No.	Treatment			Length of root system	Fresh weight	Dry weight	PO activity	IAA oxidase activity
	IAA	KIN	GA ₃					
1	—	—	—	100	100	100	100	100
2	10 ⁻⁵	—	—	98	102	99	93	98
3	—	5·10 ⁻⁷	—	111	94	98	105	95
4	—	—	2·10 ⁻⁶	159	130	117	90	81
5	—	—	5·10 ⁻⁶	101	118	99	123	92
6	10 ⁻⁵	2·10 ⁻⁷	—	122	100	104	35	71
7	10 ⁻⁵	5·10 ⁻⁷	—	106	52	100	38	73
8	10 ⁻⁴	2·10 ⁻⁷	—	78	83	53	62	90
9	10 ⁻⁴	5·10 ⁻⁷	—	173	145	118	38	64
10	10 ⁻⁵	2·10 ⁻⁷	2·10 ⁻⁶	84	58	67	63	89
11	10 ⁻⁵	5·10 ⁻⁷	2·10 ⁻⁶	71	63	65	24	79
12	10 ⁻⁴	2·10 ⁻⁷	2·10 ⁻⁶	143	73	91	94	92
13	10 ⁻⁴	5·10 ⁻⁷	2·10 ⁻⁶	163	108	94	30	54
14	10 ⁻⁵	2·10 ⁻⁷	5·10 ⁻⁶	82	49	71	34	77
15	10 ⁻⁵	5·10 ⁻⁷	5·10 ⁻⁶	93	80	75	49	87
16	10 ⁻⁴	2·10 ⁻⁷	5·10 ⁻⁶	145	106	97	63	73
17	10 ⁻⁴	5·10 ⁻⁷	5·10 ⁻⁶	111	118	108	52	52

was observed. Namely, most of the growth substance solutions, used in the experiment, inhibited completely the activity of isoperoxidase A.

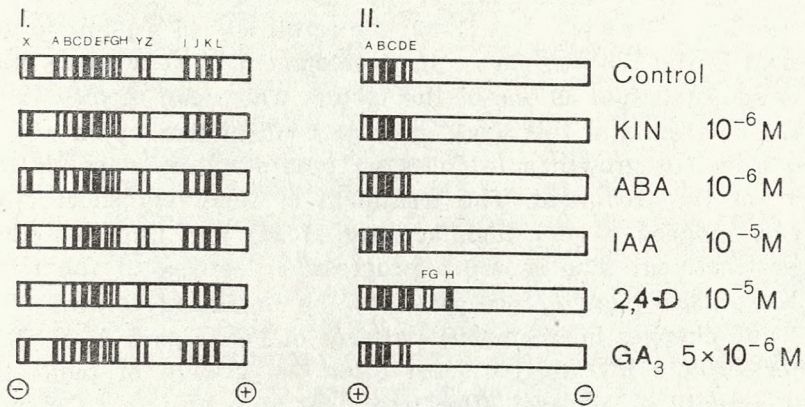
Table 3 shows that in most of variants of the experiment the fresh and dry weight of roots were lower than in the control. In some cases the presence of growth substances caused the roots to grow shorter (variants No. 2, 3, 8, 10, 11, 14, 15), however most of growth substance solutions promoted elongation of roots.

The data presented in Figure 3 and Table 3 indicate that isoperoxidase A disappeared in the roots in which elongation, and fresh and dry weight are lower than in the control. This happened in variants No. 2, 3, 8, 10, 11, 14 and 15. However, there are two exceptions (No. 6 and 7) where band A is inhibited too, but elongation and dry weight of the roots are similar to those in the control.

DISCUSSION

The results of this study indicate that the effect of growth substances on pine tissues depends, among others, on the stage of development. Embryos of imbibed seeds were more sensitive to the influence of growth substances than roots of 2 weeks old seedlings. In pine embryos the distinct qualitative changes in isoenzyme patterns of PO occurred already after 5 day of treatment with growth substances (Fig. 1), while in the roots of seedlings growing on perlite the changes in isoperoxidase

2 weeks of treatment



5 weeks of treatment

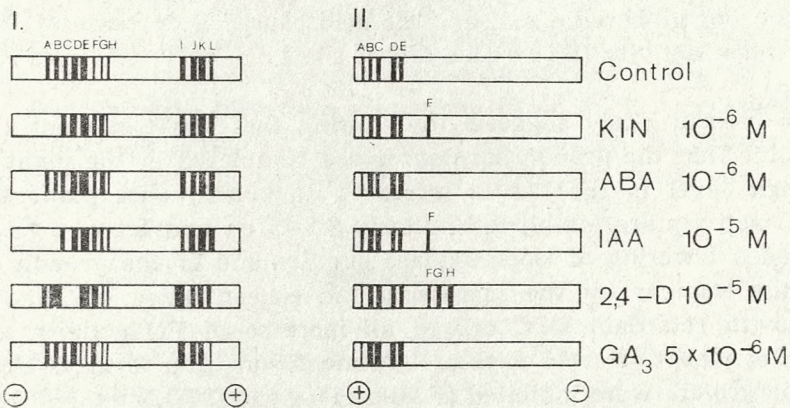


Fig. 2. Isoenzyme patterns of peroxidase in the roots of Scots pine seedlings treated with growth substances for: A. 2 weeks, B. 5 weeks. Polyacrylamide gel electrophoresis was carried out in anionic (I) and cationic (II) systems

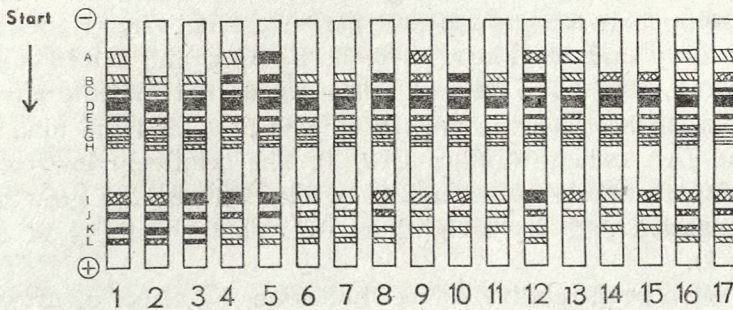


Fig. 3. Isoenzyme patterns of peroxidase in the roots of Scots pine seedlings treated for 16 weeks with growth substances as in table 3

patterns occurred only after 5 weeks of treatment (Fig. 3), but not after 2 weeks of treatment, except the case of 2,4-D (Fig. 2).

According to Trewavas (1983) the sensitivity of a plant to growth substances is the limiting factor in development. Trewavas mentioned the age of tissues as one of the factors which can modify this sensitivity. The results of this work seem to confirm that opinion.

The effect of growth substances on pine seedlings depends on the duration of the treatment. The treatment of relatively short duration (2 weeks) induced a very high activity of PO and IAA oxidase, but a longer treatment time caused a progressive decrease of the total PO and IAA oxidase activity compared to the untreated control (Tab. 1, Tab. 3) and changes in isoenzyme patterns of PO (Figs 2 A, B, 3).

Other authors investigated most often the growth of plant tissues and the activity of oxidases after treatment with growth substances of short duration (1 - 72 hours). They have found very often that IAA increased the activity of PO and IAA oxidase (Gaspar and Dinant, 1967, Meudt and Stecher, 1972, Gaspar et al., 1973, Mato et al., 1985) but gibberellin and abscisic acid caused a decrease of PO and IAA oxidase activity (Birecka and Galston, 1970, Gaspar et al., 1973).

The present study suggests that during the long treatment time it is possible that the growth substances are cumulated in the plant tissue and their level in the tissues increases. In consequence plant growth and PO activity are inhibited. Similarly Stuber and Levings (1969) observed a lowering of isoperoxidase activity and of the growth of oat coleoptile sections by the increasing the concentration of IAA. Even the growth retardant CCC caused an increase of PO activity and of growth of wheat after 10 days of treatment, but after 30 days PO activity and growth were inhibited (Flückinger, 1977).

Galston and Davis (1969) presented evidence to suggest that gibberellin, auxin, cytokinin and ethylen can interact to control the level of PO in the tissues.

Peroxidase is thought to effect growth. Some authors found an inverse relationship between growth and peroxidase activity (Penel et al., 1977, Jankay and Muller, 1976, Birecka and Galston, 1970, Liang et al., 1977). The data of this work do not indicate any simple inverse relation between the growth of pine roots and the total activity of PO and IAA oxidase (Tables 1, 2, 3). The relatively low concentrations of growth substances over 2 - 5 weeks induced the growth of the roots (elongation and dry weight) as well as the activity of enzymes (Tables 1, 2).

There have been relatively few studies on the effect of growth substances on the growth of gymnosperms. Zajączkowski and Wodzicki (1975) in *Pinus sylvestris*, Carpita and Tarmann (1982) in

Pinus taeda and Terry et al. (1982) in *Pinus ponderosa* found that auxin promoted elongation of excised sections of the pine hypocotyl. Other growth substances had little effect on elongation: GA₃ induced it a little while kinetin inhibited it a little. Various growth substances (IAA, 2,4-D, NAA) stimulated formation of new xylem cells in *Pinus sylvestris* stem segments (Zajączkowski and Wodzicki, 1975).

In this work the changes of PO activity in roots of treated pine seedlings are not proportional to IAA activity in the same roots. Similarly Elkinawy and Raa (1973) did not find proportional changes in the activity of PO and IAA oxidase in developing cucumber seedlings. Previous studies (Kieliszewska-Rokicka 1980, 1985) demonstrated that Scots pine tissues do have not any specific IAA oxidase. Not all, but some of the isoperoxidases can act as IAA oxidase.

Some investigators have found that growth of the plant is related not to the total activity of the PO but to the relative level of some isoperoxidases (Lee, 1971 a, b, Darimont et al., 1971, Gaspar and Verbeek, 1974, Runkova and Gaspar, 1976). The data obtained in the present experiments indicate that there exists a relationship between the appearance or disappearance of isoperoxidase A (Fig. 3) and the growth of roots, especially their elongation (Tab. 3). It is possible that any given endo- or egzogenic factor, which can change the isoperoxidase pattern, can also modify the elongation of Scots pine roots.

SUMMARY

Seeds and young seedlings of Scots pine (*Pinus sylvestris* L.) were treated with growth substances (IAA, 2,4-D, kinetin, ABA, GA₃). The effect of growth substances changed root growth, peroxidase and IAA oxidase total activity and isoenzyme pattern of peroxidase.

Embryos of imbibed seeds were more sensitive to the influence of growth substances than roots of 2 - 5 week old seedlings.

The effect of the growth substances on the pine roots depended on the concentration of the growth substances and on the period of treatment. A relatively short period of treatment (2 weeks) induced root growth and a very high peroxidase and IAA oxidase activity. A longer treatment caused a progressive decrease of this activity.

The data from this work does not indicate any simple relationship between the total peroxidase and IAA oxidase activity and the growth of pine roots.

Electrophoretic analyse of peroxidase bands suggests that there exists a relationship between the appearance of peroxidase band A and the root system growth.

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Wpływ traktowania siewek sosny zwyczajnej (*Pinus sylvestris* L.) fitohormonami na wzrost systemu korzeniowego oraz aktywność enzymatyczną peroksydazy i IAA oksydazy

Streszczenie

Nasiona i młode siewki sosny zwyczajnej (*Pinus sylvestris* L.) poddano działaniu substancji wzrostowych (IAA, 2, 4-D, kinetyna, ABA, GA₃). Stwierdzono, że obecność substancji wzrostowych wpływa na wzrost korzeni sosny, na całkowitą aktywność peroksydazy i IAA oksydazy oraz na obraz frakcji elektroforetycznych peroksydazy.

Wrażliwość tkanek sosny na działanie substancji wzrostowych zależy od stadium wzrostu sosny. Egzogenne substancje wzrostowe zmieniały wzrost, całkowitą aktywność enzymów i obraz frakcji elektroforetycznych w osiach zarodkowych pęczniejących nasion w krótszym czasie niż w korzeniach 2-5-tygodniowych siewek.

Działanie substancji wzrostowych na korzenie siewek sosny zależy od ich stężenia i od okresu działania. Stosunkowo krótkotrwałe (2 tygodnie) traktowanie silnie indukowało wzrost korzeni oraz aktywność peroksydazy i IAA oksydazy. Dłuższe działanie powodowało stopniowe obniżanie aktywności enzymów.

Nie stwierdzono prostej zależności między całkowitą aktywnością peroksydazy i IAA oksydazy a wzrostem korzeni.

Analiza elektroforetyczna peroksydazy sugeruje istnienie zależności między występowaniem pasma A a wzrostem korzeni sosny. Stwierdzono brak pasma A w korzeniach siewek, których wzrost został zahamowany działaniem regulatorów wzrostu i pojawianie się tego pasma w korzeniach o intensywnym wzroście.

Влияние обработки семян сосны обыкновенной (*Pinus sylvestris* L.) фитогормонами на рост корневой системы и enzymатическую активность пероксидазы и оксидазы ИУК*

Резюме

Семена и молодые сеянцы сосны обыкновенной (*Pinus sylvestris* L.) подвергли воздействию ростовых веществ (ИУК, 2, 4-Д, кинетина, АБК, ГК₃). Установлено, что присутствие ростовых веществ влияло на рост корней сосны, активность пероксидазы и оксидазы ИУК, а также характер электрофоретических фракций пероксидазы.

Чувствительность тканей сосны к воздействию ростовых веществ зависит от стадии развития сосны. Экзогенные ростовые вещества изменяли рост, активность ферментов и характер электрофоретических фракций в зародышевых

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осях набухающим семям за более короткий срок, чем в корнях 2 - 5 недельных сеянцев.

Действие ростовых веществ на корни сеянцев сосны зависит от их концентрации и периода воздействия. Относительно короткая обработка (2 недели) значительно индуцировала рост корней и активность пероксидазы и оксидазы ИУК. Более длительное воздействие вызывало постепенное понижение активности ферментов.

Не установлено прямой зависимости между активностью пероксидазы и оксидазы ИУК и ростом корней.

Электрофоретический анализ пероксидазы указывает на существование зависимости между встречаемостью полосы А и ростом корней сосны. Установлено, что полоса А отсутствует в корнях сеянцев, рост которых был остановлен действием регуляторов роста. Она появляется в корнях с интенсивным ростом.

