The acropetal effects of indole-3-acetic acid in isolated shoot segments of *Acer pseudoplatanus* L.

II. Possible regulation by a vectorial field of auxin waves

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Abstract

The acropetal effects of auxin on elongation of axillary buds and on modulation of the wave-like pattern of basipetal efflux of natural auxin to agar from *Acer pseudoplatanus* L. shoots were studied. When synthetic IAA was applied to cut surfaces of one of two branches the elongation growth of buds situated on the opposite branch was retarded, suggesting regulation independent of the direct action of the molecules of the applied IAA. Oscillations in basipetal transport of natural auxin along the stem segments were observed, corroborating the results of other authors using different tree species. Apical application of synthetic IAA for 1 hour to the lateral branch caused a phase shift of the wave-like pattern of basipetal efflux of natural auxin, when the stem segment above the treated branch was sectioned. The same effect was observed evoked by the laterally growing branch which is interpreted as an effect of natural auxin produced by the actively growing shoot. These modulations could be propagated acropetally at a rate excluding direct action of auxin molecules at the sites of measurement. The results seem to corroborate the hypothesis suggesting that auxin is involved in acropetal regulation of shoot apex growth through its effect upon modulation of the vectorial field which arises when the auxin-waves translocate in cambium.

Key words: IAA, bud growth, auxin waves, acropetal regulation, *Acer pseudoplatanus* L.

INTRODUCTION

Although the role of auxin in the control of correlative growth of shoots in tree crowns has been known for many years (Wareing 1970, Zimmermann and Brown 1971, Jankiewicz, 1979) the mechanism by which this phytoho-

hormone is involved in regulation of the activity of stem apices of branches is still little understood (Wareing and Saunders 1971, Saunders 1978, Leopold and Nooden 1984, Wareing 1986). The principally basipetal polar transport of auxin prevents its direct effect oriented from the base of the branch towards the apical meristem. In addition, polar transport of auxin has been estimated as 1-2 cm per hour (Goldsmith 1969, 1977, Thimann 1972) which, in the crowns of large forest trees, means that auxin produced at the apices when they started to grow would have to be transported for weeks before reaching the base of lateral branches that are a few meters long. Recent investigation on the acropetal effects of synthetic IAA in shoot segments of a woody plant (*Acer pseudoplatanus* L.) (Adamczyk 1991) confirmed the results of experiments performed on herbaceous plants (Snow 1937, 1940) and supplied evidence that auxin has a specific inhibitory effect upon the elongation of buds situated above the source of this substance.

Recently a theoretical model of hormonal regulation of plant morphogenesis has been proposed (Zajączkowski and Wodzicki 1978b). In it the propagation of the regulatory signals is related to a modulation of parameters of the supracellular auxin waves forming in the cambium region of stems. To function in regulation of correlative growth the morphogenetic information would have to be encoded in parameters of the auxin waves propagated as wave modulations both in basipetal and acropetal direction, regardless of the fact that transport of auxin molecules is basipetally polar. Wodzicki et. al. (1979), Wodzicki and Wodzicki (1981) demonstrated that such synthetic growth regulators as IAA, ABA, GA_3 and zeatin can modulate auxin wave parameters. The modulations caused by ABA (Wodzicki and Wodzicki 1981) and IAA (Adamczyk and Wodzicki 1987) can be propagated acropetally at a rate faster than their molecular translocation thus excluding the direct action of molecules of these substances at the site of measurement of the auxin wave.

The present paper reports further results contributing to the hypothesis according to which auxin participates in the acropetal control of shoot apex activity by its effect upon the vectorial field forming when the auxin waves are translocated in shoot cambium.

MATERIAL AND METHODS

MATERIAL

The investigations were performed on shoot segments from either 5-year-old or ca. 15-year-old *Acer pseudoplatanus* L. trees grown in forest stands (Experimental Forest Station in Rogów, Central Poland). This species was selected because of the: 1) monopodial type of growth, 2) opposite lateral branches and buds, 3) straight and sufficiently long internodes, 4) the basipetal

auxin efflux from series of successive short stem sections which form a wave-like pattern similar to that found previously in pine stem segments (Wodzicki and Wodzicki 1981). Besides, it has been found (Adamczyk 1991) that buds of this species respond to acropetal action of synthetic growth regulators by retarded or stimulated elongation.

WATER-CULTURE CONDITIONS

The methods of culture, observations and measurements were the same as described in the previous report (Adamczyk 1991). The synthetic growth regulators: indole-3-acetic acid (IAA) or triiodobenzoic acid (TIBA), each in a concentration of 0.5% were applied in lanolin-water paste to the cut surface of the shoot on the day the experiment started. Control series included treatment with pure lanolin-water paste. The shoots were positioned vertically in containers with their basal ends immersed 1 cm deep in distilled water at room temperature (about 18°C), with natural air humidity and daylight.

The effects of experimental treatment were characterized daily by determining: 1) the number of shoots on which the bud started to grow, and 2) by the time required for bud opening after the experiment had begun. The extension growth of new shoots was measured 20 days after the bud started to grow.

The results were subjected to analysis of variance and Student's *t* test at $P=0.05$.

MEASUREMENT OF GROWTH SUBSTANCE ACTIVITY ALONG THE AXIS OF THE SHOOT

Segments of main shoots (about 20 mm in diameter) with two opposite lateral branches (about 5 mm in diameter) were isolated from ca. 15-year-old trees. The main shoots were cut 110 mm above and 20 mm below the lateral branches. The branches were cut to 25 mm long stumps or left intact. Plain agar discs were applied to the cut surfaces of the stem and branches for 1 hour. Subsequently, the stem segments were cut longitudinally in half. The parts of the shoots above the node were cut to 6 mm long sections, progressing successively from the apical ends. Diffusible growth substances from the cambial region of those small sections were taken up at the basal end of the stem section into 1.5% agar strips (2.0 × 1.5 mm, length dependent on the diameter of the stem). The basipetal efflux of natural growth substances was allowed for 10 or 15 min. after which the agar strips were cut into 8 or 6 cubes and tested for growth stimulation by Went's *Avena* (cv. Seger I) coleoptile curvature test. The bioassay method followed essentially the procedure advanced by Funke (1939) and modified by Wodzicki and Wodzicki (1980).

RESULTS

EFFECT OF IAA ON BUD GROWTH ACTIVITY

Experiment 1

Segments of the main shoot with two opposite lateral branches comprising a 75 mm (24-105) long fragments of the one-year-old shoot above the lateral branches and 45 mm long fragment of the two-year-old shoot below the branches were used. The lateral branches were cut to equal lengths of 35 mm (20-50). There were two well formed axillary buds on the apical fragment 5 mm below its end. The cut surfaces of the lateral branch stumps were covered with aqueous-lanolin paste or with a lanolin paste containing IAA or TIBA. Each experimental treatment (illustrated in Table 1) comprised 8-12 replicate shoots. The whole experiment was repeated twice: January 8 and February 28 and with some of the experimental series repeated once again on April 2 and January 6 of the next season.

Table 1

Length of new shoots (mm) formed from left (B_L) and right buds (B_R) of main shoot sections after application of pure lanolin (L) or lanolin containing synthetic growth regulators to lateral branch stumps. Mean of 8-12 shoot segments

DATE THE EXPERIMENT STARTED	T R E A T M E N T S									
	B_L	B_R	B_L	B_R	B_L	B_R	B_L	B_R	B_L	B_R
Jan. 8, 1986	15.8	12.0	20.4	8.4	13.6	8.4	8.6	9.0	14.9	11.4
Feb. 28, 1986	12.8	12.9	15.5	11.2	12.5	15.6	13.8	21.6	12.8	6.6
April 2, 1986	11.8	16.1	15.8	10.1	-	-	-	-	-	-
Jan. 6, 1987	14.8	16.2	13.3	5.1	-	-	-	-	-	-
Mean	13.8	14.3	16.3	8.7	13.1	12.0	11.2	15.3	13.9	9.0
$B_R - B_L$	0.5		-7.6		-1.1		4.1		-4.9	
LSD	4.2		3.9		6.5		6.5		4.6	

Observation of bud breaking indicated that there were no differences between the left and right buds in all of the series of the experiment, irrespective of the date when the experiment started.

Measurements of the new shoots formed from the buds revealed less elongation above the lateral branch stumps treated with IAA in comparison with the other branch stumps treated with pure lanolin paste or lanolin paste containing TIBA (Table 1). Differences between the elongation of the left and right buds if both stumps had been treated with IAA or only one with TIBA and the other with pure lanolin paste, were insignificant.

Experiment 2

Several-year-old main shoots with two opposite lateral branches were cut into 10 cm long stem segments at equal distances from the node. The side branches were decapitated 0.5 cm above the two lateral buds whose growth was subsequently measured. The apical cut surface of the main shoot was covered with aqueous lanolin paste or paste containing IAA. The three experimental variants differed in the mean length of the lateral branches: 47 mm (20-74), 133 mm (70-212) and 330 mm (164-528). The experiment was repeated two times: on January 8 and February 28 (the last variant only on February 28).

The shoot treated with IAA (Table 2) exhibited smaller increments of new shoots formed from buds on the lateral branches.

Table 2

Total length of new shoots (mm) formed from 4 axillary buds of lateral branch stumps after application of pure lanolin (L) or lanolin containing IAA to apical cut surface of main shoot sections. Mean of 10 shoot segments

Mean length of lateral branch stumps		47mm		133mm		330mm	
DATE THE EXPERIMENT STARTED	T R E A T M E N T S						
	L + +	IAA + +	L + +	IAA + +	L + +	IAA + +	
Jan. 8, 1986	25.1	3.7 *	35.6	15.7	-	-	
Feb. 28, 1986	36.0	3.3 **	53.6	31.9	60.9	20.6	
Mean	30.6	3.5	44.6	23.8	60.9	20.6	
IAA - L	- 27.1		- 20.8		- 40.3		
LSD	9.2		12.5		30.0		

* only 3 buds started to grow

** only 7 buds started to grow

Experiment 3

Shoots with a forking type of branch were used in the next experiment. The shoots used for treatment had a 12 cm long segment of the two-year-old main stem with two opposite one-year-old branches located on the apical part of the segment. One of the branches was cut to a length of 15 cm. No buds were left intact on this branch. The other was cut 0.5 cm above the axillary buds whose elongation was subsequently measured. The two experimental variants differed in mean length of the lateral branch whose bud growth was investigated: 214 mm (100-288) and 487 mm (377-741). Synthetic IAA was applied in lanolin paste to the cut surfaces of 15 cm long budless branch stumps. The experiment was repeated three times: January 8 (excluding variants with longer branch stumps), February 28 and January 6 of the next season.

As before, smaller new shoots formed from the buds if the other branch was treated with IAA (Table 3), however, the differences between the auxin treated and untreated series were significant only in the variant with shorter shoots.

Table 3

Total length of new shoots (mm) formed from 2 axillary buds of one of two pseudodichotomic shoot stumps after application of pure lanolin (L) or lanolin containing IAA to apical cut surface of other shoot stump. Mean of 10 shoot segments

Mean length of lateral branch stumps		214 mm		487 mm	
DATE THE EXPERIMENT STARTED		T R E A T M E N T S

Jan. 8, 1986		47.4	18.2	—	—
Feb. 28, 1986		50.4	48.6	92.8	70.5
Jan. 6, 1987		68.8	36.7	72.3	55.8
Mean		55.5	34.5	82.6	63.2
IAA - L		- 21.0		- 19.4	
LSD		13.3		22.0	

BASIPETAL EFFLUX OF NATURAL GROWTH SUBSTANCES

Spatial pattern

Lateral branches of the shoot about 0.5 cm thick were cut to 25 cm long stumps and the cut surfaces were covered with 1.5 mm thick 1.5% aqueous agar discs for 1 hour. After that the stem segments were cut longitudinally into two halves and new agar discs were applied to the cut surfaces for the next 1 hour (Fig. 1A) and basipetal efflux of natural auxin was tested as described previously. The measurements revealed a wave-like pattern of basipetal efflux of natural growth substances (Fig. 1B) from a series of short stem sections. The length of the wave was about 20-40 mm. The phases of the oscillations as measured in the two opposite halves of the same stem usually coincided. In the second variant of the experiment the basipetal efflux of natural growth substances from the short sections of the two halves of the stem was measured as collected in agar immediately after the stem segment had been cut longitudinally (Fig. 2A). As previously, oscillations were revealed and the phases in the two opposite stem halves (Fig. 2B) coincided.

Fig. 1. Oscillation in the amount of natural auxin collected by basipetal efflux from a series of short sections obtained by successive sectioning of two opposite halves of shoot segment. A — Successive operations of shoot sectioning and collecting natural auxin for bioassay. B — Results of oat coleoptile curvature test of natural auxin efflux to agar from consecutive 6-mm long shoot sections. Average of 8 coleoptiles. C — Stimulation produced by $0.56 \mu\text{M}$ of synthetic IAA in agar with no contact with the shoot sections

Fig. 2. Oscillation in the amount of natural auxin collected by basipetal efflux from a series of short sections obtained by successive sectioning of two opposite halves of shoot segment. A — Successive operations of shoot sectioning and collecting natural auxin for bioassay. B — Results of oat coleoptile curvature test of natural auxin efflux to agar from consecutive 6-mm long shoot sections. Average of 6 coleoptiles. C — Stimulation produced by $0.56 \mu\text{M}$ of synthetic IAA in agar with no contact with the shoot sections

Fig. 3. Acropetal effects of synthetic IAA upon the wave-like pattern of the amount of natural auxin efflux from a series of short sections obtained by successive sectioning of two opposite halves of shoot segment. A — Successive operation of shoot sectioning and collecting of natural auxin for bioassay. B — results of oat coleoptile curvature test of natural auxin to agar from consecutive 6-mm long shoot sections. Average of 8 coleoptiles. Plain agar applied to lateral branch stump — solid line, agar containing $0.56 \mu\text{M}$ IAA to lateral branch stump — dotted line. C — Stimulation produced by $0.56 \mu\text{M}$ of synthetic IAA in agar with no contact with the shoot sections

Effect of auxin

Analogous shoots as above were used in the following experiment. After the stem segments had been cut longitudinally, the plain agar discs were replaced: plain agar was applied to the lateral branch of one half of the shoot, while the agar discs containing IAA in a concentration $0.5 \mu\text{M}$ were applied to the other half for 1 hour (Fig. 3A). Measurements of natural auxin efflux from the two series of short stem segments revealed a phase shift of the wave-like pattern between the two shoot halves corresponding to each other (Fig. 3B).

Acropetal effects of the growing lateral branch

One of the lateral branches of the shoot selected as described previously was cut to a 25 mm stump and the other was left intact for 1 hour (Fig. 4A). The main shoot was then cut longitudinally and basipetal efflux of natural auxin was bioassayed. The results of measurements from a series of short stem sections revealed a phase shift in oscillations in the wave-like pattern between the two halves of the shoot (Fig. 4B).

Basipetal effects of the growing lateral branch

The main stem segments (15-20 cm long) with two nodes were selected from the crown as shown in Fig. 5A. The lateral branches of the apical node were situated exactly above the two basal branches, respectively. Two basal and one apical branch were cut to 25 mm long stumps and the apical branch was left intact for 1 hour. Subsequently, the 60 mm long internode segment of the main shoot was cut longitudinally into two halves and basipetal efflux of natural auxin to agar was tested as previously. The results of measurements corresponding to the two series of short stem sections revealed a phase shift of the oscillations of the wave-like pattern (Fig. 5B). Moreover, the same increase of stimulation in the stem half corresponding to the side of the intact lateral branch was noticeable.

DISCUSSION

The specificity of the oat coleoptile curvature bioassay for detecting natural IAA (auxin) collected by diffusion from stem tissues to agar gel is high enough (Wodzicki et al. 1987) to support the supposition that the natural growth stimulators measured in this study (at least in many of their effects) are the natural auxin of maple (*Acter pseudoplatanus* L.). The high level of sensitivity and low variability of the replicate measurements obtained using test (Wodzicki et al. 1984) as well as the close correspondence of the stimulation

Fig. 4. Acropetal effects of growing lateral branch upon the wave-like pattern of amount of natural auxin efflux from a series of short sections obtained by successive sectioning of two opposite halves of shoot segment. A — Successive operation of shoot sectioning and collecting natural auxin for bioassay. B — Results of oat coleoptile curvature test of natural auxin to agar from consecutive 6-mm long shoot sections. Average of 6 coleoptiles. The shoot half above the lateral branch stump — solid line, the shoot half above the intact lateral branch — dotted line. C — Stimulation produced by $0.5 \mu\text{m}$ of synthetic IAA in agar with no contact with the shoot sections

Fig. 5. Basipetal effects of growing lateral branch upon the wave-like pattern of amount of natural auxin efflux from a series of short sections obtained by successive sectioning of two opposite halves of shoot segment. A — Successive operation of shoot sectioning and collecting of natural auxin for bioassay. B — Results of oat coleoptile curvature test of natural auxin to agar from consecutive 6-mm long shoot sections. Average of 6 coleoptiles. Shoot half below the lateral branch stump — solid line, shoot half below the intact lateral branch — dotted line. C — Stimulation produced by $0.56 \mu\text{M}$ of synthetic IAA in agar with no contact with the shoot sections

patterns when two tangentially adjacent stem segments are measured (Wodzicki and Wodzicki 1981, Zakrzewski 1983, Adamczyk and Wodzicki 1987) permit the conclusion that the oscillations reveal the true rate of basipetal transport of natural auxin.

The present results revealed that the basipetal efflux of endogenous growth substances from the cambial region of the successive short sections of the maple internode, measured by the coleoptile curvature test, changes along the shoot axis, thus forming the wave-like pattern such as was found earlier in the cambium of *Pinus sylvestris* L. (Zajaczkowski and Wodzicki 1978a), *Picea abies* Karst., *Larix* sp., *Acer pseudoplatanus* L. (Wodzicki and Wodzicki 1981), *Quercus robur* L. (Zakrzewski 1983), *Fraxinus excelsior* L. (Adamczyk and Wodzicki 1987). These oscillations could result from differences in natural IAA efflux to agar due to a variable expression of the stem polarity, as was recently discovered in the cambium of *Pinus sylvestris* L. by Wodzicki et. al. (1988).

The phases of oscillations measured along two opposite halves of the shoot segments above the node in the control series, in which the lateral branches were not treated with IAA, usually coincided. The isophasic surfaces of these oscillations were nearly orthogonal to the stem axis revealing synchronization of the rate of basipetal auxin efflux around the stem circumference. Application of synthetic IAA (in a physiological concentration) to a cut surface of one of two laterals caused a phase shift of the oscillations between the wave-like pattern measured along the opposite halves of the stem segment above the node and, consequently, the orthogonality of the isophasic surfaces in respect to the stem axis was lost. When one growing lateral branch (irrespective of its position above or below the place of measurements) was not decapitated, the phase shift of the wave-like pattern of natural auxin basipetal efflux was clearly manifested. Thus, the natural auxin, produced in the active, growing shoot apex, probably affected the auxin-wave vectorial field analogously to the acropetal effects of synthetic IAA applied to one of the lateral branches. All the results described above provide further evidence for the earlier suggestion by Wodzicki et. al. (1979) that auxin modulates parameters of the wave-like pattern of the basipetal efflux of natural auxin to agar from stem sections. Although translocation of the applied IAA was not studied, there is good reason to believe that the observed effects were not the result of direct action of the molecules of the synthetic auxin. Firstly, because auxin transport in the shoot of woody plants is always found to be basipetally polar (Leopold 1961, Thimann 1977) and secondly, because propagation of the phase shift of the wave-like pattern of basipetal efflux of natural auxin was faster than the known rates of auxin translocation in plant tissues (Goldsmith 1969, 1977, Thimann 1972).

The acropetal retarding effects of synthetic IAA on elongation of new shoots in each of the three experiments were documented, and confirmed the

results of the study where IAA was applied to unbranched stem segments (Adamczyk 1991). Taking into account the phenomenon of predominantly basipetal transport of auxin in plant tissues it seems probable that the observed acropetal effects of IAA upon shoot elongation were associated with such a system of plant growth regulation which does not require translocation of the same auxin molecules from the place of their application to the site of their reaction. The coincidence of occurrence of the two above-described effects of auxin (1) bud elongation, and 2) auxin wave configuration change) may suggest a causal relationship. The modulation of the oscillations of the natural auxin wave in response to application of IAA, observed in the present investigation, can possibly be involved in the mechanism of propagation of the morphogenetic message for apical meristems, as has already been proposed by Zajączkowski and Wodzicki (1978b). Such a mechanism could control the growth activity of apices of various shoots in the tree crown, acting fast and without limits upon the direction of transfer of morphogenetic information.

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Akropetalny wpływ kwasu indolilo-3-octowego w wyizolowanych odcinkach pędów *Acer pseudoplatanus* L.

II. Możliwość regulacji przez pole wektorowe fal auksynowych

Streszczenie

Badano akropetalny wpływ syntetycznego kwasu indolilo-3-octowego (IAA) na wydłużanie pąków rozgałęzionych odcinków pędów w kulturze wodnej, i na oscylacje bazypetalnego transportu naturalnej auksyny w strefie kambialnej ładygi. Stwierdzono zmniejszenie przyrostu długości nowych pędów utworzonych z pąków pachwinowych znajdujących się na odcinku jednej osi, gdy IAA dostarczono do odcinka innej osi tego samego układu pędowego, w porównaniu z analogicznymi seriami kontrolnymi. Wynik ten sugeruje udział dostarczonego IAA w akropetalnej regulacji aktywności wzrostowej wierzchołków pędów, która, z uwagi na bazypetalny transport auksyny w tkankach roślinnych, może być związana ze zjawiskami sygnałowymi nie wymagającymi przemieszczania się molekuł IAA. Badany za pomocą zmodyfikowanego testu Went'a, bazypetalny wpływ naturalnej auksyny z serii kolejnych 6-mm. odcinków dwóch naprzeciwleg-

łych części pędu wykazał zsynchronizowane obwodowo zmiany o charakterze oscylacyjno-falowym, korespondujące z wynikami otrzymanymi wcześniej dla innych gatunków drzew. Obecność źródła auksyny (syntetyczny IAA dostarczony do odcinka bocznego pędu lub rosnący boczny pęd) powoduje przesunięcie fazy oscylacji w nadległej części pędu głównego, wskazując na okropetalną propagację zmian synchronizacji fazy oscylacji w komórkach strefy kambialnej pędu pod wpływem bodźca auksynowego, i to znacznie szybciej niż znane prędkości przemieszczania się auksyny w tkankach roślinnych. Otrzymane wyniki sugerują możliwość udziału naturalnej auksyny w akropetalnej regulacji aktywności wzrostowej poszczególnych wierzchołków wzrostu w rozgałęzionym systemie pędowym korony rośliny drzewiastej, poprzez modyfikację pola wektorów propagacji fal auksynowych w układzie komórek przejawiających polarność w transporcie auksyny.