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Apical control of xylem formation in the pine stem. I. Auxin effects and distribution of assimilates

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Abstract

The effect of IAA upon cambial activity, xylem differentiation and translocation of assimilates from the lateral shoot was investigated in spring and late summer in decapitated and ring-barked young trees of *Pinus silvestris* in the forest stand. Decapitation interrupted cambial xylem production in the uppermost part of the main stem of decapitated trees in spring and late summer, regardless of whether lateral branches below were growing, dormant or disbudded, and the contact through phloem with the roots was maintained or severed. Auxin supplied to the decapitated stems caused an increasing stimulation of cambial xylem production in spring. It also stimulated cambial activity in August but was ineffective in September. Apical control of cambial xylem production was strongly dependent upon the continuity of phloem and/or cambial tissues of the decapitated main-stem-section with lower parts of the plant. Decapitation of the stem strongly reduced the daily rate of cell wall deposition in the cambial xylem derivatives which on the day the experiment started constituted the zones of radial enlargement and maturation. This reduction limited progressively secondary wall deposition in consecutive maturing tracheids even though the cells differentiated longer. Irrespective of the season, auxin prevented the effect of decapitation in cells which were already differentiating when the experiment started as well as extension of the maturation phase. The effect of auxin was somewhat reduced when the lateral branches were additionally decapitated in early summer. In early summer auxin caused a significant increase of the daily rate of cell wall deposition in cells of the cambial zone or the newly produced ones, thus resulting in formation of progressively thicker secondary walls. Late in summer assimilates were transported mostly to the lower part of the stem. Decapitation changed the intact tree pattern of assimilate distribution, increasing the transport in spring and reducing it later in the summer. Prevention of the contact with roots via phloem and cambium in spring (by ring-barking the stem at tree base) decreased decapitation-induced downward transport of assimilates. Application of auxin to the decapitated uppermost

segment of the main stem resulted in a significant increase of assimilate translocation into the stem. At least two mechanisms of auxin involvement in regulation of the rate of secondary wall deposition in pine stem tracheids can be considered: (a) induction (or activation) of the cell wall metabolic potential which seems to occur during meristematic or early radial enlargement phases of tracheid differentiation, and (b) regulation of substrate availability during the phase of tracheid maturation.

INTRODUCTION

Investigation of the auxin effect in decapitated or ring-barked trees of *Pinus silvestris* L. (W o d z i c k i and W o d z i c k i 1973, W o d z i c k i and Z a j ą c z k o w s k i 1974) raised several questions concerning the mechanism by which this hormone is involved in the control of stem xylem differentiation, especially in phases further than meristematic. It was observed that auxin-treated plants produced thick-walled tracheids. However, the experiments did not answer the question if auxin affected the daily rate of cell wall deposition or the duration of maturation phase of differentiating tracheids. The possibility of both effects was reported for other tree species (N i x and W o d z i c k i 1974, D e n n e and W i l s o n 1977). Neither was it known whether the applied treatment, especially application of auxin, could be related to any effects on distribution of assimilates, as suggested by others (S e t h and W a r e i n g 1967).

Two experimental approaches to these problems were tested: a) application of auxin to decapitated stems with simultaneous removal of the bark and phloem ring, thus separating the portion of the stem exposed to auxin, or of the root system from the rest of the plant (experiments were performed during three consecutive seasons 1973-75); b) tracing of transport of radioactive derivatives of photoassimilation of CO_2 to the stem portion decapitated and exposed to auxin (experiments performed during three seasons: 1973, 1974 and 1977).

MATERIAL AND METHODS

Two seasonal experiments were started in May and August in each of the three seasons 1973-75, with 5- to 6-year-old plants of *Pinus silvestris* L. in the plantation of Experimental Forests in Rogów. Trees were decapitated about 18 cm above the 3rd, or 4th whorl of branches and some of them were ring-barked (1 cm wide strip of phloem and cambial zone removed around the stem) at the base of the decapitated yearly stem increment, or at the tree base. Lateral branches in a few series were decapitated and disbudded. Each experimental series comprised 5 trees.

IAA (conc. 0.5 per cent) in lanolin-water paste (3 : 1, w/v) was applied to the cut surfaces of decapitated stems. Control series with no auxin treatment and intact trees were included. Lanolin was changed every 10 days and after periods of 10 to 50 days the treated stem segments were collected for anatomical examination. The small segments of the stem removed by decapitation (corresponding to the decapitated stem segment remaining with plant) were collectd on the days the experiments started as reference for investigation of xylem increment. All the material was preserved in formol-calcium fixative (Barka and Anderson 1962) or in 70 per cent ethanol until sectioned. After staining with safranin and light green the tranverse stem sections were mounted in Canada balsam and the extension of the zones of differentiating xylem distiguished according to Wilson et al. (1966) was investigated under the light microscope as described earlier (Wodzicki and Zajączkowski 1974). The sections for investigation were obtained 2 cm below the decapitated surface of the stem, and the control stem pieces (collected on the day the experiment started) were sectioned as close to the cut surface as possible. The complete list of treatments and dates of experiments are summarized in Table 1 and Fig. 1.

Experiments concerning translocation of radioactive assimilates were performed in a small plantation of 3- and 4-year-old *Pinus silvestris* in the park of the Warsaw Agricultural University. The main stems of the plants were decapitated 12 cm above the 2nd or 3rd whorl of branches and some were additionally ring-barked at the tree base. All needles were removed from the decapitated main stem yearly increment segments. IAA was applied in lanolin as previously described. One of the well-developed lateral branches just below the decapitated stem section in each plant was enclosed in a 30 × 35 cm polyethylene bag and sealed with plasticin. $Na_2{}^{14}CO_3$ was introduced into the bags and $^{14}CO_2$ (60 μCi per bag) was liberated in the bags by lactate. In each of the 3 years (1973, 1974 and 1977) exposures started early in the morning at 6 or 7 a.m. and ended 1.5-2 hrs later by removal of the bags. The transport of labelled assimilates was allowed for 11 to 12 consecutive hours, and the plants were harvested for measurements.

The bark, consisting mainly of the first periderm, phloem and some of the cambial zone was collected from the main stem yearly increments above and below the $^{14}CO_2$-exposed branch separately. As measure of total radioactivity assimilated by the trees, the needles (separately young and mature) were analysed. The differences between trees were not significant. All samples were homogenized in 80% ethanol and radioactivity of the soluble fraction was estimated. Averages of three replicate trees were calculated per 1 g of fresh weight. Radioactivities in particular years are not directly comparable because of different conditions of the experiments.

Table 1

Increment of new xylem cells formed from cambial zone in radial direction. Means of five trees. Description of symbols below table. Except for intact controls, trees were decapitated or also ring-barked at the tree base or below the place of decapitation of the main stem. Auxin /IAA/ was applied in lanolin paste to decapitated stems in some series. In brackets - daily increment

Early-summer experiment				Late-summer experiment			
Experimental series	period of treatment			Experimental series	period of treatment		
	May 20-June 19, 1973	May 21-June 30, 1974	May 21-July 10, 1975		Aug. 21-Oct. 1, 1973	Aug. 7-Sept. 16, 1974	Aug. 11-Sept. 19, 1975
	40 days		50 days		40 days		
	31/0.8/	45/1.1/	51/1.0/		10	40	33
	4±1/0.1/	5±1/0.1/	- x		4±1	4±1	2±1
	10±3/0.2/	-	8±3/0.16/		-	4±1	
IAA 	63±4/1.6/	62±7/1.6/	95±6/1.9/	IAA 	16±2	29±6	28±6
IAA IAA IAA 	-	-	108±8	———	-	-	-
	7±2	-	-		10±4	9±5	-
IAA 	95±13/2.4/	57±4/1.4/	94±7/1.9/	IAA 	19±1	48±4	40±8
IAA 	121±8/3.0/	-	137±10/2.7/	IAA 	-	32±4	-
IAA 	-	89±2/2.2/		IAA 	-	49±5	-

Description of symbols.

 - growing shoot apex;

 - terminal bud;

 - decapitated shoot;

 - needles

 - ring-barked shoot

x/ The series was not represented in this season

The experimental treatments with $^{14}CO_2$ are summarized in Fig. 5. Dates of the treatments are specified below.

Season 1973. Decapitation of the main stem on: May 29 and June 5 in spring, and on August 20 and 27 in late summer. IAA applied to decapitated stem segments on: May 29 and August 20, and exposures to $^{14}CO_2$ on June 6 and August 28.

Season 1974. Decapitation of the main stem, ring-barking at the tree base, and application of IAA on May 30 and August 12 in two seasonal experiments. Exposure to $^{14}CO_2$ on May 31 and August 13, respectively.

Season 1977. Decapitation and application of IAA to all shoots and/or to main shoot or lateral branches only on May 14 and 25 respectively. Exposure to $^{14}CO_2$ occured on May 26.

RESULTS AND DISCUSSION

CAMBIAL PRODUCTION OF XYLEM

Decapitation interrupted cambial xylem production in the uppermost part of the main stem of all decapitated trees in spring and late summer, regardless of whether the lateral branches below were growing, dormant or disbudded, and the contact through phloem with the roots was maintained or severed (Table 1). After decapitation only few additional cells were deposited. Periodic collection of the plants treated with auxin at the decapitated stem revealed that in spring the auxin caused an increasing stimulation (Fig. 1A) and by the end of the experiment the daily rate of xylem formation doubled the mean rate of cambial activity of intact trees (Table 1). Also in late summer, auxin stimulated a greater daily xylem production than in intact controls but only until mid-August (Fig. 1B), and the final rate did not reach the level of stimulation observed in spring. In September, auxin treatment became ineffective. The experiments confirmed the previous suggestions that cambium of some conifers is less sensitive to auxin late in the season than in spring (Zajączkowski 1973, Wodzicki and Zajączkowski 1974, Denne and Wilson 1977).

Apical control of cambial xylem production was strongly dependent upon phloem and/or cambial contacts of the decapitated main stem section with the lower parts of the plant (demonstrated in plants ring-barked at the base of the decapitated stem segment, Table 1). Decapitation of lateral branches in spring additionally increased cambial activity. Moreover, the differentiation of the cambial xylem derivatives in these plants altered. Many shorter tracheids with horizontally bent ends differentiated in radial rows instead of long axial tracheids, and xylem parenchyma (both of xylem rays and associated with resin canals) proliferated. As the new underdeveloped shoots were removed by decapitation the investigated parts of the main stem were freed, first of all,

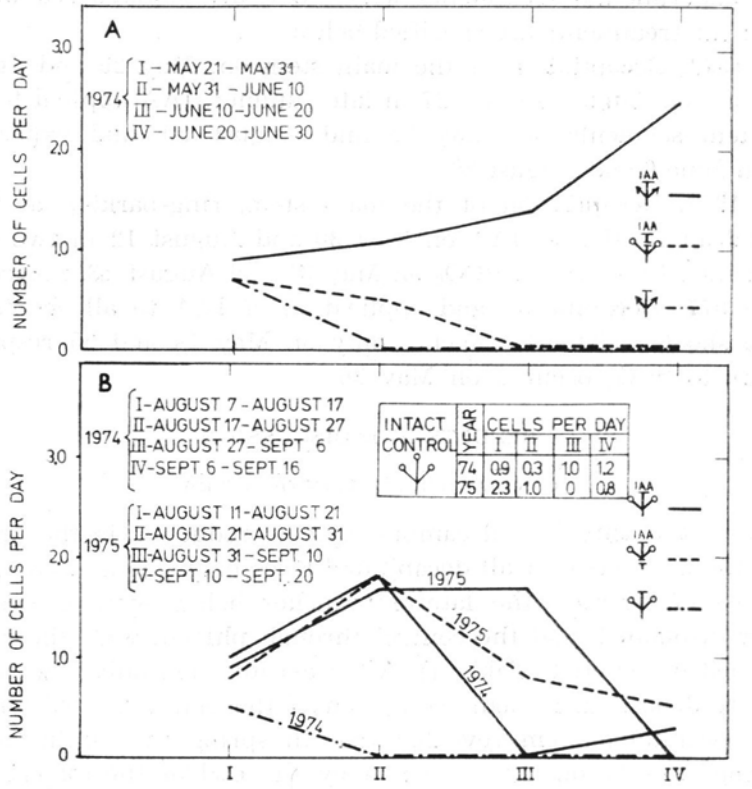

Fig. 1. Effect of main stem decapitation (with or without IAA treatment) and ring-barking of pine upon cambial xylem production. Measurements at 10-day intervals. A — spring, B — late summer experiments. For description of symbols see Table 1

Fig. 2. Effect of main stem decapitation, ring-barking and disbudding of lateral branches of pine with or without IAA application to the decapitated stems, upon radial diameter of tracheids

I — spring experiments started in May and ended 40 (1973, 1974) or 50 (1975) days later. A, B, C, — mean of three seasonal experiments 1973, 1974, 1975; E — mean of two seasonal experiments 1973, 1975; D, F — mean of one seasonal experiments 1975, 1974, respectively

II — late summer experiments started in August and ended 40 days later. A, B, E — mean of three seasonal experiments 1973, 1974, 1975; C, D — mean of one seasonal experiments 1974

Cells which on the day the experiment started were undergoing division, radial growth and maturation are marked C, G, D, respectively; T_1, T_2, T_3 refer to tracheids which completed maturation before the experiment started; X_1, X_2 represent tracheids which differentiated from cambium after the experiment started; the oldest are noted T_1 and X_1. For description of symbols see Table 1

A
B
C
D
E
F
G
IAA
RADIAL DIAMETER, µm
40
30
20
10
0
I
T D G C X1 X2
T D G
T1 T2 T3 D G C X1 X2
T1 T2 T3 D G
T1 T2 T3 D G C
II

from their competition for assimilates. In August, when lateral shoots were already terminated by buds, the effect of decapitation of the branches was not observed, however, prevention of eventual transport of assimilates to roots by ring-barking of the stem at the tree base, appeared stimulating and extended somewhat the period of xylem formation (Fig. 1 B). Application of IAA to all decapitated shoots in May 1975 (Table 1) limited somewhat the previously described effects, indicating that, except for competition for assimilates, some other "correlative growth phenomena" were probably involved.

DEVELOPMENTAL CHANGES IN THE MORPHOLOGY OF TRACHEIDS

Cambial xylem derivatives grow radially and form the secondary wall during two consecutive phases of differentiation following the meristematic stage. On the transverse sections of the stem the differentiating tracheids form three destinguishable zones: cambial, radial growth and maturing (W i l s o n et al. 1966). By measuring the diameter and cell wall thickness of mature tracheids which at the beginning of the experiment were still differentiating (or could be located in the particular zones of differentiation and the zone of mature tracheids by comparison of the radial cell numbers in transverse sections of stem segments collected at the start and end of the experiments) it is possible to trace at which stage of differentiation the mechanism controlling final dimensions of the tracheids is affected by the experimental treatments.

Radial growth of differentiating tracheids

Decapitation affected but little (Fig. 2) the final radial diameters of the tracheids which on the days the experiments started were in the stage of radial enlargement (or could be located in the zone of enlarging xylem). Neither did auxin or any other treatment applied in the experiments performed in 1973 or 1974 produce a significant growth response of these cells irrespective of the part of the season. These conclusions are supported by an similar lack of auxin stimulation of growth of the cells which at the time of decapitation constituted the cambial zone. In fact, in early summer the diameter of these cells did not reach even the size of the tracheids differentiated in intact trees, or before stem decapitation, in spite of auxin treatment. A slight stimulation could be ascribed to experimental treatments only in trees decapitated on all branches in spring or ring-barked at the ground level in late summer if auxin was simultaneously applied to decapitated main stem.

As seen, the results gave little information on the mechanism controlling radial growth of differentiating tracheids in pine. The substances translocated acropetally in phloem seem to play a secondary role, and auxin is probably not the sole substance involved in apical control of radial growth of tracheids.

Secondary wall formation

Decapitation of stem strongly reduced the daily rate of cell wall deposition in the xylem cambial derivatives which on the day the experiment started constituted the zones of radial enlargement and maturation (Figs. 3 and 4). This reduction limited progressively secondary wall deposition in consecutive maturing tracheids even though originally the cells differentiated longer. Auxin treatments prevented extension of the maturation phase (induced by decapitation). The effect of auxin was somewhat reduced when lateral branches were additionally decapitated in early summer.

Replacement of apical stem parts with IAA in lanolin paste caused a significant increase of the daily rate of cell deposition in early summer which resulted in formation of progressively thicker secondary walls not seen in intact trees. The thickest cell walls were formed by cells which on the day of first auxin application were meristematic of formed from cambium still later. In August-September, these effects, of auxin were hardly noticeable or were not manifested, thus the suggested earlier seasonal change in response of differentiating tracheids to auxin was fully confirmed. The effects of auxin upon the rate of cell wall deposition, the insignificant effects upon duration of the tracheid maturation phase, additional stimulation of the rate of cell wall formation caused by removal (or separation) of the organs competing for assimilates, all suggest involvement of auxin in apical control of distribution, availability and utilization of carbohydrate substances.

CONTROL OF DISTRIBUTION OF ASSIMILATES

Experiments performed in 1974 revealed a seasonal change of assimilates distribution in intact trees. Late in summer assimilates were transported mostly to the lower part of the stem (and probably to the roots), (Fig. 5 C). Decapitation changed the intact-tree pattern of assimilate distribution increasing transport in spring and reducing it later in summer (Fig. 5 D). The effect, however, was manifested only shortly after (1 day) decapitation. The effect did not subsist for a long time because after 12 days transport into the main stem was lower than in intact plants (experiments in spring 1977, Fig. 5 F, C). Application of auxin to

Table 2

Effect of main stem decapitation and auxin treatment upon translocation of radioactive assimilates in cortical tissues of young pine trees. Dates of $^{14}CO_2$ exposure: May 31 and August 13, 1974. Trees were decapitated, ring-barked and treated with IAA 1 day before exposure to $^{14}CO_2$. Radioactivity was measured above and below the whorl to which $^{14}CO_2$ was applied (average of 3 trees)

Experimental treatment of main stem	Radioactivity, 10^3CPM/g.fr.wt.			
	May		August	
	above	below	above	below
Decapitation	2.50	12.14	0.0	0.06
Decapitation plus IAA	6.38	21.60	trace	0.16
Decapitation and ring-barking	2.52	4.04	0.06	0.16
Decapitation plus IAA and ring-barking	2.52	0.40	1.68	0.44
Intact trees	0.12	0.14	0.0	0.79

the decapitated uppermost segment of the main stem resulted in a significant increase of assimilate translocation, provided the exposure was long enough. Auxin applied for 10 to 24 hrs following the 12-day decapitation period increased translocation slightly (Fig. 5 G, H). Eight-day auxin treatment highly increased transport of assimilates to a decapitated segment in spring (Fig. 5 B). Unfortunately in 1973 only upstem transport was studied. If in 1974 auxin was applied in spring simultaneously with decapitation, the increase of transport to the main stem was observed already after 24 hrs (Fig. 5 D, E). None of the described auxin effects was observed in autumn (Fig. 5 A, B, D, E). Prevention of contact with roots via phloem and cambium in spring (by ring-barking the main stem at the tree base) decreased decapitation-induced downward transport of assimilates (Fig. 5 D, Table 2). Application of auxin decreased even this down-ward transport (Fig. 5 E). Later in summer, combined effects of ring-barking and auxin resulted in increasing the upward transport of assimilates into the main stem (Fig. 5 E). If auxin was not applied, the effects of ring-barking were not manifested.

CONCLUDING REMARKS

At least two mechanisms of auxin involvement in regulation of the rate of secondary wall deposition in pine stem tracheids can be considered: a) induction (or activation) of the cell wall metabolic potential which seems to occur during the meristematic (or early radial enlargement) phase of tracheid differentiation, and (b) regulation of substrate

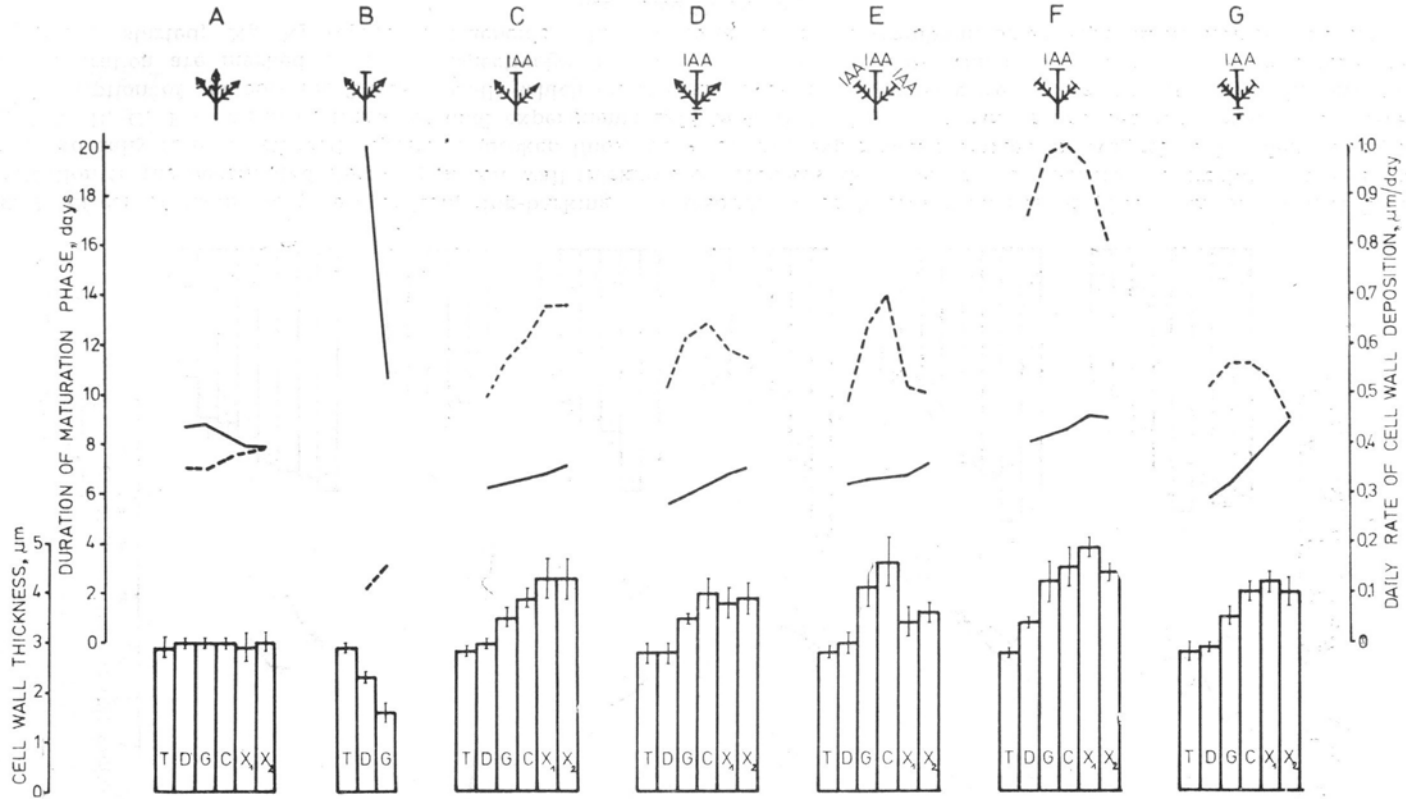

Fig. 3. Effect of main stem decapitation, ring-barking and disbudding of lateralbranches of pine with or without IAA application to the decapitated stems, upon cell wall thickness of tracheids, duration of the tracheids maturation phase (solid lines) and daily rate of cell wall deposition (broken lines). Spring experiments started in May and ended 40 (1973, 1974) or 50 (1975) days later. A, C, D — mean of three seasonal experiments 1973, 1974, 1975; B, F — mean of two seasonal experiments 1973, 1974 and 1973, 1975, respectively; F, G — mean of one seasonal experiments 1975, 1974, respectively cells which on the day the experiment started were undergoing division, radial growth and maturation are marked C, G, D, respectively; T refer to tracheids which completed maturation before the experiment started; X_1, X_2 represent tracheids which differentiated from cambium after experiment started; the oldest are noted X_1. For description of symbols see Table 1

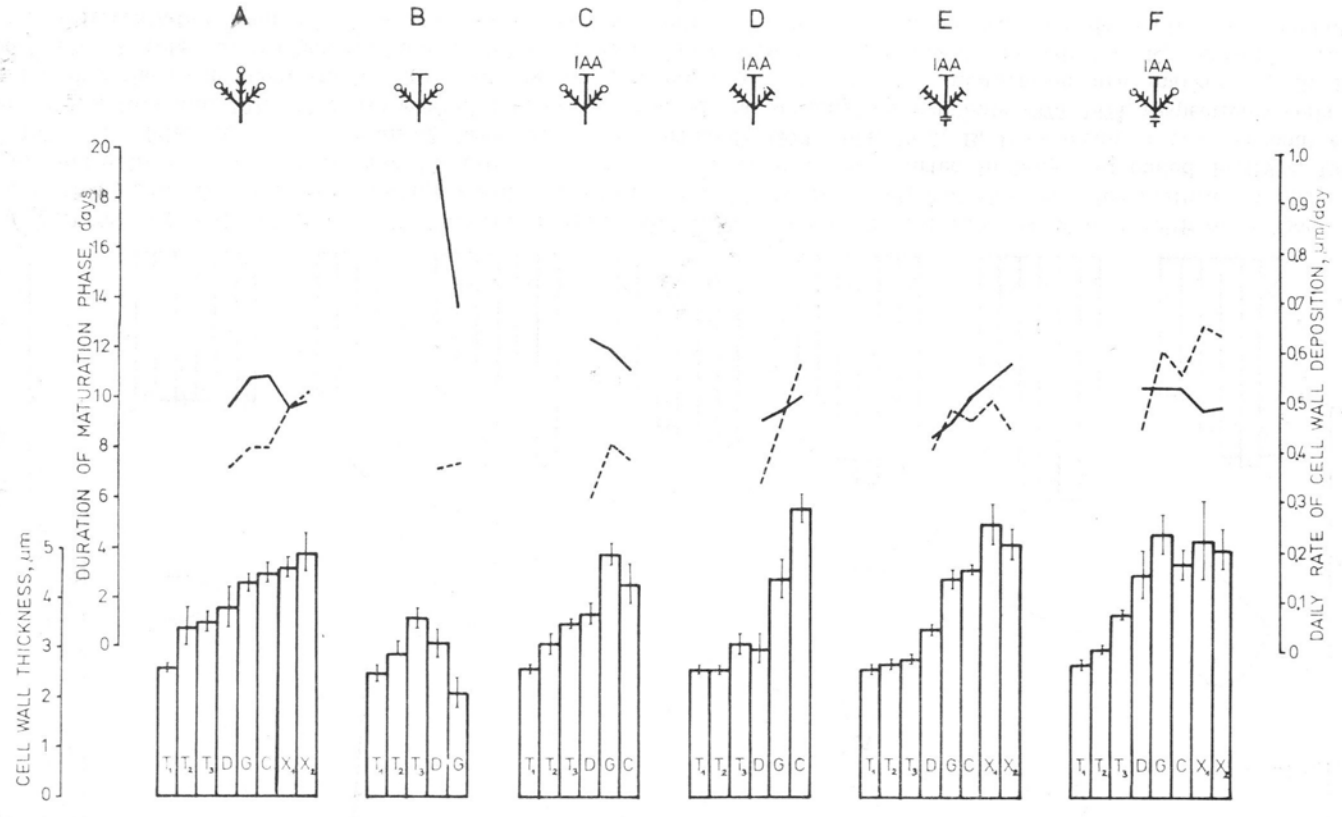

Fig. 4. Effect of main stem decapitation, ring-barking and disbudding of lateral branches of pine with or without IAA application to the decapitated stems, upon cell wall thickness of tracheids, duration of the tracheid maturation phase (solid lines) and daily rate of cell wall deposition (broken lines). Late summer experiments started in August and ended 40 days later. A, B, C, F — mean of three seasonal experiments 1973, 1974, 1975; D, E — mean of one seasonal experiments 1974 For description of symbols see Table 1. Cells which on the day experiment started were undergoing division, radial growth and maturation are marked C, G, D respectively; T_1, T_2, T_3 refer to tracheids which completed maturation before the experiment started; X_1, X_2 represent tracheids which differentiated from cambium after experiment started; the oldest are noted T_1 and X_1

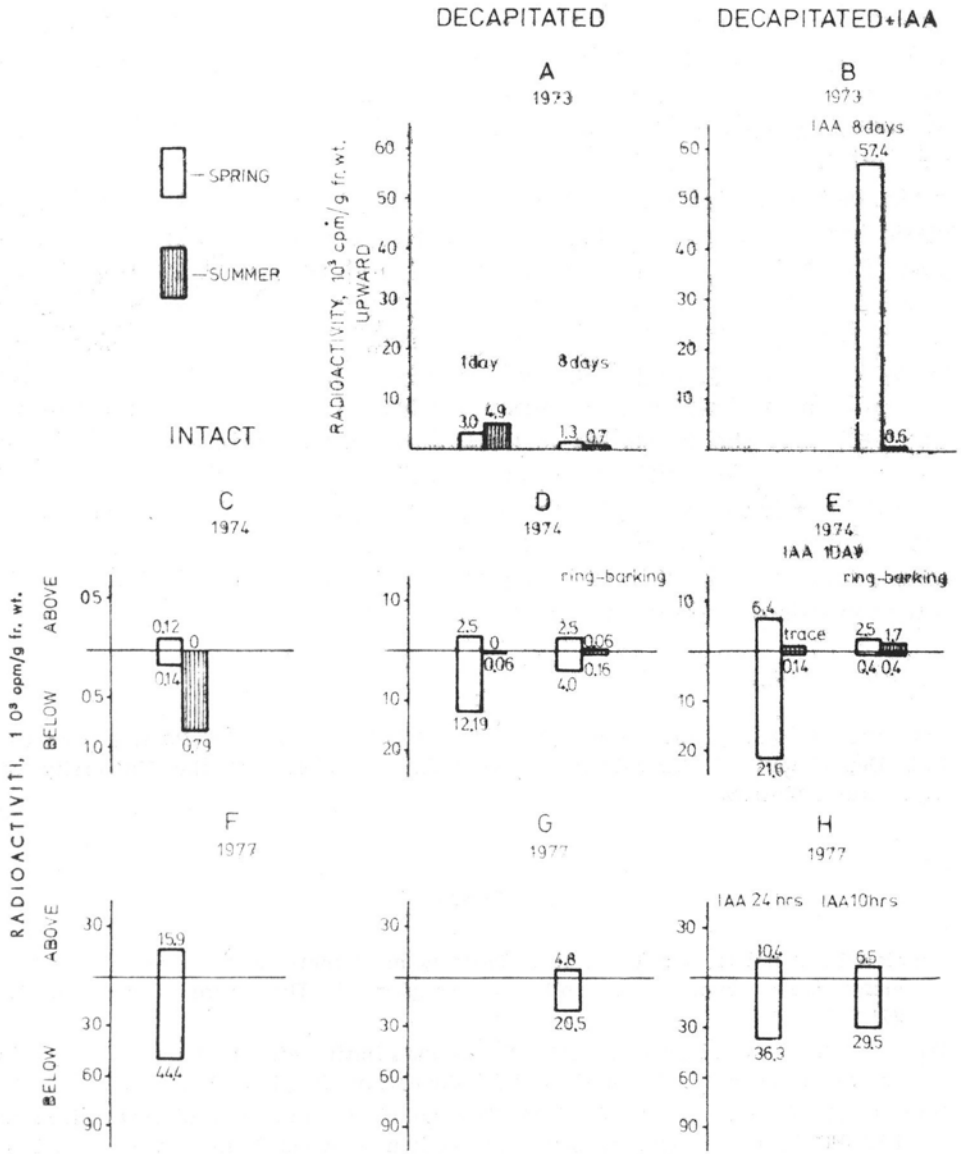

Fig. 5. Effect of main stem decapitation and auxin treatment upon translocation of radioactive assimilates in cortical tissues of young pine trees. Means of three replicate trees. Dates of $^{14}CO_2$ exposure; June 6 and August 26, 1973 upper row; May 31 and August 13, 1974 middle row; May 26, 1977 bottom row. Trees were decapitated and treated with IAA 1 or 8 days before exposure to $^{14}CO_2$ in 1973 and 1 day in 1974; in 1977 trees were decapitated 12 days before IAA application and exposed to $^{14}CO_2$ 10 or 24 hours after application of IAA. Radioactivity was measured above and below the whorl to which $^{14}CO_2$ was applied

availability during the phase of tracheid maturation. The progressively increasing response of cells less advanced in differentiation may mean that the cells which constituted the cambial zone on the day the experiment started may use both ways of auxin involvement in apical control of xylem differentiation. The cells with longer developmental history constituting the original zone of maturation and most of the zone of enlarging xylem benefitted only from a better supply of cell wall substrates.

In fact, both influences, increase of supply of substrates, and enzymatic induction, could result from a single effect of auxin upon transport of assimilates to the place of auxin application. Indeed, the expected attraction of assimilates by auxin was observed only in early summer which corresponds to the seasonal difference in the morphological response of differentiating tracheids. However, little is known about the way in which, in this case, auxin controlled transport of assimilates. The fact that the responses to decapitation and auxin were relatively fast, and the additional modifying effects produced by decapitation of lateral branches (and replacement of lateral buds with auxin) indicate the possibility of involvement of another system of information transfer than simply the creation of a negative concentration gradient of assimilates towards the activated cambial meristem.

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REFERENCES

Barka T., Anderson P. J., 1962. Histochemical methods for acid phosphatase using hexazonium pararosanilin as coupler. J. Histochem. Cytochem. 10: 741-753.

Denne M. P., Wilson J. E., 1977. Some quantitative effects of indoleacetic acid on the wood production and tracheid dimensions in picea. Planta 134: 223-228.

Nix L. E., Wodzicki T. J., 1974. The radial distribution and metabolism of IAA-^{14}C in *Pinus echinata* stems in relation to wood formation. Can. J. Bot. 52: 1349-1355.

Seth A. K., Wareing P. F., 1967. Hormone-directed transport of metabolites and its possible role in plant senescence. J. Exp. Bot. 18: 65-77.

Wilson B. F., Wodzicki T. J., Zahner R., 1966. Differentiation of cambial xylem derivatives: proposed terminology. Forest Sci. 12: 438-440.

Wodzicki T. J., Wodzicki A. B., 1973. Auxin stimulation of cambial activity in *Pinus silvestris*. II. Dependence upon basipetal transport of auxin. Physiol. Plant. 46: 97-100.

Wodzicki T. J., Zajączkowski S., 1974. Effect of auxin on xylem tracheids differentation in decapitated stems of *Pinus silvestris* L., and its interaction with some vitamins and growth regulators. Acta Soc. Bot. Pol. 43: 129-148.
Zajączkowski S., 1973. Auxin stimulation of cambial activity in *Pinus silvestris*. I. The differential cambial response. Physiol. Plant. 29: 281-287.

Wpływ wierzchołka pędu na różnicowanie drewna sosny. I. Wpływ auksyny i dopływu asymilatów

Streszczenie

Badano wpływ IAA na aktywność podziałową kambium, różnicowanie cewek drewna wtórnego oraz przemieszczanie asymilatów, w młodych, dekapitowanych i obrączkowanych drzewach *Pinus silvestris* L. Dekapitacja powodowała zahamowanie aktywności podziałowej kambium zarówno wiosną, jak i późnym latem. Dostarczenie auksyny do apikalnego końca dekapitowanego pędu głównego wiosną, powodowało stymulację tworzenia drewna. Efekt ten ujawnił się również w sierpniu, natomiast nie wystąpił we wrześniu. Stymulujący wpływ auksyny nie ujawnił się w przypadku zaobrączkowania dekapitowanego pędu powyżej ostatniego okółka pędów bocznych. Dekapitacja pędu znacznie ograniczyła dzienny przyrost wtórnej ściany komórkowej cewek, które w dniu rozpoczęcia doświadczenia znajdowały się w fazie wzrostu promieniowego i dojrzewania. Spowodowało to wytworzenie cieńszej ściany komórkowej tych cewek, pomimo, iż w wyniku dekapitacji następowało wydłużenie okresu dojrzewania zarówno wiosną jak i późnym latem. Dostarczenie auksyny zapobiegało wpływom dekapitacji. Wydłużenie okresu dojrzewania cewek wystąpiło jednak w przypadku dostarczenia auksyny w okresie wiosennym u drzew, którym zdekapitowano pędy boczne.

Zastosowanie auksyny wczesnym latem powodowało znaczne zwiększenie dziennego tempa formowania ściany komórek, które w dniu dekapitacji znajdowały się w strefie merystematycznej oraz pochodnych kambium utworzonych później. W związku z tym kolejne cewki, utworzone z tych komórek, charakteryzowały się coraz grubszą ścianą komórkową. Doświadczenia przeprowadzone z dostarczeniem $^{14}CO_2$ do aparatu asymilacyjnego odgałęzień bocznych, wskazały że u drzew niedekapitowanych, w okresie późnego lata, asymilaty transportowane są do dolnej części pędu. W wyniku dekapitacji transport ten zwiększał się w okresie wiosennym, natomiast ulegał zmniejszeniu późnym latem. Przerwanie kontaktu z korzeniami poprzez zaobrączkowanie drzew u podstawy pędu głównego w okresie wiosennym zmniejszało wywołany przez dekapitację transport do dolnej części pędu. Dostarczenie IAA powodowało znaczne zwiększenie transportu asymilatów do górnej części pędu głównego.

Otrzymane wyniki wskazują na to, że szybkość formowania ściany komórkowej w okresie różnicowania zależy zarówno od warunków określanych już w fazie merystematycznej cewek (indukcji lub aktywacji potencjału metabolicznego związanego z syntezą ściany komórkowej) jak również od mechanizmu kontrolującego dystrybucję asymilatów. Stwierdzono, że procesy te znajdują się pod wyraźną kontrolą nie tylko wierzchołka tego pędu, w którym tworzy się drewno lecz także od korelacji wzrostowych wynikających ze współdziałania wierzchołków całego układu pędów korony. Stwierdzono, że interakcje te mogą być zastąpione działaniem auksyny.