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Growth and Epinasty of Marigold Plants Maintained from Emergence on Horizontal Clinostats[1]

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ABSTRACT

Dry weight, leaf number, and leaf size of marigold plants (*Tagetes patula*) grown from emergence for 18 days on horizontal clinostats rotating at 15 revolutions per hour (rph), were similar to those of plants grown for the same period on vertically oriented clinostats rotating at 15 rph. The horizontally grown plants exhibited some epinasty which disappeared when plants were placed upright for 24 hours. Vertically grown plants when placed on horizontal clinostats for 24 hours exhibited more epinasty than plants grown from emergence on horizontal clinostats.

Data are provided to demonstrate that leaves undergo movement (bending) during each rotation cycle that leads to the development of a leaf curvature that is oriented away from the direction of rotation. The results of this study suggest that epinasty of plants placed on horizontal clinostats could be due to uncontrolled movement of plants during rotation rather than controlled by gravity nullification. The usefulness of horizontal clinostats for gravity nullification or simulating weightlessness on plants is questioned.

Clinostats have been utilized for nearly 100 years to negate gravity and thus provide information on the significance of gravity to the growth of plants. The negative geotropic response of stems, positive geotropic response of roots, and plageotropic response of leaves have been established with clinostat experiments. In more recent years, clinostats have been utilized to simulate or duplicate the weightless environment of space flight (6, 17, 19, 20) to provide understanding of possible growth effects upon plants in space stations. Clinostats theoretically negate gravity if the rotational speed is 0.1 rpm or greater so that the presentation time for plants to sense and respond to a changed gravity field is not significantly exceeded at any particular part of the rotation cycle (13). On the other hand, rotational speed cannot produce more than 0.01*g* upon the plant or centrifugal forces will control and direct the orientation of the growing organs (17, 22, 24). The biosatellite experiments which placed germinating wheat seeds and developing *Capsicum* plants in space for 2 days demonstrated that the horizontal clinostats produce growth responses similar to those observed on plants maintained in space (12, 16) and thus, it was concluded that clinostat rotation effectively duplicates space flight conditions (25). However, Brown *et al.* (3) reviewed the data collected from the biosatellite flight and demonstrated that there were significant differences between clinostatted control plants and space flight plants. Additional arguments against the usefulness of clinostats for nullifying gravity were presented by Brown *et al.* (5) in experiments with centrifugation of horizontally rotating plants.

The epinasty that develops with rotation on horizontal clinostats has been shown to result from differential auxin distribution within the petiole (18). Greater accumulation of auxin on the adaxial side of the petiole compared to the abaxial side causes the downward bending of the leaf. Researchers have also found increased ethylene production with horizontal rotation and, therefore, have proposed that this is an intermediate step between the change in orientation and altered auxin transport which induces the epinasty of the plant leaves (14). The lack of epinasty upon horizontally rotated plants that were maintained in an atmosphere of elevated CO_2 which inhibits ethylene production (14) indicates that ethylene is a controlling factor in the epinastic response.

The recent reports of growth suppression of plants by light shaking (11, 21) has raised the concern that rotation of plants on a clinostat may cause sufficient vibration of plants to stimulate growth responses, and that some responses of plants in space flight may have been due to vibrational effects during liftoff.

This study was undertaken to study carefully and compare plants that were grown continuously on horizontal clinostats with plants placed for only short periods on horizontal clinostats.

MATERIALS AND METHODS

Set-up. All experiments were conducted in the University of Wisconsin Biotron. A single growing room was divided in half with an opaque plastic screen. The front half of the room was maintained with overhead lighting for the vertically oriented plants and the back half with wall lighting for horizontally oriented plants. A divided room was utilized in preference to separate rooms to avoid room to room variation. Lighting was continuous, utilizing cool-white fluorescent bulbs. Both areas had a Plexiglas barrier between the lamps and plants. Environmental levels were balanced as closely as possible to have similar conditions at the top of the plant canopy for the vertically oriented plants in the front half of the room and for the horizontally oriented plants in the back half of the room. The experimental levels over the course of the study in the front half of the room were 16.5 ± 0.5 nE $cm^{-2}sec^{-1}$, 22.1 ± 1.4 C and 69 ± 4% RH and in the back half of the room were 17.0 ± 0.3 nE $cm^{-2}sec^{-1}$, 23.0 ± 0.9 C and 66 ± 4% RH.

Marigold seed (*Tagetes patula* cv. Petite Gold) was obtained from Ferry Morse Seed Company. The growing medium was a commercial blend of peat and vermiculite manufactured by Grace and Company. Each plastic pot of 7.5 cm diameter was filled with peat-lite. A 5-cm section of Tygon tubing (wide bore flexible PVC tubing of 2.2 cm o.d.) was filled with peat-lite and partially buried in each plastic pot so that the top of the tube extended 2 cm above the container rim. The medium of all of

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the containers was slightly compacted by hand to prevent movement of the medium during rotation on horizontal clinostats. The medium of all containers, except for that within the protruding tube, was covered with light colored 40 denier spun Dacron screening to prevent loss of medium. Seed was then planted 3 mm under the surface of the medium in the exposed end of the Tygon tube. The Tygon tubing provided elevation for the plants to prevent leaves from contacting the container rim during epinastic movements.

The seeds were then allowed to germinate while all of the containers were in an upright stationary position with overhead lighting in the front half of the Biotron room, to insure uniformity of seedling growth at the start of the experiment.

The containers were watered with one-half-strength Hoagland nutrient solution, once every 6 hr using an automatic watering system. At least 30 ml of solution was applied with each watering which provided an excess and prevented soluble salt buildup in the media. Horizontally oriented containers were watered through screen-covered openings in the sides of the container (Fig. 1) and containers with vertically grown plants were also fitted with these openings to provide adequate controls.

Plants were thinned to a single plant per container 4 days after seeding. At the start of the 9th day after seeding, white foam supports (2-cm foam test tube plugs) were secured with wire around, and pressing against, the hypocotyls of plants to prevent stem movement and maintain stem orientation perpendicular to the plane of rotation for plants on horizontal clinostats. These supports were placed on all plants in all treatments.

Experimental Procedures. At the emergence of the seedlings (3 days after seeding), 15 uniform containers were chosen and randomly divided into the three treatments. The three treatments were: horizontal orientation on a rotating clinostat (treatment H), vertical orientation on a rotating clinostat (treatment V), and vertical orientation without clinostats (treatment S). Clinostats were set at either 0° (vertical clinostat) or 90° (horizontal clinostat) to the plumb line, and mechanized rotation was provided by 15 rph synchronous electric motors. These treatments were maintained for 18 days, for a total of 21 days of growth after seeding.

At the beginning of the 21st day after seeding, treatment H plants were removed from the horizontal clinostats and placed in an upright stationary position in the front half of the room. At the same time, plants of treatments V and S were moved to the back of the room and positioned on horizontal clinostats for 24 hr. Following this 24-hr period on horizontal clinostats, treatment V and S plants were removed from the clinostats and situated in the front half of the room with treatment H plants for an additional 24-hr period. The plants' tops were then harvested at the end of this period, 23 days from seeding, and fresh weights were immediately taken. Plants were then dried at 70 C for 72 hr, and dry weights taken.

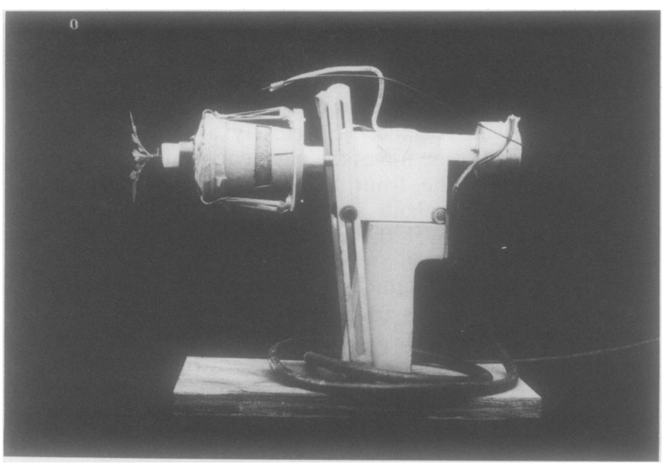

FIG. 1. Marigold plant in container attached to horizontally rotating clinostat, illustrating the automatic system utilized for watering these plants.

Data Collection. Data on plant growth and leaf orientation were collected from photographs taken during the course of the experiments. The leaves of marigolds arise in opposite pairs with each successive leaf pair arising at right angles to the preceding pair. To obtain data for both the first and second pair of true leaves, it was necessary to have photographs of two different sides of each plant. This was accomplished in a single photograph for each plant through the use of a mirror positioned to give a side view of the plant in combination with the front view image. Photographs were taken at the start of the 7th, 14th, and 21st day after seeding to give the developmental sequence of each of the treatments. Photographs were also taken at the start of day 22 to get the leaf orientation changes that occurred when the treatments were changed, and at the start of day 23 to get the final recovery positions. The plants had to be taken off the clinostats for photographing, but this required no more than 60 sec for each plant.

Data on the length of leaves and cotyledons were taken from the photographs by measuring the linear distance from each leaf tip to its respective node and correcting the value according to the magnification of the projected image. By day 21, it was difficult to observe the position of each of the leaf nodes due to the size of the plants; therefore, the second true leaf node was utilized as the center point for all leaf measurements. Individual leaf nodes were visible and utilized for all 7- and 14-day measurements. Data on leaf epinasty were taken from the photographs by measuring the angular deviation from an upright vertical orientation for each leaf. The orientation of each leaf was defined by a line drawn from the node to each leaf tip. The leaf angle was the angular deviation of the leaf orientation line from a vertical line that ran through the plant axis.

It has been observed that the plant leaves bend downward slightly during rotation on horizontal clinostats. To verify and quantify this bending of leaves on horizontal clinostats, plants were photographed from the front side facing into the growing tip at four times during a single rotational cycle. The first photograph was taken when the first leaf pair was oriented perpendicular to the direction of the force of gravity and successive photographs taken after 90°, 180° and 270° of rotation. The amount of movement of each leaf was determined when the leaves were perpendicular to the direction of the force of gravity by comparing the two photographs taken 180° out of phase with each other. The difference in the angular position of the leaves in these reciprocal photographs was recorded as the bending response. These photographs were taken of treatment H plants just before their removal from the horizontal clinostats on day 21; and of treatments V and S plants, at two times, just after they were secured on horizontal clinostats at the start of day 21 and just before removal from clinostats at the start of day 22.

Statistical significance of treatment mean squares was determined using Duncan's Multiple Range Test at either the 0.05 or 0.01 level of significance. Data for the two leaves of each leaf pair were averaged together prior to testing for significance.

RESULTS AND DISCUSSION

Plant Growth. Growth of the plants maintained on horizontal clinostats from emergence to bud formation at 21 days was similar to growth of the plants maintained in a vertical orientation over this period (Table I). There were no significant differences in the hypocotyl length, cotyledon length, leaf length, fresh weight, dry weight, or number of true leaves per

TABLE I

Growth of marigold plants maintained for 18 days after emergence in horizontal orientation on clinostats (H), in upright vertical orientation on clinostats (V) and in upright vertical orientation without clinostats (S).

Days after Seeding	H	V	S
Day 7			
Hypocotyl length (mm)	15	15	13
Cotyledon length (mm)[z]	20a	17b	17b
Day 14			
Hypocotyl length (mm)	17	17	15
Cotyledon length (mm)	30	30	30
1st leaf length (mm)[z]	43a	40b	40b
Day 21			
Hypocotyl length (mm)	17	17	15
Cotyledon length (mm)	30	30	30
1st leaf length (mm)	59	63	59
2nd leaf length (mm)	61	63	66
Day 23			
Fresh weight (g)	4.320	3.973	3.884
Dry weight (g)	.450	.405	.403
Number of leaf pairs	2.4	2.6	2.8

[z]Mean separation within rows by Duncan's Multiple Range Test. Values with no common letters are significantly different at the 5% level. Values in the other rows are not significantly different at the 5% level.

plant. There was a small but significant increase in the cotyledon length measured on day 7 and in the first leaf length measured on day 14 during enlargement of the plants on the horizontal clinostats compared to plants in the vertical position. This small difference in growth rate was probably due to the slightly higher temperatures around the horizontally oriented plants, and did not appear as differences in the final developed size of hypocotyl or first leaves. Foliage color and growth habits of the plants were similar for all three treatments. It appears that the effects of long term growth on a horizontal clinostat have little effect on the gross morphology or rate of growth of plants.

The lack of significant effects of horizontal rotation on leaf enlargement and number of developing leaves is in agreement with previous studies by Brian (2) and Brown *et al.* (4) with several different plant species. A study by Hoshizaki *et al.* (9) did demonstrate differences in leaf elongation and node number but these data were taken upon plants grown for a period in an upright position before being placed on clinostats, as compared to this study and studies by Brian (2) and Brown *et al.* (4) that were conducted with plants grown from emergence on clinostats. Scientists have reported significant effects of horizontal rotation upon root and stem elongation. Both increases and decreases have been demonstrated for hypocotyl growth (2, 4, 20). Decreases in elongation have been reported for the stems and roots of most plants (2, 9). Reductions in stem and root elongation would be expected with the increased production of ethylene noted both with horizontal rotation on clinostats (14) and with vibration and shaking (7, 15, 23). The lack of a significant increase or decrease in stem elongation of marigold plants in this study is not completely unexpected for there is essentially no internode elongation in this marigold species.

Small differences in growth of plants on horizontal clinostats *versus* growth of plants in an upright position are to be expected because of the difficulty in maintaining similar radiation, temperature, and air movement environments around horizontally and vertically maintained plants for extended periods of growth.

Leaf Angle. Leaves of plants grown on horizontal clinostats from emergence exhibited a slight epinasty when compared with vertically grown plants (Table II). This difference became more significant as the plants became older and larger. The first statistically significant difference in leaf angle was recorded on day 14 for the first leaf pair. However, there was no significant difference in the orientation of the cotyledons on this date. At day 21, there was again recorded a significant difference in the orientation of the first leaf pair. In plants of treatment H, the first leaf pair angle was 121° from vertical, while leaf angles of treatments V and S were 98 and 102°, respectively; thus, demonstrating about 20° of epinasty. However, for the second leaf pair, there was no significant difference in epinasty under the different treatments.

A greater amount of leaf epinasty developed in plants that were grown in a vertical orientation and placed on horizontal clinostats for only a 24-hr period, treatments V and S (Table II). Both the first and second leaf pairs of 21-day-old plants given a 24-hr period of horizontal rotation exhibited much greater epinasty than similar leaves of plants of treatment H maintained from emergence on horizontal clinostats. The first leaf pairs of plants in treatments V and S were at angles of 138 and 135°, respectively, compared to an angle of 121° for plants of treatment H at the end of horizontal rotation on day 21. The second leaf pair had angles of 115 and 120° for treatments V and S, respectively, compared to the angle of only 86° for the treatment H plants.

Another indication that plants grown from emergence on horizontal clinostats do not develop as much epinasty as plants placed on horizontal clinostats for short periods of time is demonstrated in the recovery response of the leaves. A reversal of epinasty occurs when plants are removed from the clinostats and maintained in an upright orientation for 24 hr. The recovery responses for the leaves of plants of treatment H plants were only 4 and 7° for the first and second leaf pairs, respectively, which were significantly less than the recovery response between 22 and 28° for the first and second leaves of treatment V and S plants (Table II). Figure 2 shows the leaf orientation of plants before and after recovery from horizontal rotation for plants of treatments H and V.

At no time during the experiment were there any significant differences in leaf angles between plants grown on vertical clinostats and plants grown in a vertical stationary orientation for 21 days. Growth rates and morphology of V plants and of S plants were similar. This would lead to the conclusion that rotation of plants on a vertically oriented clinostat has no measurable growth effect upon the marigolds.

The photographs taken facing into the top of plants while being rotated on horizontal clinostats showed that leaves bend sidewise during each rotation on the clinostat (Fig. 3). The

TABLE II

Leaf angles of marigold plants grown for 18 days after emergence under the indicated treatment conditions of Table I.

Days after seeding	H	V	S
Day 7			
Cotyledon angle (degrees)	84	79	84
Day 14			
Cotyledon angle (degrees)	101	98	102
1st leaf angle (degrees)[y]	90a	81b	82b
Day 21			
1st leaf angle (degrees)[y]	121a	98b	102b
2nd leaf angle (degrees)	86	91	94
Day 22			
1st leaf angle (degrees)[y]	117a	138	135
2nd leaf angle (degrees)[y]	79a	115b	120
Day 23			
1st leaf angle (degrees)[z]	120a	110b	114ab
2nd leaf angle (degrees)	86	93	96
Recovery response	(day 21 - day 22)	(day 22 - day 23)	(day 22 - day 23)
1st leaf recovery (degrees)[y]	4a	28b	22b
2nd leaf recovery (degrees)[y]	7a	22b	24b

[y]Mean separation within rows by Duncan's Multiple Range Test. Values with no common letters are significantly different at the 1% level.
[z]Mean separation within rows by Duncan's Multiple Range Test. Values with no common letters are signifícnatly different at the 5% level. Values in other rows are not significantly different at the 5% level.

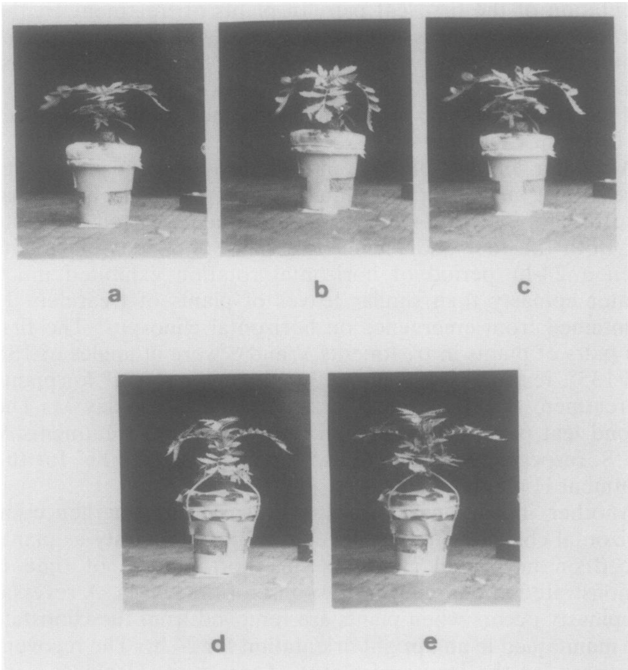

FIG. 2. Orientation of leaves of marigold plants, cv. Petite Gold. a: Plant having 18 days of upright vertical orientation and rotated on upright clinostat. b: Plant of (a) after 24 hr on horizontal clinostat. c: Same plant after 24 hr in upright position on bench. d: Plant after 18 days of horizontal orientation and rotation on horizontal clinostat. e: Plant of (d) after 24 hr in an upright position on bench.

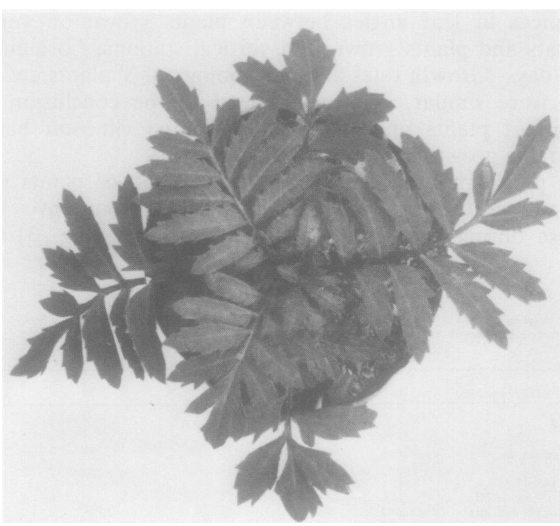

FIG. 3. Top facing photograph of a marigold plant of treatment H at 21 days just before removal from a horizontal clinostat. This depicts the curved growth of leaves that develops with rotation in the direction the leaf tips are oriented.

average angular leaf bending during each rotation on horizontal clinostats is given in Table III. Leaf-bending values for a given leaf pair in treatment H plants were similar to those of treatment V and S plants. Leaf-bending averages ranged from 7 to 9° for the first leaf pair of all treatments and 18 to 23° for the second leaf pair of all treatments. The amount of bending during each rotation was the same during the 1st hr of horizontal rotation as during 24th hr of horizontal rotation. This bending was sufficiently slow so that it was not possible to observe any obvious movement or "flopping" of the leaves.

The pattern of bending response was not uniform during the rotation cycle of each leaf. The sidewise bending response was greatest when a particular leaf was in a position perpendicular to the gravity force vector and negligible when in a position aligned with this vector. In addition, the leaf was bent for a shorter period of time during the lowering portion of the rotation cycle than during the rising part of the rotation cycle. The explanation for this response can be most easily demonstrated by comparing the bending response of the two leaves of each pair. The leaf lowering with the gravity force vector reaches a position parallel with the vector before the leaf rising against the vector (b of Fig. 4). This is because the leaf lowering with the gravity force vector bends toward a position parallel with the gravity force vector while a leaf rising against that vector bends away from a position parallel with the vector. The leaf in the down position would tend to maintain a downward orientation parallel with the gravity force vector as the leaf rotates upward against this vector. The leaf in the up position would immediately start its descent, aided by gravity as soon as it passed the upright position (c of Fig. 4). As a result of this, each leaf is parallel with gravity force vector for a greater portion of each cycle in the down position than parallel with vector in the up position. Also, each leaf is in the ascent part of the rotation on a horizontal clinostat for a greater period than in a descent part. This causes unequal distribution of the gravitational force vectors acting on each leaf, for the vectors are not uniformly distributed during the 360° of each rotational cycle. These cumulative effects are best demonstrated by the curved orientation that leaves assume when rotated for several

TABLE III

Sidewise bending of leaves of marigold plants on horizontal clinostats after being grown for 18 days under the indicated treatment conditions of Table I.

	SIDEWISE LEAF BENDING (DEGREES)		
	H	V	S
Day 21			
1st leaf bending (degrees)	7(3)[x]	8(5)	9(5)
2nd leaf bending (degrees)	18(5)	22(5)	23(5)

[x]Number in parentheses indicates the number of single plant replicates (On two plants, the first leaves could not be accurately measured because they were partially covered by the second pair of leaves).

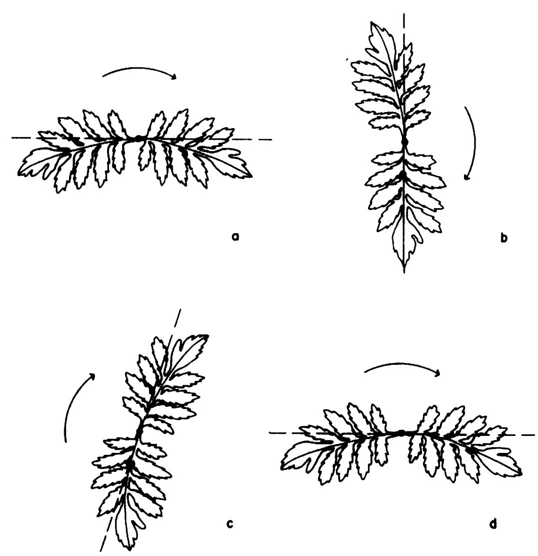

FIG. 4. Top facing diagrams of a pair of marigold leaves at four different positions; a, b, c, and d, during 180° rotation on a horizontal clinostat demonstrating unequal sidewise bending. The dotted line indicates theoretical orientation of leaf midrib if no bending was occurring.

days on a horizontal clinostat (Fig. 4). The leaf tips of horizontally rotated plants tend to curve back away from the direction of rotation. Vertically rotated plants do not develop this leaf configuration. Plants with this curved configuration tend to lose it after being placed vertically for 24 hr.

A previous report has documented a similar type of curvature in developing radicles with bending of the tip away from the direction of rotation (26). Induction of the curvature has likely resulted also from unequal gravity force vectors during rotation as discussed in this paper. Another report (10) describing a curvature of plant stems in the direction of rotation is difficult to explain with the concepts developed in this paper. However, the plants were oriented perpendicular rather than parallel with the direction of rotation.

The data obtained in these studies raise serious questions about the assumption that nullification of gravity with horizontal rotation causes epinasty of leaves. One might assume that the bending and wobbling of the leaves during horizontal rotation induce the epinasty of the leaves. Mechanical stimulation has been found to increase the production of ethylene, a plant hormone produced under stressful situations (1, 7, 8, 15, 23). The leaf movement during clinostat rotation may be encouraging the production of ethylene and this growth hormone-inducing epinastic response of the leaves. The low amount of leaf epinasty in plants grown from seedling stage compared with plants placed on horizontal clinostats for 24 hr might be explained by the studies of Leather *et al.* (14) on tomatoes. They showed that there is a peak of ethylene production within a few hr after plants are placed on horizontal clinostats that would encourage epinasty. The increased level slowly returns to a normal, low level of production with resulting reduction of epinasty.

The studies reported indicate that rotation of plants on horizontal clinostats does not negate the force of gravity upon plant leaves that are free to bend. Therefore, the use of clinostats for simulating weightlessness or zero gravity upon plants with expanded leaves must be questioned.

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