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The Effects of Light and Gravity on the Horizontal Curvature of Roots of Gravitropic and Agravitropic *Arabidopsis thaliana* L.

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ABSTRACT

In an attempt to study and distinguish the effects of light and gravity on the direction of horizontal root growth, wild-type and an agravitropic mutant of *Arabidopsis thaliana* L., *aux-1* were examined. The mutant *aux-1* seedling roots are agravitropic but do respond to light, thus allowing the effects of light and gravity on roots to be studied separately. It is shown that in addition to the recognized negative phototropic and positive gravitropic responses of the root, there are also horizontal curvatures (clockwise or counterclockwise) induced by both unilateral light and gravity. The effects of light and gravity in inducing the horizontal curvature of roots are synergistic when both act in the same direction, and are antagonistic when acting in opposite directions. The results indicate that light and gravity interact to determine the direction and magnitude of the horizontal curvature of roots.

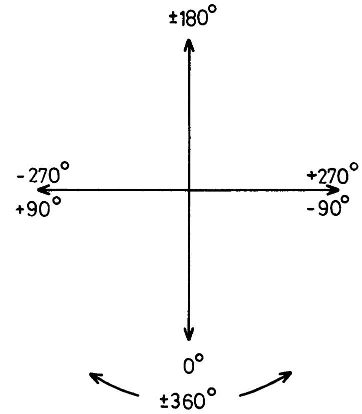

FIG. 1. Conventions for expressing the curvatures of roots. Positive curvatures in the clockwise direction and negative curvatures in counterclockwise direction. An angle of +540° thus means the root tip has completed 1½ circles in the clockwise direction.

Light and gravity are important environmental factors in the growth of plant roots. Darwin (1) noticed that in nature, most of the seeds which germinate on the surface of the soil receive light and gravity acting perpendicular to the plane of root growth until roots penetrate the soil. How do roots react to these dual stimuli? Due to the technical problem of clearly separating light and gravity responses, the information available on this aspect is scarce (2).

The microgravity environment of spacecraft provides unique opportunities for conducting research on the responses of plants to light. On earth, the presence of gravi-responsiveness often modifies or masks these responses (3). However, the agravitropic mutant *aux-1* (4, 5) of *Arabidopsis thaliana* provides an opportunity to study the responses of plant roots to light within the gravitational field of the earth.

In the present paper, advantage has been taken of the agravitropic nature of *aux-1* roots to study and distinguish light and gravity effects on the direction of horizontal root growth of *aux-1* and its isogenic WT.[2]

MATERIALS AND METHODS

The mutant *aux-1* was induced and isolated in *Arabidopsis thaliana* L., ecotype Landsberg (*erecta* mutant) on the basis of its resistance to the herbicide, 2,4-D (4). The parent plant itself is here designated as WT.

WT and *aux-1* seeds of the same size (250–300 μm, using Endecott test sieves) were sown with random orientation either on the surface of agar (1% by w/v), or sandwiched between two thin layers of agar in 9 cm polystyrene Petri dishes. The dishes were stored at 4°C for 2 d before incubation (agar surface vertical or horizontal) at 25±1°C either in darkness or in light (from white fluorescent tubes 30 cm above or below the dishes with photon flux density of 160 $\mu E\ m^{-2}\ s^{-1}$ at the level of dishes). To illuminate one face of the dish, the other face was covered with black filter paper. After incubation, the dishes were directly exposed on to photographic paper and root curvature angles were measured from the enlarged photographs according to the scheme given in Figure 1.

RESULTS AND DISCUSSION

Light and Horizontal Curvature of *aux-1* Roots. Mutant *aux-1* roots are agravitropic and negatively phototropic. When *aux-1* seedlings were grown on the surface of horizontal agar with illumination from above, the roots developed clockwise curvatures as seen from above. In contrast, *aux-1* roots developed counterclockwise curvatures (as seen from above) when illuminated from below. The clockwise or counterclockwise curvatures were more prominent when the face of the Petri dish opposite to illumination was covered with black filter paper (to prevent reflection of light) than when uncovered. To equalize the agar conditions on both sides, *aux-1* seedlings were then grown sandwiched between two layers of horizontal agar with illumination from above (Fig. 2A) and below (Fig. 2B). In the latter case, some roots appeared to grow straighter because of the interference of light by the wire mesh shelf on which dishes were placed. This could explain the difference in the mean curvature values given in Table I. It can be seen that the curvature which developed was always clockwise when viewed in the direction of

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[2] Abbreviation: WT, wild-type.

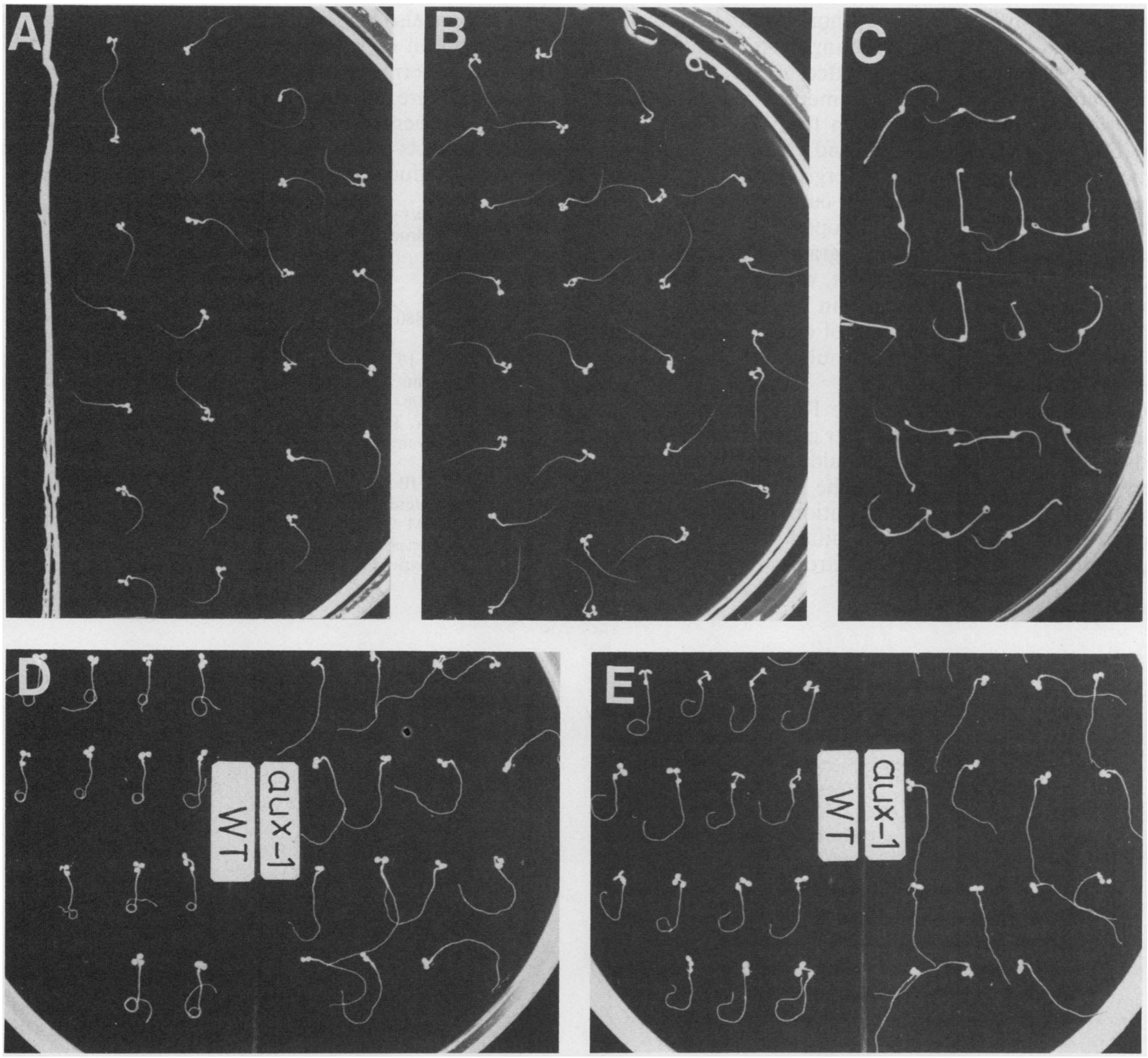

FIG. 2. Horizontal curvatures of WT and *aux-1* roots induced by light and gravity. A, *aux-1* seedlings grown sandwiched between two layers of horizontal agar after 72 h incubation with illumination from above (×1.1); and B, from below (×1.1); C, WT seedlings grown on the surface of horizontal agar after 72 h incubation in darkness (×1.0); D, WT and *aux-1* seedlings grown on the surface of agar in a Petri dish which was first held in the vertical position for 72 h with illumination from above and was then turned to the horizontal position for 48 h with illumination from above (×1.0); and E, from below (×1.0).

Table I. *Mean Curvatures of Horizontal aux-1 Roots with Illumination from Above or Below*

Seeds were sown sandwiched between two thin layers of agar and incubated for 72 h. Clockwise curvatures are assigned as (+) and counterclockwise curvatures as (−). Each value represents 42 seedlings.

Illumination from Above/Below	Mean Curvatures as Seen from Above
	degrees ± SEM
Above	(+) 104.05 ± 5.12
Below	(−) 59.31 ± 6.09

Table II. *Mean Curvatures of Horizontal WT and aux-1 Roots with Illumination from Above or Below*

Seedlings were grown as described in Figure 2, D and E. Clockwise curvatures are assigned as (+) and counterclockwise curvatures as (−). The number of seedlings in each case is given in parentheses after the curvature values.

Genotype	Mean Curvatures as Seen from Above	
	Illumination from above	Illumination from below
	degrees ± SEM	
WT	(+) 507.31 ± 35.96 (27)	(+) 181.78 ± 15.43 (28)
aux-1	(+) 51.25 ± 9.36 (31)	(−) 42.79 ± 4.59 (30)

incident light.

Gravity and Horizontal Curvature of WT Roots. When WT seedlings were grown in horizontal dishes incubated in darkness (either by switching off the lights of the growth chamber or by wrapping the dish in aluminum foil), the roots which grew on the surface of agar (Fig. 2C), developed distinct clockwise curvatures (mean degrees ± SEM of 30 seedlings, 117.17 ± 5.33). Thus, horizontal WT roots developed a clockwise curvature perpendicular to the direction of gravity vector.

Synergistic and Antagonistic Effects of Light and Gravity on the Horizontal Curvature of Roots. To see if there is any interaction of light and gravity in inducing horizontal curvatures of roots, WT (and *aux-1* as a control) seedlings were initially grown in the vertical position (to avoid the effect of the direction of radicle emergence, if any, on the development of root curvatures) and then horizontally with illumination from above (Fig. 2D) and below (Fig. 2E). When both light and gravity vectors acted in the same direction (Fig. 2D), a synergistic effect (clockwise coiling) was produced on the horizontal curvature of WT roots, whereas, an antagonistic effect (with an opening tendency of the coiling) was produced when light and gravity vectors acted in opposite directions (Fig. 2E). In contrast, with horizontal *aux-1* roots, light and gravity, whether acting in the same or opposite directions, produced similar low levels of clockwise or counterclockwise curvatures, respectively, as would be expected by the light alone (Table II).

In these experiments, one face of the Petri dish opposite to illumination was covered with black filter paper. It would, therefore, be expected that each treatment would yield seedlings which maintained equivalent temperatures. The horizontal curvature of roots are thus not attributable to variation in temperature.

The present results show that, in addition to the recognized negative phototropic and positive gravitropic responses of the root, there are also horizontal clockwise curvatures perpendicular to the direction of light and gravity vectors. Light and gravity interact to determine the direction and magnitude of the horizontal curvature of roots. In nature, however, both light and gravity act synergistically on germinating seeds as long as the developing roots are on the soil surface and would therefore be expected to induce clockwise coiling.

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