Short Communication

Abscisic Acid as a Root Growth Inhibitor: Physiological Analyses

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Summary. Abscisic acid (ABA) moves basipetally and laterally in maize (*Zea mays* L.) root segments placed horizontally; its transport properties are thus similar to those of the growth-inhibiting substances produced by the root cap. The two opposite flows af ABA and of indolyl-3-acetic acid (IAA) — substances both present in the cap — may control elongation and georeaction of the root.

The root cap of maize produces at least one growth inhibitor (Gibbons and Wilkins, 1970) which is not species specific (Pilet, 1972). It is transported basipetally to the extension zone (Shaw and Wilkins, 1973) and can move laterally in the root cap (Pilet, 1973). This inhibitor is responsible for the georeaction (Gibbons and Wilkins, 1970; Pilet, 1971). Although indolyl-3-acetic acid (IAA) has been detected in the maize root cap (Rivier and Pilet, 1974), it is unlikely to be the inhibitor because its transport is highly polar in the acropetal direction (Pilet, 1964; Bowen *et al.*, 1972; Shaw and Wilkins, 1974). On the other hand abscisic acid (ABA), which strongly inhibits root elongation (Pilet, 1970; Milborrow, 1974; Newton, 1974), has also been identified in the maize cap (Kundu and Audus, 1974a, b). The aim of the work reported in this paper was to determine, by physiological experiments, whether ABA could act as the growth inhibiting substance.

The conditions for the germination of maize (*Zea mays* L. cv. Kelvedon 33) fruits have been described previously (Pilet, 1974). When the primary roots reached a length of 15 ± 3 mm, 10 ± 0.2 mm apical segments were exised and decapitated at 0.6 ± 0.1 mm, *i.e.* only the cap was taken away (Juniper and French, 1970). The segments were mounted in plastic frames with their basal cut ends covered with a moist filter paper (buffered solution at pH 6.1 with or without IAA or *cis-trans*-DL-ABA at 10^{-6}M). Their apical cut ends were half covered (lower or upper part) by an agar half block. The cylindrical agar blocks (diameter, 2.5 mm; thickness, 1 mm) contain IAA or ABA at 10^{-6}M. A buffered (pH 6.1) agar (Difco purified) at 1.8% was used. In a few assays, mica barriers ($2 \times 2 \times 0.4$ mm) were inserted into the side of the root (0.9 ± 0.2 mm behind the tip). The frames, with the decapitated root segments placed horizontally, were kept in closed boxes ($22 \pm 1°$; relative humidity $90 \pm 5\%$; white light from Osram L 13 W/25 lamps, 0.9 ± 0.006 J m^{-2} s^{-1}). Curvature of the root segments was recorded after 7 ± 0.5 h, by shadow photographs. To reduce the standard error of the mean, a control assay with moist filter paper and agar blocks without IAA and ABA was run for each series of experiments. Because the control assay varied slightly from one experiment to another, the data are expressed in percent of the control. The results represent the mean response of 25 ± 6 roots for the "treated" material.
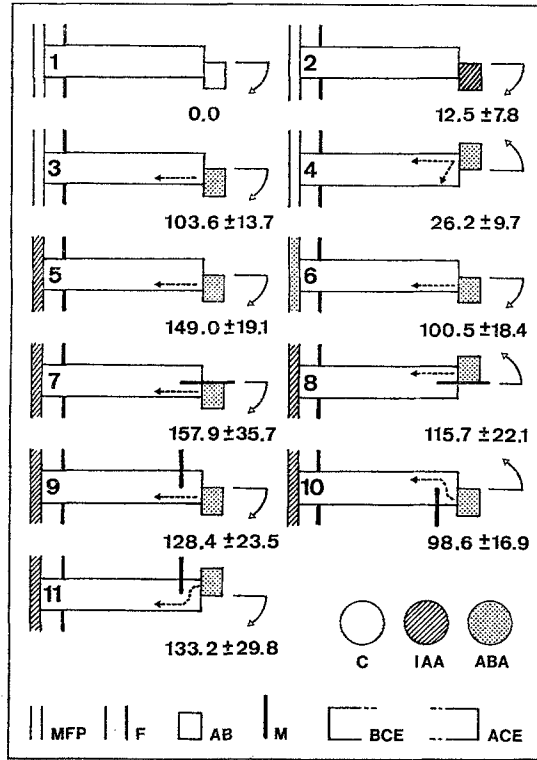
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Fig. 1. Curvature (relative values with ± standard error) after 7±0.5 h of horizontally placed maize root segments decapitated at 0.6±0.1 mm. *MFP* moist filter paper, *F* frame, *AB* agar block, *M* mica barrier, *BCE* basal cut end, *ACE* apical cut end, *C* control (without IAA and ABA). Initial length: root, 15±3 mm; segment: 10±0.2 mm. Root segments and blocks not to scale. The broken arrows indicate the transport of ABA from the donor block. For further explanation see text

All experiments are summarized in Fig. 1. For the control (1), although the relative values are 0%, a downward bending was always obtained; for 14 different assays, the curvature varied between 7 and 23°. The curvature developed by such root segments but without an agar block was 3.9±2.8°. With IAA in the block (2), the reaction was slightly enhanced, but the concentration effect (10^{-8}–10^{-4} M) was not significant. With ABA (3), in contrast, a dramatic bending was obtained at 10^{-6} M, and this ABA effect on the georeaction depends on the ABA concentration (10^{-8} M: 60.2±10.1%; 10^{-4} M: 136.8±16.9%). When the ABA block was placed on the upper half of the cut end (4), a small upward curvature was obtained. These results indicate that ABA can move lengthwise in the basipetal direction, and also laterally.

The downward curvature caused by ABA can be significantly increased when IAA is applied on the basal cut end (5), while if ABA is substituted for IAA in the
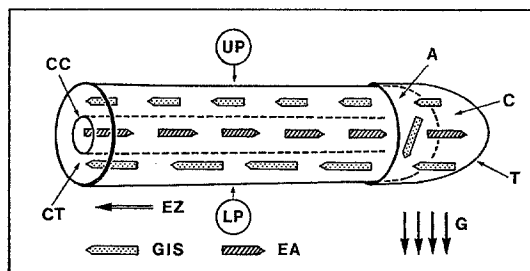
Fig. 2. Diagram showing the basipetal and lateral transport of the growth inhibiting substances (*GIS:* ABA, *etc.*) and the acropetal transport of endogenous auxins (*EA:* IAA, *etc.*) in an apical root segment placed horizontally. *UP* upper part (flank); *LP* lower part (flank), *T* tip, *C* cap, *A* cortex, *CC* central cylinder, *EZ* extension zone, *G* gravity

moist filter paper (6) the reaction is not altered (compare 3). It thus appears that the transport is polar basipetally for ABA and acropetally for IAA, both substances acting in the extension zone of the root segments.

When a mica barrier was inserted horizontally into the apical cut end of the root segment with an ABA block in the lower position (7) the curvature was not significantly different from that in similarly treated roots without a barrier (see 5), except that the standard error was greater: the barrier therefore does not induce any wounding effect. But when the ABA block was placed on the upper part of the cut end (8) a large upward bending occurred. The barrier thus prevents ABA from moving down laterally in the root apex (compare 4). Inserting the mica into the upper flank (9) did not change the reaction (compare 5), confirming that insertion of such a barrier into the root tip results in no significant injury. In contrast, the mica barrier caused a significant inversion of the bending when it was inserted into the same side of a root on the apical end of which an ABA block had been placed (10, 11).

From these data it can be concluded that ABA can move laterally in the root apex. This would partly explain an increase of ABA level in the lower flank of the extension zone of horizontally placed roots, causing downward curvature. On the other hand, it appears from experiments using mass fragmentography now under way that the production of ABA by the cap of horizontal roots was greater in the lower than the upper part.

As stated, ABA has been found in maize caps. Its transport properties appear to be very similar to those observed for the growth inhibitors which are also formed in the cap. One can assume that ABA is one of the growth-inhibiting substances. It should also be said that the acropetally polarized transport of IAA only occurs in the presence of the central cylinder (Shaw and Wilkins, 1974). Consequently root growth and the georeaction of the root could be controlled by at least two opposite flows: a basipetal transport of ABA and other growth inhibitors the level of which increases in the lower part of roots placed horizontally, and an acropetal transport of auxin (see Fig. 2).

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