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Acropetal effects of IAA upon the wave-like pattern in the basipetal efflux of natural growth substances of *Fraxinus excelsior* L.

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Abstract

Basipetal efflux of natural growth substances from the cambial region of a successive series of short sections of the stem of *Fraxinus excelsior* L. was measured by Went's oat coleoptile curvature bioassay. A wave-like pattern of stimulation by natural growth substances collected after efflux of only 10 min in agar containing 0.56 μM synthetic IAA was observed, confirming to earlier findings in other species. Both inhibitory and stimulatory effects were recorded, however, the oscillations were manifested in stimulation, which is probably due to natural auxin. IAA applied for 1 h directly to the cut surface of the lateral branch, distal to the stem segment used for the measurements of natural auxin efflux, caused acropetal modulations of the wave-like pattern. The results seem to indicate that the auxin-wave system analogous to that already described for other trees operates also in the cambial region of the *Fraxinus excelsior* L. stem. Modulations of such waves caused by IAA (seen as phase shift) can be propagated acropetally at a rate excluding direct action of molecules of auxin at the site of measurement.

Key words: *auxin-wave, Fraxinus excelsior, IAA acropetal effects*

INTRODUCTION

Basipetal efflux of natural auxin to agar from a series of consecutive short sections of the stem of pine and of other tree species forms a wave-like pattern (Zajączkowski and Wodzicki 1978a, Wodzicki

and Wodzicki 1981, Zakrzewski 1983). This pattern, according to Zajączkowski and Wodzicki (1978b), reveals a morphogenetic vectorial field which forms when the auxin waves are propagated in the stem cambial region.

The required high efficiency and precision of any system of coordination of growth and differentiation in the whole plant depends on the condition that it acts fast and without limits upon the direction of transfer of morphogenetic information. Thus, if the morphogenetic information is encoded in parameters of the auxin waves, propagation of wave modulations should be expected in both basipetal and acropetal directions, regardless of the fact that transport of auxin molecules is basipetally polar (Thimann 1972, Goldsmith 1977). Wodzicki et al. (1979), and Wodzicki and Wodzicki (1981) demonstrated that phytohormones can contribute to the morphogenetic message by modulation of the auxin waves, thus, the present investigation is devoted to the question whether such modulations are translocated acropetally in isolated stem segments.

MATERIAL AND METHODS

Segments of stems from four to about fifteen-year-old trees (*Fraxinus excelsior* L.) in a forest plantation of the Experimental Forest in Rogów were investigated. The stem segments were cut in series of 12 consecutive 6 mm long sections. Diffusible growth substances from the cambial region of these sections were taken up at the basal ends of stem sections into 1.5% agar rings of about 8 mm outer diameter and about 1.5 mm thick with 0.56 μM IAA (analytical grade) added to allow expression of interaction effects by inhibitors.

The basipetal efflux of the natural growth substances was allowed for 10 min., after which period the agar strips were cut into 8 cubes and tested for growth stimulation by Went's *Avena* (cv. Seger I) coleoptile curvature test. The method of bioassay followed essentialy the procedure advanced by Funke (1939).

RESULTS AND DISCUSSION

WAVE-LIKE PATTERN OF STIMULATION MEASURED IN WENT'S BIOASSAY

To check the hypothesis that in young shoots of ash the basipetal auxin efflux conforms to the wave-like pattern described earlier for other tree species, segments of internodes (72 mm long, about 8 mm in diameter)

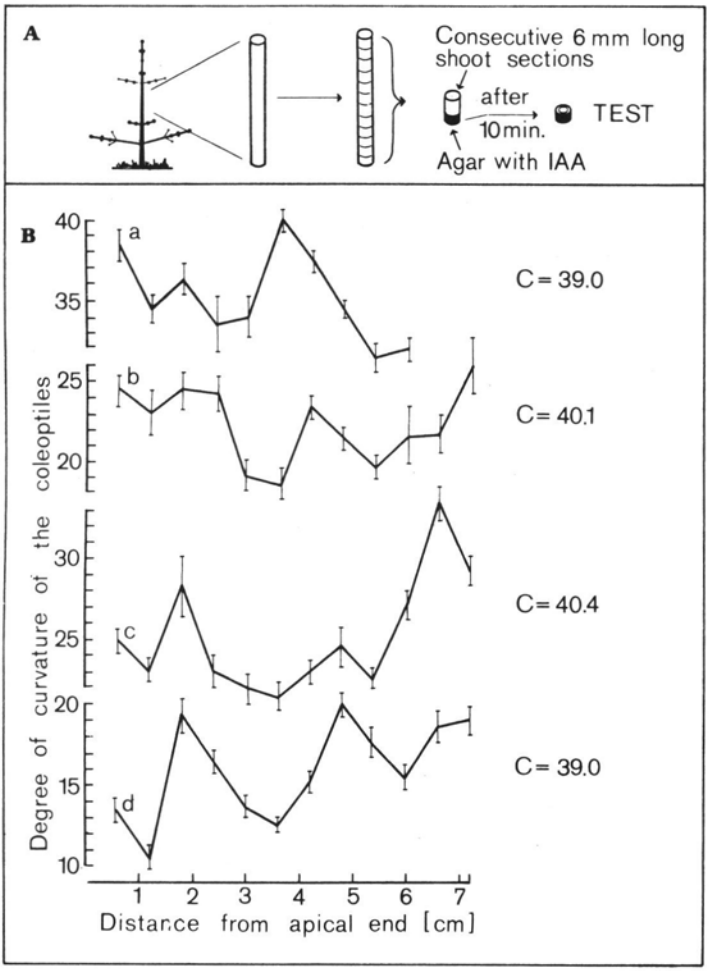

Fig. 1. Oscillations in the amount of *Fraxinus excelsior* L. natural growth substances collected by basipetal efflux from a series of short sections of stem into agar. A — Successive operations of stem sectioning and collecting of growth substances for bioassay. B — Results of Went's oat coleoptile curvature test of natural growth substances from consecutive 6 mm long shoot sections to agar containing IAA 0.56 μM. C — Stimulation produced by 0.56 μM of synthetic IAA in agar with no contact with the shoot sections. Averages of 8 coleoptiles. Vertical lines indicate standard errors. Dates of experiments: a — Sept. 8, b — Sept. 15, c — Sept. 1, d — July 17, 1981

were isolated from four-year-old trees four times during July and September 1981. Measurements of the basipetal efflux of natural growth substances revealed indeed a wave-like pattern of growth response of coleoptiles (Fig. 1A, B).

However, stimulation of coleoptile growth produced by the agar rings containing both synthetic IAA and the stem endogenous growth substances

was reduced as compared to IAA effects alone in controls. In the experiment of September 8 (Fig. 1Ba) all stem sections were first placed for 10 min. on agar rings without IAA and only then transferred to fresh rings of agar containing IAA for another 10 min. The stimulatory effect on growth of coleoptiles increased but the wave-like pattern persisted. This suggests an interaction of a diffusible growth inhibitor(s) from the tissue, however, the variable growth responses of oat coleoptiles seem rather to reflect oscillations in the amount of natural auxin collected in agar rings.

EFFECT OF AUXIN

Segments of main shoots, about 20 mm in diameter and 110 mm long above the node, with two opposite lateral branches cut to 25 mm long stumps, and a 20 mm long stem section below the node were isolated from approximately fifteen-year-old trees. Plain agar rings were applied to the cut surfaces of the stem and branches for 1 h. Subsequently, the stem segments were cut longitudinally in halves (Fig. 2A) and the plain agar of the cut surface of a lateral branch in one half of the shoot was replaced with agar containing IAA 0.56 μM for 1 h. A fresh ring of pure agar was applied to the other. For the control pair of halves, pure agar was applied to the stumps of both lateral branches. After 1 h the parts of the shoots above the node were cut to 6 mm long sections. To remove the excess of the inhibitor(s) from the tissue, the agar half-rings containing IAA 0.56 μM were first applied to the basal ends of the short sections for 20 min. and then fresh agar half-rings also containing IAA were applied for 10 min. to the same surfaces. Measurements of the natural growth substances activity were done only in this second collection of agar half-rings.

As previously, oscillations in basipetal efflux of the natural growth substances were found. Phases of oscillations in the control series measured in two halves of the shoot segment above the node usually coincided (Fig. 2B, a, b, c). However, in the case of auxin applied to the cut section of the lateral branch of one of the stem halves, a shift of the oscillation phases was noticeable (Fig. 2B, d, e, f).

Taking into account that the lateral branch segment was about 25 mm long and the time of IAA application was only 1 h, the molecules of applied synthetic auxin, for which the basipetal transport rate is estimated to be 10–15 mm h^{-1} (Goldsmith 1969, Thimann 1972), most probably could not move, not only into the cambial region of the sampled stem section above the node, but even to traverse the distance to the node.

The results seem to evidence that an auxin-wave system analogous

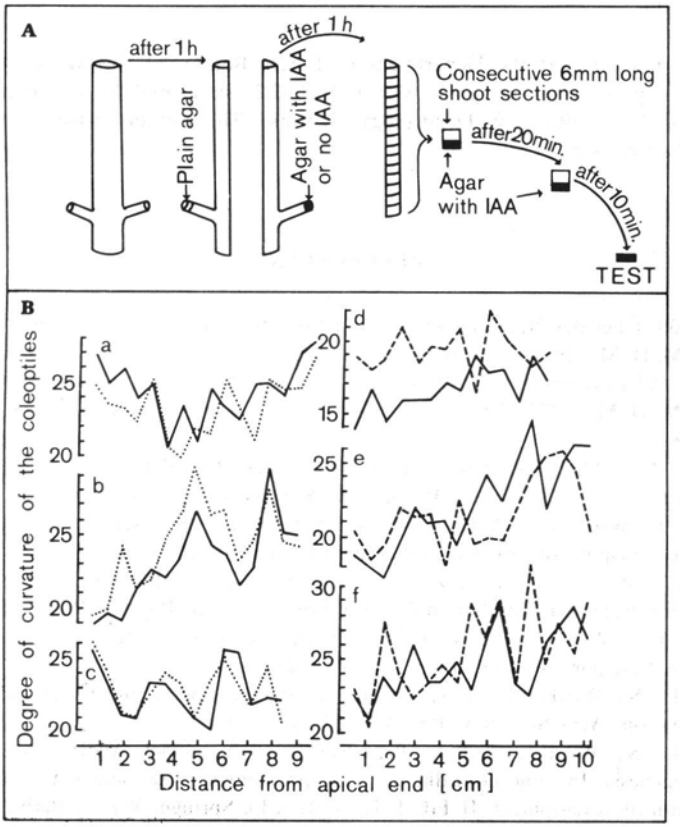

Fig. 2. Acropetal effects upon wave-like pattern of amount of natural growth substances basipetal efflux from a series of short stem sections of *Fraxinus excelsior* L. caused by IAA application to a lateral branch. A — Successive operations of stem sectioning and collecting of growth substances for bioassay. B — Results of Went's oat coleoptile curvature test of natural growth substances from consecutive 6 mm long shoot sections to agar containing IAA 0.56 μM. Averages of 8 coleoptiles. Plain agar applied to lateral branches — solid or dotted lines, agar with IAA to lateral branches — broken lines. Dates of experiments: a — Dec. 25, 1983; b — Jan. 20, c — Feb. 3, d — Jan. 13, e — Jan. 27 and f — Feb. 9, 1984

to that already described for other trees operates also in the cambial region of the *Fraxinus excelsior* L. stem. Modulations of such waves caused by IAA (seen as a phase shift) can be propagated acropetally at a rate excluding direct action of molecules of auxin at the site of measurement.

This acropetal propagation of signals coupled to the phenomena of basipetal polar transport of the auxin molecules, but faster than the known velocities of such transport, corroborate the hypothesis (Zajączkowski et al. 1984) that the measured "auxin-waves" constitute part of the system of positional information in plant morphogenesis.

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Akropetalny wpływ IAA na falowy wzór polarnego transportu naturalnych substancji wzrostowych w pędach Fraxinus excelsior L.

Streszczenie

Mierzony za pomocą zmodyfikowanego testu Wenta, bazypetalny 10 min. wypływ endogennych substancji wzrostowych z serii kolejnych 6 mm odcinków pędu jesiona wyniosłego (*Fraxinus excelsior* L.) wykazuje cykliczne zmiany o charakterze falowym wzdłuż osi pędu. Badania wykazały obecność w tkankach pędów jesiona inhibitora wzrostu koleoptyli owsa, który ogólnie obniża poziom stymulacji, jednak nie wpływa na falowy wzór wypływu stymulatora, prawdopodobnie auksyny. Zastosowanie syntetycznego IAA do odcinka bocznego odgałęzienia wyizolowanego fragmentu systemu pędowego powoduje modyfikacje stymulacji przez naturalne substancje wzrostowe, zebrane z części pędu głównego nadległej do miejsca rozgałęzienia. Otrzymane wyniki ujawniły, że w pędach jesiona wyniosłego funkcjonuje system oscylacyjno-falowy, związany z polarnym transportem auksyny, analogiczny do opisanego wcześniej dla innych gatunków drzew. Ponadto rezultaty doświadczeń potwierdzają hipotezę,

że fala auksynowa może być modulowana akropetalnie i to znacznie szybciej niż znane szybkości polarnego transportu molekuł dostarczonego egzogennie IAA wyzwalającego te modulacje. Ujawniony tu brak ograniczeń w kierunku akropetalnym dla przenoszenia sygnałów przez falę, mierzoną jako oscylacje związane z polarnym transportem auksyny, przyczynia się do dalszego utwierdzenia hipotezy o znaczeniu "fal auksynowych" jako składnika systemu informacji pozycyjnej w morfogenezie roślin.