Short Communication

Lateral Transport of Auxin Mediated by Gravity in the Absence of Special Georeceptor Tissue

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Georeceptor tissue in the root cap is essential for the geotropic response of a typical root (5, 6). A coleoptile has statolith cells in a hollow cylinder of parenchyma near its apex (4), but aerial parts of typical vascular plants show at least some effects of negative geotropism without the mediation of a special georeceptor mechanism.

Growth curvatures in plagiotropic leaves and branches, with and without an effect of gravity, provide an opportunity to study the mechanism which governs geotropic responses in immature tissues for which discrete georeceptors are unknown. One component of this mechanism in leaves has been shown to be controlled by biochemical processes (13). An essential feature of geotropic response in both leaves and branches is lateral transport of auxin (IAA) from the upper side into the lower side of the growth zone (10–12). Without disturbing the chemical phase of the mechanism, it is possible to vary the physical component of gravitational force and to measure the resultant effect of both the growth responses and changes in the distribution of auxin within a growth zone.

Results of experiments with tilted clinostats in this study of branches and leaves show a direct, nonlinear relationship between their geotropic responses and vectors of gravity downward along the axis of a plant. Distribution of auxin in the two organs shows the same quantitative relationship between gravity and an imbalance of IAA when the force is less than 1g.

MATERIALS AND METHODS

Plants used for experiments with growth curvatures of branches were units from the clone of *Coleus blumei* Benth. grown in our greenhouse for over 15 years. Plants with several pairs of immature branches had developed from cuttings in 4-inch pots of fertile soil. Tests of branch curvatures were made at 24 ± 0.5°C in darkness on 1 rpm clinostats with rotation axes tilted at different degrees of elevation from the horizontal, as illustrated by a typical set of plants in Figure 1. Data for degrees of growth curvature in such defoliated branches were obtained as before in our studies of epinasty (10) from superimposed shadowgraphs drawn manually on a sheet of paper. Each measurement of curvature was made by a goniometer at the intersection of lines drawn tangent to the two shadow tracings of the youngest internode as the plant was set upright against a lighted wall at the start and again at the close of an experiment 23 to 24 hr later.

Tritiated IAA (98% purity; specific radioactivity 3.6 × 10^6 cpm/mg; Schwarz-Mann, Orangeburg, N. Y.) was supplied to the branches from thin terminal caps of 1% (w/w) IAA-5-H in lanolin. The curved sections of the branches were collected after shadowgraphing, bisected into upper (convex) and lower (concave) halves by weight, and soluble materials were extracted by grinding the tissues with ethanol in a mortar. Distribution of tritiated compounds between the convex and concave sides of the curved organs was determined from liquid scintillation counting of radioactivity in the ethanol extracts. Auxin imbalance between the two counts of radioactivity was recorded and shown graphically in Figures 2 and 3 as percentage of excess auxin in the convex half in comparison with the smaller amount of auxin extracted from the concave half of the organ.

A study of comparable growth curvatures in leaves was carried out with 15 tomato plants (*Lycopersicon esculentum* Mill.) in the first bud stage. Each potted plant bore six to eight medium-aged leaves; other leaves were cut away. The procedures for attaching the pots to a tilted clinostat in sets of five, rotation in darkness for 23 to 24 hr, and measuring the distribution of radioactive auxin in the curved leaf axes were essentially the same as for experiments with branches. Differences included the use of a light-weight needle glued to the upper surface of each terminal leaflet for accuracy in shadow records, and application of the tritiated IAA to a small area of the lower surface of that leaflet (10, 13).

RESULTS

Epinastic Curvatures. The growth effects of rotating branched *Coleus* plants on a horizontal clinostat and at eight different angles of tilting the rotation axis are shown graphically in Figure 2. All data points were derived from branches on 15 plants. The epinastic curvature of the immature part of a branch decreases rapidly as the angle of axis elevation is increased from 0 to 17.5° (see Fig. 1). At that point the mean curvature is only about 18% of the maximum induced on a horizontal clinostat. As the clinostat axis is set at greater angles of upward tilt, the curvature of a branch decreases more slowly and reaches zero for the erect position of the rotating axis and plants.

Changes in curvatures of tomato leaves with differences in tilting of the clinostat appear in Figure 3. The form of the graph of curvatures from 0 to 90° tilt is much like that for branch curvatures. Decrease in leaf curvature with increase in angle of tilt is rapid between 0 and 17.5°, as for branches, although the leaf curvature still remains at 40% of the maximum at 0°. This difference and failure of the curve of leaf

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2 Dr. Lyon died on August 6, 1971.
Fig. 1. Coleus branches with small epinastic curvatures after growth for 24 hr in darkness on a clinostat with its axis inclined at 17.5° above the horizontal.

Fig. 2. Epinastic curvatures of Coleus branches and corresponding excesses of auxin in convex halves of branches after 24 hr of growth in darkness on a clinostat with its rotation axis tilted to expose plants to a range of gravity vectors along their axes. Brackets show the standard errors for means of data measurements.

Fig. 3. Epinastic curvatures of tomato leaves and corresponding excesses of auxin in convex halves of leaf axes after 24 hr of growth in darkness on clinostat with rotation axis tilted to expose plants to a range of gravity vectors along their axes. Brackets show the standard errors for means of data measurements.

Curvature to fall away at an even rate for axis elevations greater than 17.5° may be due to strong curvatures in the terminal leaflets of the younger leaves.

Auxin Distribution. Measurements of radioactivity from IAA and its degradation products extracted from the two halves of epinastic curvatures showed an excess of IAA in the convex half for both leaves and branches as expected (10, 11). The plot of this excess auxin in the upper half of a curved leaf axis (Fig. 3) followed very closely that for leaf curvature over the entire range of gravity vectors. The critical point of about 0.3g for change of decrease in percentage of excess auxin in the convex side of the organ coincided with the point of change of rate of decline in leaf curvature.

The corresponding curves for growth curvature and excess auxin in the convex half of a curved branch (Fig. 2) agree well in general trend and in the range of rates of decrements at 0.3g. The pattern of auxin distribution is similar to that for curvatures over the lower third of the vector range. With greater vectors of force the agreement between the angle of curvature and excess of auxin is not so close, but the same trend indicates a direct effect of gravitational force in moving excess IAA downward in the branch as the force approaches its maximal value.

DISCUSSION

Growth Curvatures. Development of epinastic curvatures in leaves and branches on a tilted clinostat contradicts the prediction of Larsen (7) and of Rawitscher (15) that the effect would be hyponasty. Larsen believed that stimuli from the transverse component of gravity do not cancel out during ro-
tation about a tilted axis. On the contrary, it was assumed by Dedolph et al. (3) that the rotation would free *Avena* seedling organs from effective gravitational force except for that of the longitudinal component along the tilted axis of the clinostat and seedling.

This vector of gravity is determined by the sine of the angle of elevation. The effect of variations in the vector on the orientation of immature branches was reported in 1961 by Lyon to be epinastic curvatures (8). The only other such experiments are reported by Conrad and Yokoyama (2) for epinastic curvatures in leaves of *Phaseolus* and *Capsicum* with gravitational forces increased by steps from 0 to 1g on tilted clinostats. The epinastic curvatures in their leaves, as in ours, decreased gradually as the effective gravitational force on the plant was increased to 1g for the erect position.

**Auxin Transport.** Most of the evidence for downward transport of IAA under the influence of gravity has been obtained from tests with roots and coleoptiles. Results comparable with those of this report came from work with sections of *Pisum* stems in 1966 (1) and from geotropic curvatures of intact *Coleus* branches in 1965 (12). Special georeceptor tissues were lacking in both cases but IAA moved downward through solid cylinders of tissue.

The curves for reduction of excess IAA in the upper side of a plagiotropic organ (Figs. 2 and 3) with increasing vectors of gravity show a proportionately larger effect of small vectors than from those closer to 1.0g. There is no critical effect, however, from exposing organs to a vector slightly greater than one showing no auxin transport action and getting a strong lateral movement of auxin. Such a vector could be called a threshold such as that reported for seedling organs with special receptor tissues (2, 8). This threshold effect is lacking in both leaves and branches for any gravity vector below 1.0g. This seems to be a characteristic of lateral transport without special georeceptor tissues, a point supported by the data reported by Conrad and Yokoyama (2) for leaf curvatures with gravity vectors less than 1.0g.

There is no obvious reason for the large difference between the maximal percentages (at zero g) of excess auxin in the convex side of a curved leaf (81%) and in that of a branch (35%). The mean maximal curvature of a tomato leaf axis (about 125°) is actually smaller than that of a *Coleus* branch (about 170°) with the same environment of zero g. This difference in epinastic curvatures may be due to the unequal elongation of tissues in three branch internodes on the average while the corresponding growth zone in a leaf extends along the entire axis and has a lower capacity for elongation in some regions. From the functional viewpoint, one result of the greater amount of excess auxin in the uppermost half of a leaf is to provide a greater potential for opposing the stronger tendency to negative geotropism caused by the synthesis of much more auxin in a tomato leaf blade than in a *Coleus* branch.

**LITERATURE CITED**