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Effect of auxin on xylem tracheids differentiation in decapitated stems of *Pinus silvestris* L. and its interaction with some vitamins and growth regulators*

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Summary

The effects of several vitamins and substances known as important agents in regulation of cell metabolism upon secondary xylem differentiation were studied in interaction with auxin (IAA) as applied in lanoline to decapitated stems of 5-year-old *Pinus silvestris* trees in early and late-summer. Tested substances were: gibberellic acid, kinetin, nicotinic acid, thiamine, pyridoxine, calcium panthotenate, choline chloride, riboflavin, inositol, ascorbic acid, vitamin A (alcohol), vitamin A (ester), saponin. None of the effects of these substances appeared significant enough to indicate the involvement in the seasonal variation of the response of cambium or differentiating tracheids to auxin. However, several effects, especially those of inositol, vitamin A and pyridoxine upon cambial xylem production and further stages of tracheid differentiation were observed. Auxin (IAA) affected cambial activity and subsequent differentiation of tracheids during the earliest stages of cell ontogenesis. At these stages auxin treatment induced quantitative expression of the developmental processes involving radial growth and secondary wall formation by tracheids. In this respect, auxin did not affect cells advanced in differentiation, however, it proved to be an essential factor in the completion of the full cycle of tracheid ontogenesis.

INTRODUCTION

Differential response of the cambium to auxin has been proposed as a possible mechanism involved in formation of reaction wood (W a r e-

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ing et al. 1964), or explaining the seasonal differences in xylem production and the spring basipetal initiation of cambial activity in tree stems (Zajączkowski 1973). Among numerous possible ways in which variable cambial sensitivity to auxin may develop, the interaction with other active substances is one of the most probable. In many attempts to find the specific regulators of xylem differentiation, various substances were tested. Künning (1950) studied the effect of ascorbic acid and aneurin, Morey and Cronshaw (1968 b) 2,4-dinitrophenol, Hejnowicz and Tomaszewski (1969) l-tryptophan, and the role of cyclitols was investigated by Torrey and Loomis (1967), and Robards et al. (1969). Special attention was given to the effect of growth regulators such as gibberellins (Bradley and Crane 1957; Wareing 1958 a; Larson, 1960; Wareing et al., 1964; Doley and Leyton, 1968; Farrar and Fan, 1970), cytokinins (Pieniążek and Jankiewicz, 1966, 1967; Pieniążek, 1968; Robards et al., 1969; Zajączkowski, 1973) and inhibitors (Larson, 1964; Cronshaw and Morey, 1965; Kennedy and Farrar, 1965 a; Morey and Cronshaw, 1966; Balatinecz and Farrar, 1968; Hejnowicz and Tomaszewski, 1969). Interactions of many of these substances with several synthetic auxins were studied (Morey and Cronshaw, 1968 a; Hejnowicz and Tomaszewski, 1969) above all, with idole-3-acetic acid, as the changes in concentration and distribution of this native auxin are known to correlate with variation of cambial activity and xylem differentiation in tree stems (see reviews by: Wareing, 1958 b; Larson, 1962 Reinders-Gouwentak, 1965; and Brown, 1970). The effects of gibberelic acid, 6-furfurylaminopurine, 6-benzylaminopurine and 2,3,5-tri-iodobenzoic acid were demonstrated in xylem formation by angiosperms but rarely in conifers. Except for TIBA, application of which may induce formation of xylem elements classified as reaction wood, and which is known to interfere with basipetal transport of auxin (Kuse, 1954; Niedergang-Kamien and Leopold, 1957) very little is known on the mechanism of interaction of the above mentioned substances with auxin.

The study reported here was concerned with the effect of several vitamins and other substances known as important agents in the regulation of cell metabolism or affecting the stability of cytoplasmic membranes (Dingle 1963). Such substances could possibly be involved in conditioning the cambium response to auxin and play a role in the regulating corollary of ontogenetic stages differentiation of axial elements of xylem and initiation of the autolytic processes which terminate their maturation.

MATERIALS AND METHODS

The tested substances were: (1) two growth regulators: gibberellic acid (GA) and kinetin (Kin), (2) vitamins: nicotinic acid (NA), thiamine (B_1), pyridoxine (Pi), calcium panthotenate (CP), choline chloride (CC), riboflavin (Rf), inositol (Io), ascorbic acid (AA), vitamin A-alcohol (Aa), vitamin A-ester (Ae), and (3) saponin (Sa). The effects of these substances were studied in interaction with indole-3-acetic acid (IAA). Lanoline pastes were prepared with all substances to final 0.5 per cent concentration, and applied to the cut surface of decapitated 5-year-old pines in the forest. The decapitated end of the stem was subsequently sealed with aluminium and plastic foil to protect the paste against light and rainfall. The internodes of the main stems to which the pastes were applied were 3 years old. Apical parts of the trees were cut off 15 cm above the node with well developed assimilating branches. The pastes were reapplied four times at ten-day intervals in the course of two experiments started on June 3rd and August 27th, 1970. Each combination of substances was applied to five trees.

After 40 days, at least 12 cm long uppermost pieces of stem exposed to paste were collected and fixed in 70 per cent ethanol. Transverse free-hand sections of these segments at a distance of 2 and 12 cm below the place of paste application were stained with safranine and light green SF, mounted in Canada balsam and examined under a light microscope. In addition, transverse sections were prepared from the removed apical stem segments at the surface facing the pasted stump at the beginning of the experiment to serve for reference measurements. The investigation concerned the effect upon the following processes:

1. Production of axial tracheids of secondary xylem from the cambial zone.

2. Radial growth which determines the final radial diameter of the tracheids.

3. Maturation of tracheids during which secondary wall is deposited.

The latter two processes were studied in respect to the cells newly formed from the cambium after the experiment had started, and to those which were already differentiating at the time the experiments started, with distinction of their ontogenetic stage. For this purpose the following groups of cells were distinguished:

1. Newly formed tracheids: x_1, x_2, x_3, (the youngest, last formed — marked x_1).

2. Tracheids which corresponded to the cambial zone (C) at the beginning of the experiment (nomenclature after W i l s o n et al. 1966).

3. Tracheids which corresponded to the zone of enlarging xylem (G).

4. Tracheids which corresponded to the zone of maturation (D).
5. Mature tracheids formed before the experiment started.

The total radial number of tracheids formed during the season in each of the zones of differentiating xylem was determined before and after the experiments. For measurements, the positions of the above listed groups of cells were determined with the use of apical stem segments of each tree collected on the day the experiment started, as reference. The cells corresponding to each zone of differentiation were measured in respect to their radial diameter and cell wall thickness. The same measurements were performed on cells formed before, or after decapitation. Averages for each group were calculated from four tracheids measured in 2 radial files on each slide and for five trees in each treatment. The significance of the results was tested at a 95 per cent level of confidence. Statistical data were omitted in presentation of the material, as the variability among treatments was sufficiently manifested in the diagrams.

RESULTS

1. Production of axial xylem elements

The data concerning cambial xylem production are presented in Fig. 1. It is seen that decapitation greatly reduced or even arrested formation of new xylem cells from the cambial zone. Supply of auxin in lanoline promoted further cambial activity in spite of decapitation only in early-summer. Substances other than auxin did not allow more cambial xylem production. Neither did the applied substances produce an effect synergistic with auxin stimulation. On the contrary, several substances seemingly decreased the effect of auxin in early-summer. Later in season, a slight stimulating effect was observed in the series with inositol, vitamin A (alcohol) and pyridoxine applied with auxin. The high variability among trees does not warrant the reliability of the latter results.

2. Zone of enlarging xylem

Decapitation resulted in a decrease of the number of cells undergoing radial enlargement under most treatments in the early-summer experiment (Fig. 2). The decrease was more pronounced 12 cm below the surface to which lanoline was applied than at a 2 cm distance. The number of cells in this zone remained seemingly unaffected, or little affected by decapitation, when gibberellic acid, ascorbic acid, inositol, pyridoxine, riboflavin or auxin were separately applied. The

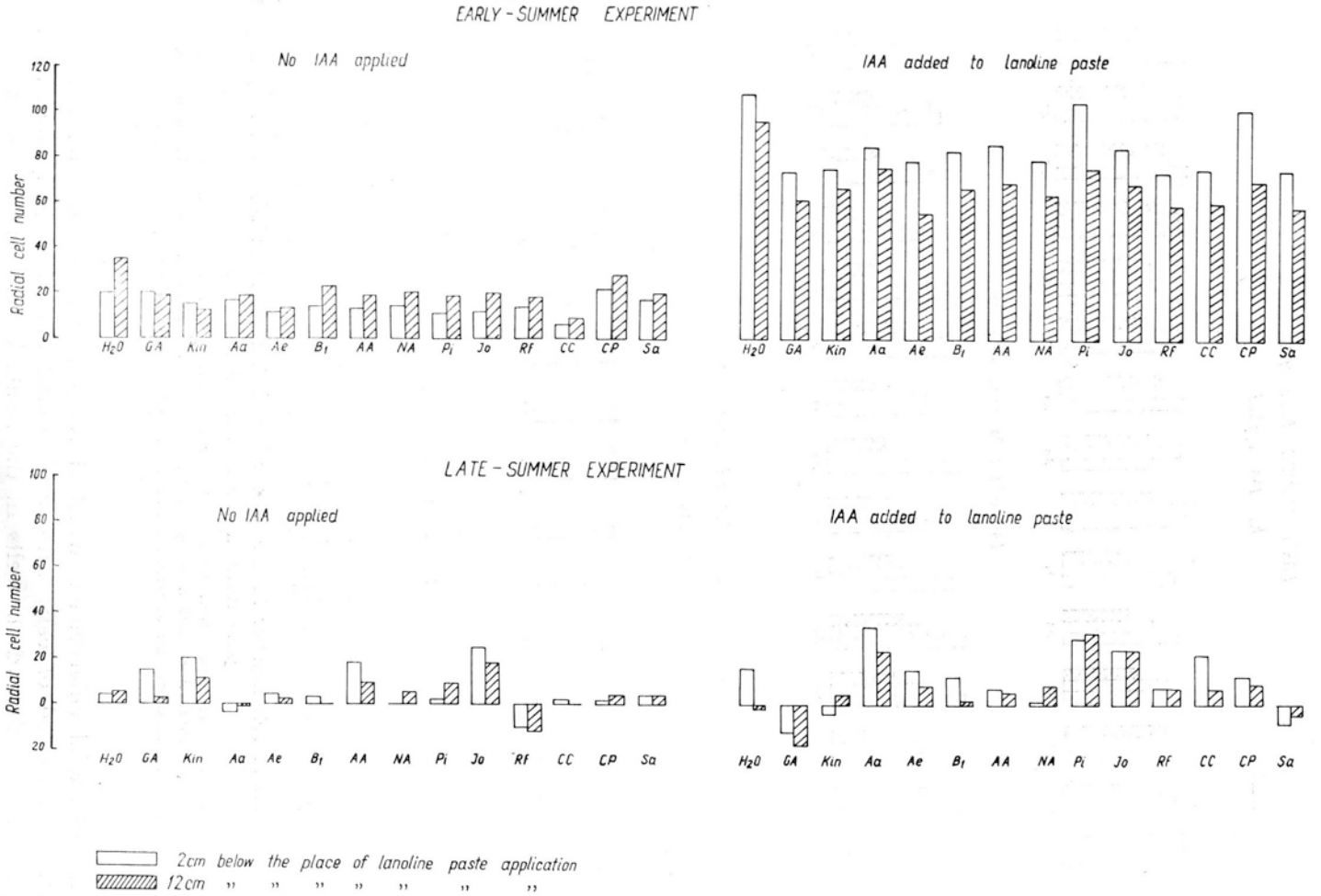


Fig. 1. Increment of total radial cell number after 40 days following decapitation of young pine trees at 3-year old main stem internode

Averages of 5 trees. For description of abbreviations see text

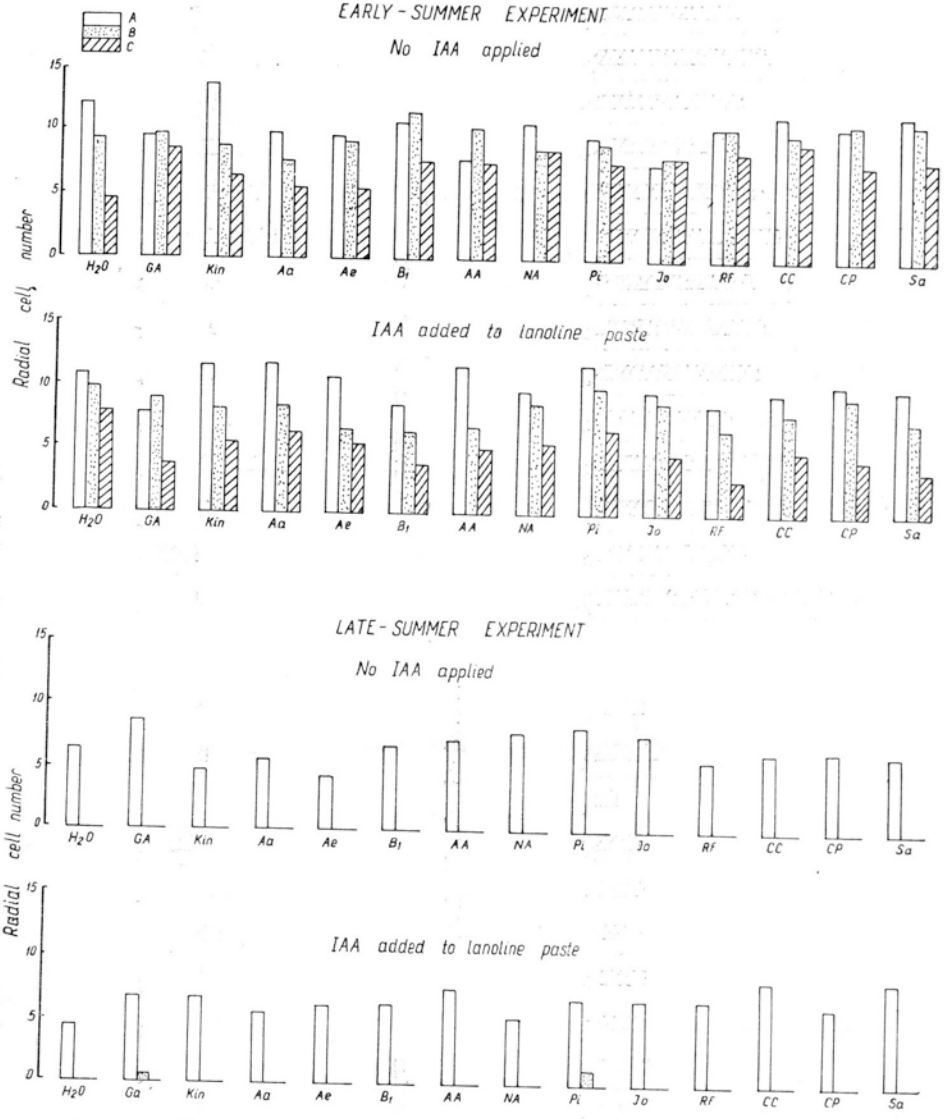


Fig. 2. Radial cell number in the zone of enlarging xylem in the stem of young pine trees at the 3-year-old internode

A — on the day the experiment started, B — 2 cm and C — 12 cm below the cut surface, 40 days after decapitation, followed by application of various substances in lanoline paste. For explanation for substances abbreviations see text. Averages of 5 trees

zone of radial enlargement which developed in these cases (except for auxin) consisted of cells with small radial diameters (only somewhat greater than that of the cells in the cambial zone). Formation of the normal zone of enlarging xylem (although reduced in cell number) was observed only if IAA was present in addition to the substance

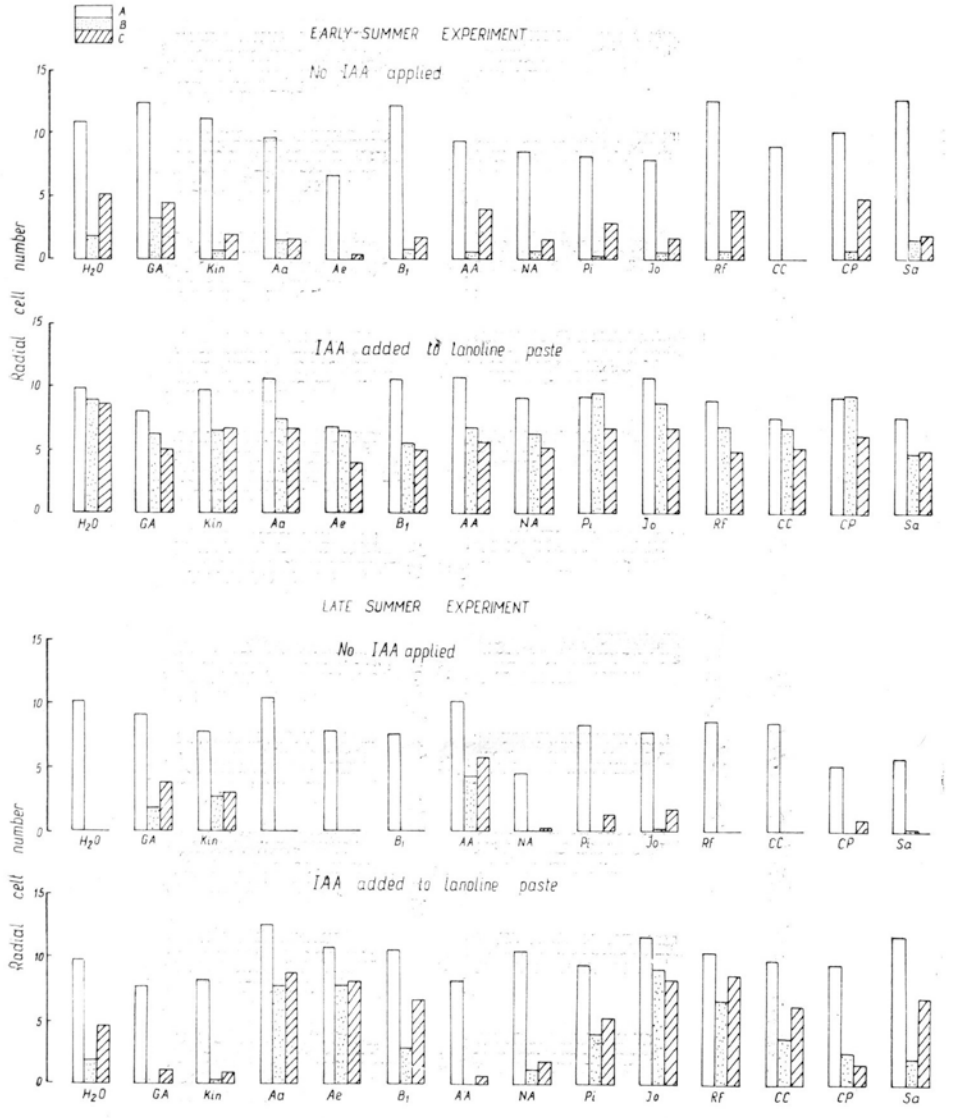
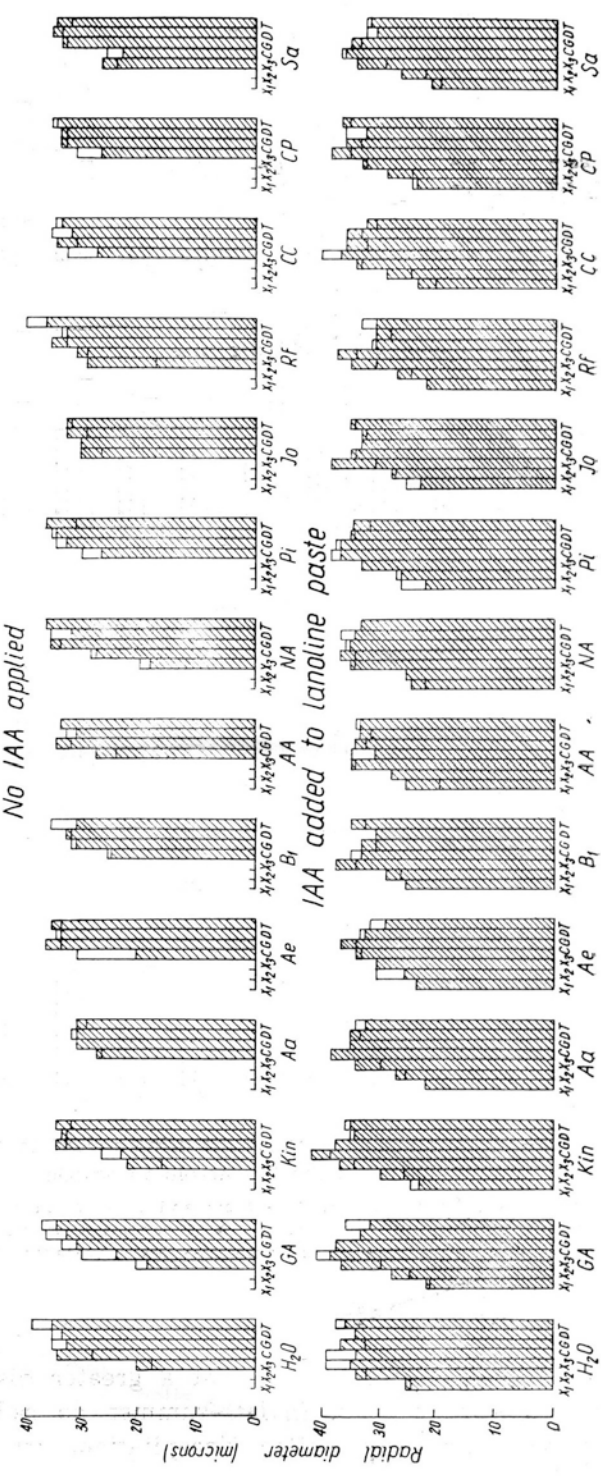


Fig. 3. Radial cell number in the zone of maturing xylem in the stem of young pine trees at the 3-year-old internode

A — on the day the experiment started, B — 2 cm and C — 12 cm below the cut surface, 40 days after decapitation followed by application of various substances in lanoline paste. For abbreviations of substances names see text. Averages of 5 trees

tested. However, this effect of auxin at a greater distance from the cut surface was also reduced. In late-summer no radially enlarging xylem could be distinguished after decapitation, irrespective of the substance applied.


Experiment started June 3rd, ended July 13th, 1970
No IAA applied
IAA added to lanoline paste
Radial diameter (microns)
0
10
20
30
40
H_2O
GA
Kin
Aa
Ae
B_1
AA
NA
P_i
Jo
Rf
CC
CP
Sa

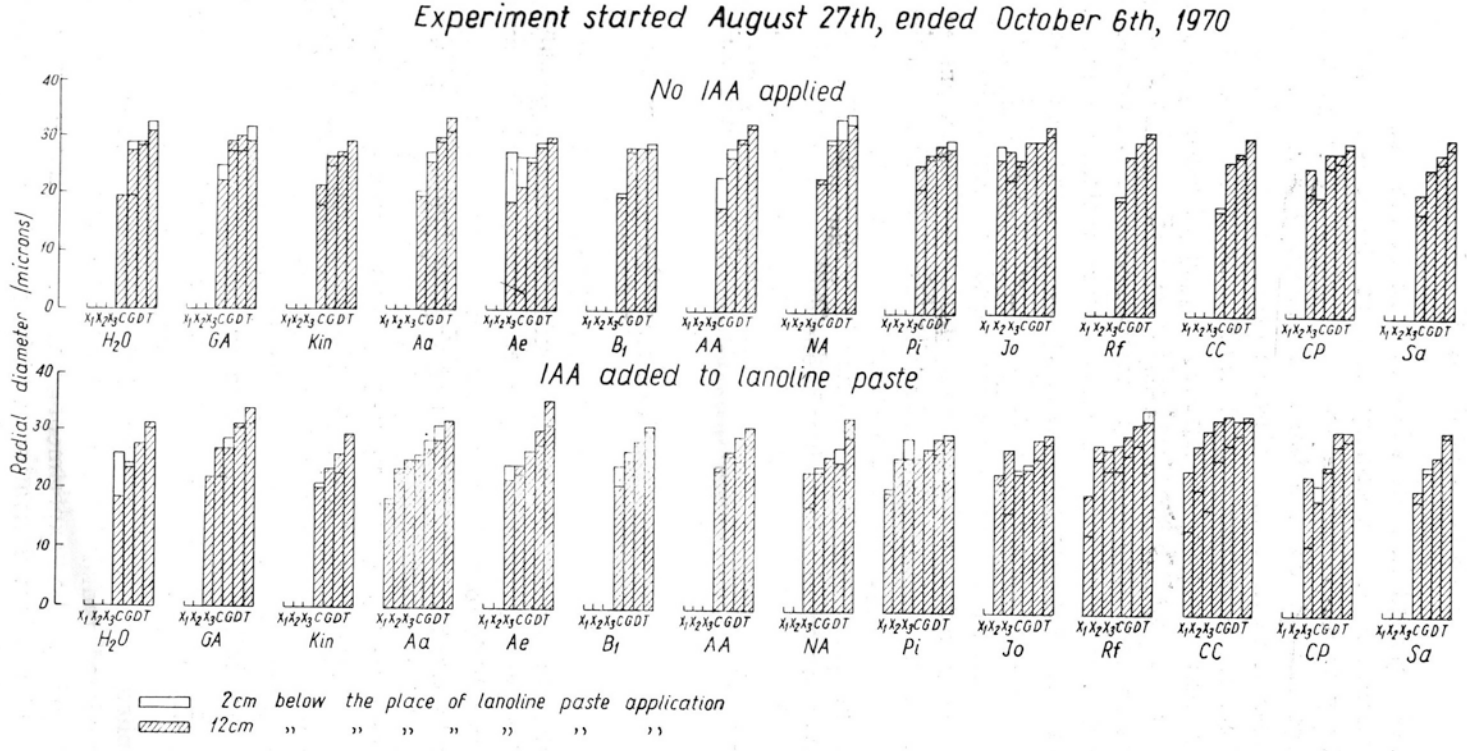


Fig. 4. Eeffect of removal of upper part of crown and application of various substances in lanoline paste upon final diameter of tracheids which at the time of decapitation were still not fully differentiated

Cells which were undergoing division, radial growth and maturation are marked C, G, D respectively. T — refers to tracheids which completed maturation before the experiment started. x_1, x_2, x_3 — represent tracheids which differentiated from cambium after experiment started, the oldest are noted x_3. For abreviations of substances names see text

3. Zone of maturing xylem

Decapitation resulted in a drastic reduction of the number of cells undergoing formation of a secondary wall, in all series in which the cambial activity was also suppressed in early-summer (Fig. 3). In contrast to the effect upon the zone of enlarging xylem, this effect was always less pronounced at a distance of 12 cm than at 2 cm from the cut surface. No substance, except auxin, among the applied series could prevent this effect of decapitation. Supply of auxin resulted in maintenance of the same radial number of maturing tracheids at both levels as that in the intact stem at the beginning of the experiment in early summer. In most series in which other substances were given together with IAA, the effect of auxin was suppressed and reduction of the cell number in the zone occurred.

Few, or no maturing tracheids were found in most series of the late-summer experiment. Auxin alone was little effective in preventing the reduction of the zone of maturation at this time of the season. In series which were supplied with vitamin A (both alcohol and ester form) or inositol and riboflavin, in addition to IAA, the zone of maturation was clearly preserved. The reduced zone could be also distinguished in series supplied with ascorbic acid, gibberellic acid and kinetin applied separately,

4. Radial growth of tracheids

Measurement at the end of experiment of the radial diameter of tracheids which at the beginning were undergoing radial growth (i.e. constituted the zone of radial enlargement) and of those of the cambial zone, or those which formed from cambium in the course of experiment reveals to what extent the cells at various early stages of ontogenesis respond by growth to the applied treatment. It is seen from Fig. 4 that decapitation which limited cambial activity, affected but little the final radial diameter of the tracheids which at that time were undergoing radial enlargement. Neither did separate application of the tested substances produce a significant growth response of these cells. Slight stimulation by auxin alone or in interaction with other substances was detected in the early-summer experiment. Later in summer this effect of auxin was not observed.

Auxin applied alone or with most of the other substances in early-summer stimulated radial enlargement of cells which occupied the cambial zone when the experiment started. It stimulated also the growth of cambial xylem derivatives which formed immediately afterwards. This effect of auxin was not observed in late-summer. In no case,

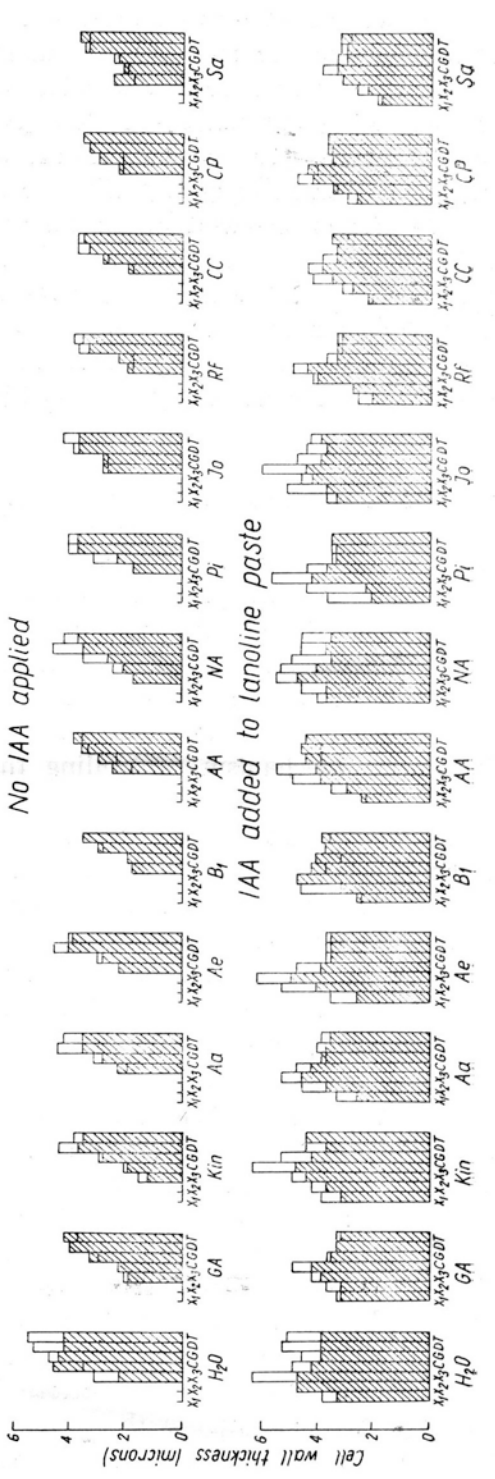
by applying auxin it was possible to maintain this higher level of radial growth stimulation over a longer period, and tracheids differentiated later during the experiment had smaller and smaller diameters. No specific effect of other interacting substances in this respect was significant in early-summer. Slight positive interaction with auxin was noted later in summer with inositol and maybe a few other substances. However, all these observable effects are well in the limits of possible error of measurements. In the case of application of all substances studied alone (except for inositol and water in early-summer) the diameter of the cells which occupied the cambial zone at the time of decapitation was reduced, although they grew above the original size which for the cells in the cambial zone rarely reaches 15 microns.

5. Formation of secondary wall

The final cell wall thickness of tracheids is determined during their maturation which ends by autolysis of protoplast. By measuring at the end of the experiment the cell wall thickness of the tracheids which at the time of decapitation were present in the zones: cambial, of radial enlargement, of maturation and of cells formed still later, it is possible to trace at which stage of cell ontogenesis the applied treatments affected the mechanism controlling the final thickness of the cell wall.

It is seen from Fig. 5 that cell wall formation was not affected, irrespective of the substances applied to the cells which at the time of decapitation occupied the zone of maturation. Greater cell-wall thickness of these tracheids than that of the previously formed mature tracheids in the late-summer experiment reflects probably only the natural seasonal pattern of transition to thick-walled late-wood.

The cell wall of cells undergoing radial enlargement at the time of decapitation and especially of those in the cambial zone was found to be thinner than of the tracheids previously formed. However, if auxin was supplied (alone or in the presence of other substances) the cell wall of these tracheids reached the thickness of that formed by the preceding tracheids or even exceeded it. Ironically the only exception from this rule in the late-summer experiment is the series treated with IAA alone. This was probably due to an abnormally high differences between the number of cells at the stem level studied and the control sections and as such must not be taken into account in further discussion. Some substances (inositol, kinetin, vitamin A, pyridoxine) seem to interact slightly with auxin in stimulating formation of thicker cell walls by tracheids of the cambial zone in early--summer. Auxin induced the first series of new cambial derivatives


Experiment started June 3rd, ended July 13th, 1970
No IAA applied
IAA added to lanoline paste
Cell wall thickness (microns)
0
2
4
6
H2O
GA
Kin
Aa
Ae
B1
AA
NA
Pi
Jo
Rf
CC
CP
Sa

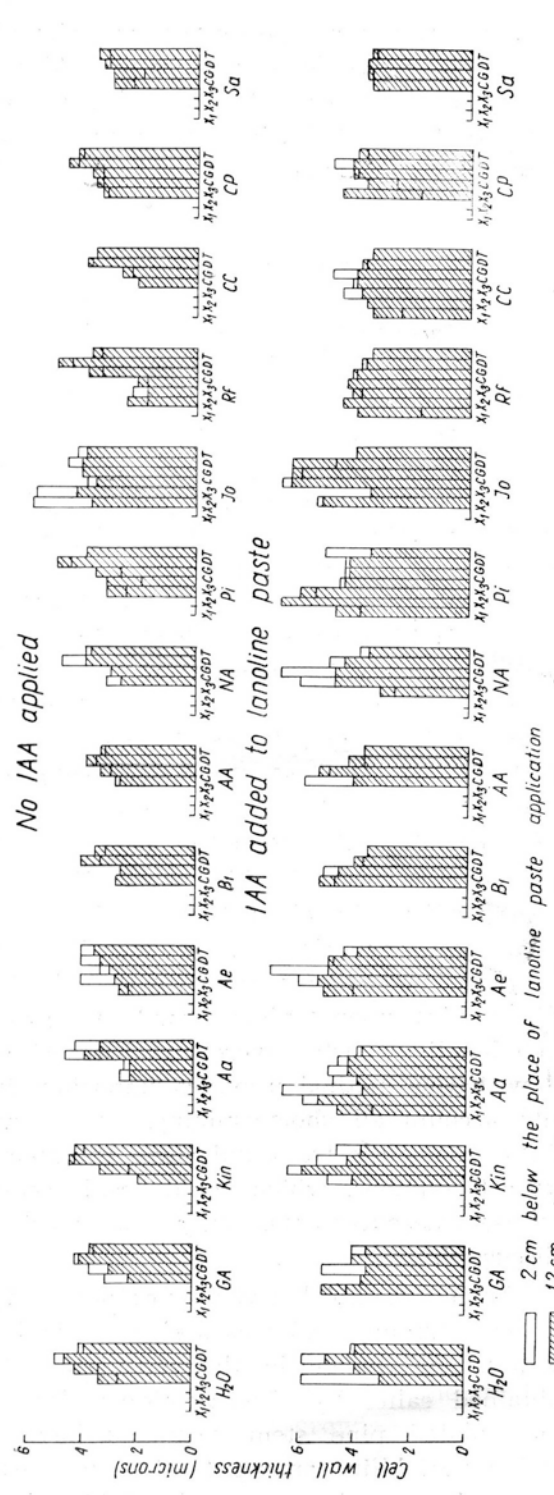


Fig. 5. Effect of removal of upper part of crown and application of various substances in lanoline paste upon the final cell wall thickness of tracheids which at the time of decapitation were not yet fully differentiated

Cells which were undergoing division, radial growth and maturation are marked C, G, D respectively. T — refers to tracheids which completed maturation before experiment started. x_1, x_2, x_3 — represent tracheids which differentiated from cambium after experiment started, the oldest are noted x_3. For abbreviations of substances see text

formed after decapitation in the early-summer experiment to form thicker cell walls during subsequent maturation. Also this effect could be somewhat increased by the substances mentioned above. Over an extended period, the effect of auxin, inducing formation of a thicker secondary wall, decreased to the original lower level.

DISCUSSION

Owing to its simplicity, the method of application of various substances in lanoline paste to decapitated stems is commonly used in large-scale experiments concerning regulation of cambial activity. Decapitation removes the shoot apex, the source of natural auxin, and arrests cambial divisions providing a convenient system for studying the cambial response. Unfortunately, except for nutrients, little is known how decapitation affects the level of substances other than auxin essential for growth, transported from different parts of the plant especially the roots (W e n t, 1938, 1943). Studies by C a r r, R e i d and S k e n e (1964), and M u l l i n s (1967) indicate that cytokinins and gibberellins may be among such substances. The lanoline-paste method does not supply information as to the degree of absorption of the applied substances by the tissues, unless a morphogenetic response is observable. Even then, the actual concentration of the active substances in the shoot remains unknown. The use of labelled compounds in large-scale experiments is rarely possible. Of necessity, the concentrations of substances applied in lanoline must be high (exceeding physiological concentrations) and may affect the absorption by the exposed tissue. Still, for reconnaissance-type experiments, the method proved to be valuable and most of our knowledge concerning the effect of various substances (especially auxin) upon xylem formation came from the experiments in which lanoline pastes were applied. Also presently, the results obtained with this method provided important information. However, taking into account all shortcommings of the method, the considerable variability among the trees and along the stem in respect to the radial xylem cell number, which could result occasionally in not sufficiently precise measurements, only the most convincing responses will be discussed.

Auxin promoted further cambial xylem production in spite of decapitation only in early-summer and was ineffective in late-summer, revealing distinctly seasonal change in the sensitivity of cambium. Thus the results obtained ealier by Z a j ą c z k o w s k i (1973) with a sterile culture of isolated pine stem segments have been fully confirmed. Considerable variability among treatments does not allow a positive conclusion whether the observed slight stimulation by

inositol, vitamin A (alcohol) or pyridoxine in interaction with IAA were really significant, although later measurements seem to confirm the effects of those substances. In any case, none of the applied substances was capable of restoring the early-summer sensitivity of cambium to auxin and probably was not a limiting factor in respect to cambial cell division. On the contrary, most of the substances in the concentration applied seemingly retarded somewhat this response of cambium to auxin in early-summer. Among these, the effects of gibberellic acid and kinetin are among the most pronounced. The finding concerning GA agrees with the observations by Zajączkowski (1973) obtained in pine stem culture. Kinetin was reported, however, to interact synergistically if applied together with auxin and gibberellic acid to pine decapitated shoots at the time of spring initiation of cambial activity (Hejnowicz and Tomaszewski 1969). It was demonstrated by these authors that kinetin and gibberellin could increase the rate of auxin transport in the shoot. On the other hand kinetin was found to reduce the induced growth of pine hypocotyl in bioassays (Zakrzewski, 1971).

Seasonal differences in response to the applied treatments were observed also in respect to the cells advanced in differentiation.

The radial diameter of the cells which were already in the zone of radially enlarging xylem at the time of decapitation was not reduced. Also, only insignificant effects of the applied substances (including auxin) upon the growth of tracheids at this ontogenetic stage were observed. The cells which responded to treatment as regards their radial growth were only those which at the time of decapitation occupied the cambial zone or were formed later. Decapitation limited their subsequent growth and auxin promoted it. However, the stimulating effect of auxin decreased progressively, and none of the applied substances could prevent this decline. An analogous short duration of the stimulation of radial enlargement of tracheids by auxin was earlier observed in pine by Larson (1960).

No relation was observed between the width of the zone of enlarging xylem observed at the end of the early-summer experiment and the radial diameter of tracheids which formed from the cambial zone. The zone of radially enlarging xylem was reduced and large-diameter cells formed in the case of auxin treatment. A wide abnormal zone of flattened cells was observed if gibberellic acid was applied, but the diameter of cells was reduced. The zone was not reduced and the diameter of tracheids remained constant in the treatment with inositol. In late summer when no zone of growing tracheids was distinguished, the interaction of inositol, pyridoxine, riboflavin and calcium chloride with auxin seemed beneficial in stimulating enlargement of tracheids.

This lack of correlation of the radial diameter of tracheids which formed from the cambial zone with the width of the zone of enlarging xylem (which may be used as an index of duration of growth) lends support to the hypothesis that decapitation and auxin affect primarily the rate of growth and less its duration. Moreover, the small effect upon the growth of cells which at the time of decapitation occupied the zone of enlarging xylem may indicate that most of the radial growth was accomplished soon after emergence of the cells from the cambial zone.

In plants treated with auxin, the tracheids originated from cells constituting the cambial zone at the time of decapitation, and those formed immediately afterwards produced thicker cell walls than all previous tracheids. Tracheids in the stage of maturation or radial growth remained unaffected. Thus, it seems reasonable to conclude that the effect of auxin upon the final cell wall thicknes of tracheids is the result of alteration of the developemental pattern of the tracheids while they are still in the meristematic stage. It may be pertinent to mention that the result obtained earlier in experiments concerning the effect of photoperiodic conditions upon xylem differentiation (Wodzicki, 1961) lead to similar conclusion. Induction concerning determination of some features characteristic for reaction wood in gymnospersms, is also reported to occur at early stages of tracheid differentiation (Wardrop and Davies, 1964; Kennedy and Farrar, 1965 b; Casperson and Zinsser, 1965; Westing, 1968; Scurfield, 1973).

In all cases in the early-summer experiment, decapitation drastically reduced the zone of maturing tracheids, as reported also by Farrar and Fahn (1970) in their experiments. In both studies the effect was observed as late as 35—40 days after decapitation, but certainly it had to develop gradually if the cells in the zone of maturation at the time of decapitation completed their secondary wall unaffected.

The width of the zone of maturation was not extended after auxin application what would indicate extension of the time of secondary wall deposition. In this case, auxin seemingly induced changes in the rate of cell wall deposition. This seems to be a different mechanism from that controlling formation of thick-walled late-wood in nature which operates through extension of the maturation period (Wodzicki 1971). It is rather similar to auxin induction of reaction-wood observed by Wershing and Bailey (1942) and others. Especially that, the thick-walled tracheids of reaction-wood were reported to differentiate in shorter time than normal tracheids, and this implies an increased rate of cell wall deposition. Unfortunately it was not possible at present to trace changes in the width of the zones soon after decapitation and calculate the exact time of differentiation

of tracheids which would allow more conclusive information. It has been observed that reduction of the zone of maturing xylem after decapitation in early-summer was less, with greater distance from the cut surface of the stem. This effect of decapitation could also be prevented by auxin. Other substances (vitamin A, inositol and riboflavin) appeared beneficial in extending this effect of auxin also to the later part of the summer. From these facts a rather indirect effect of auxin upon termination of tracheid differentiation may be tentatively concluded. The attraction of transport of other substances, as postulated by other authors (Seth and Wareing, 1967), could be provisionally accepted for the described short-term effects of auxin resulting in formation of thick-walled tracheids.

Auxin alone or in interaction with any of the applied substances was not capable of stimulating extension of the zone of maturation in early-summer, neither was it capable of preventing reduction of this zone in late-summer. On the other hand, in late-summer, inositol alone proved sufficient for stimulation of normal thickening of the cell wall, and in interaction with IAA prevented reduction of the zone of maturation. In the latter process riboflavin, pyridoxine and vitamine A in interaction with IAA were also effective. These effects, especially the role of inositol which was found to stimulate cambial activity in roots (Loomis and Torrey, 1964) deserve further investigation.

CONCLUSIONS

From the discussion of the experiments presented above the following generalizations seem possible:

1. None of the effects of the substances studied appeared significant enough to indicate the involvement in the seasonal variation of the response of cambium or differentiating tracheids to auxin. However, several effects, especially those of inositol, vitamin A and pyridoxine upon cambial xylem production and further stages of tracheid differentiation were observed and deserve further attention.

2. Synthetic auxin (IAA) affects production of xylem derivatives from the cambial zone and their subsequent differentiation in decapitated stems of pine during the earliest ontogenetic stages. At these stages auxin may induce quantitative expression of the developmental processes involving radial growth and secondary wall formation, probably by affecting the programming of the rate of these processes. In this respect auxin affects but little the xylem cells advanced in differentiation.

3. Cells of the cambial zone undergo seasonal change in response to auxin. Their response in late-summer is greately reduced. This change

concerns production of cambial xylem derivatives and completion of the full cycle of their differentiation. In the latter effect an indirect action of auxin is suspected.

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Wpływ auksyny na różnicowanie cewek drewna w dekapitowanych pędach głównych Pinus silvestris L. i jej interakcja z niektórymi witaminami i regulatorami wzrostu

Streszczenie

Badano wpływ kilku witamin i substancji czynnych w procesach regulacji metabolizmu komórki na różnicowanie wtórnego ksylemu u 5-letnich dekapitowanych drzewek *Pinus silvestris*. Badano interakcje tych substancji z auksyną (IAA) dostarczonych do pędów w lanolinie wczesnym i późnym latem. Testowano następujące substancje: kwas giberelinowy, kinetyna, kwas nikotynowy, tiamina, pyridoksyna, pantotenian wapnia, chlorek choliny, ryboflawina, inozytol, kwas askorbinowy, witamina A (alkohol), witamina A (ester), saponina. Żaden z efektów wywołanych przez te substancje nie okazał się wystarczająco istotny, by można było uznać jego znaczenie dla określenia sezonowych zmian w responsywności kambium lub różnicujących się cewek na działanie auksyny. Niektóre efekty, szczególnie wpływ inozytolu, witaminy A i pyridoksyny na tworzenie się ksylemu z kambium i różnicowanie pochodnych zasługują na dalszą uwagę. Wpływ auksyny (IAA) na aktywność kambialną i różnicowanie cewek obserwowano tylko w najwcześniejszych stadiach ontogenezy. W tych stadiach działanie auksyną indukowało ilościowy aspekt procesów rozwojowych takich jak wzrost radialny i tworzenie wtórnej ściany komórkowej. Pod tym względem auksyna nie wpływała na komórki zaawansowane w różnicowaniu, okazała się jednak ważnym czynnikiem potrzebnym do tego, by cykl różnicowania komórki był kompletny.