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Causal Basis of Gravity Stimulus Nullification by Clinostat Rotation[1]

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Summary. Using appropriate clinostat rotation methods, it has been shown that increases in root growth and geotropic curvature of oat coleoptiles are related to and explained (within the limits of auxin economy) by increased rates of plant respiration imparted by nullification of the gravitational stimulus. Increased respiration with decreased gravitational stimulus, in turn, is explained by increased uniformity in intracellular distribution of metabolically active graviprecipitable particles.

Oat seedlings grown with nullification of the gravitational stimulus show a more uniform distribution of graviprecipitable protoplasmic inclusions. Respiration involves reactions between particles of sufficient mass to be precipitated in 1 $\times$ g unidirectional force field and particles of such size that they are distributed throughout the protoplasm due to thermal energy. When plants are grown without nullification of the gravitational stimulus, graviprecipitable protoplasmic inclusions tend to accumulate in the lower portions of the cells. Respiration rates are consequently limited due to a relatively low concentration of the smaller particles in the region of high concentration of the larger particles. Distribution of the larger particles throughout the protoplasm negates the reaction rate limiting effects of these intracellular concentration gradients.

It has been shown using starch particles to index graviprecipitation of intracellular particles that enhancement of respiration by nullification of the gravitational stimulus may be induced, maintained, discontinued, and reinduced by treatments which concomitantly result in the more uniform distribution of graviprecipitable protoplasmic inclusions, the maintenance of this uniform distribution, the discontinuation of this uniform distribution and its reinduction.

The degree of uniformity of intracellular particle distribution in response to treatments only partially nullifying the gravitational stimulus is shown wholly consonant with growth responses of roots and coleoptiles when the growth is measured as the expression of increased respiration in the absence of auxin limitation.

The findings collectively indicate that gravity sensing by plants is broadly based on the physicochemical relationship between particle distribution and the expression of respiratory metabolism as growth.

Oat seedlings grown on horizontal-axis clinostats show increased root growth and a greater curvature in response to unidirectional geotropic stimulation than either plants grown on a vertical-axis clinostat or those grown vertically without rotation (3). Though neither of these differences are direct consequences of modified auxin economy (4), they are direct consequences of increased metabolic activity (5). This manuscript shows that more uniform distribution of graviprecipitable protoplasmic inclusions is the probable cause of enhanced metabolism which governs attendant phenomena associated with quantitative nullification of the directional component of the gravitational stimulus.

Materials and Methods

Particle Distribution Studies. Hulled imbibed oat seeds (*Avena sativa* cv. Victory 1, Svalof, Sweden) were planted in moist quartz sand (15 % H_2O by wt) in the bottom of 250-ml beakers. The geometry

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of seed placement, use of red light to inhibit mesocotyl development, 2 rpm clinostat rotation rates, and other general cultural practices employed in these experiments were the same as those previously described (3,4).

The axes of the clinostats used in studying the influence of gravity on intracellular particle distribution were tilted at angles which imposed a unidirectional gravity stimulus of 0.00, 0.02, 0.04, 0.06, 0.08, 0.10, 0.12, 0.14 or 1.00 × g (6). In addition to these gravity treatments involving clinostat rotation, a stationary vertical treatment was employed to index the effect of rotation per se on starch particle distribution.

Plants grown under each of these gravity treatments for about 72 hours were exposed to 0, 5, 10, 15 or 20 minutes of stationary transverse geostimulation. Half of the plants exposed to each of the times of stimulation were harvested at the end of the transverse geostimulation period. Plants not then harvested were returned to the gravity treatment imposed during their growth and harvested 1 hour later.

The harvested coleoptiles were quickly sectioned longitudinally along the cross-sectional axis which was vertical during transverse geostimulation. Sections were immediately fixed and stained with Lugol's iodine solution (8). After 1 to 2 minutes they were washed with distilled water. Two or 3 drops of glycerine water solution (1:1 v/v) were then placed over the section and a cover slip applied. Over the next few days following restaining microphotographs of these sections were made.

Using these microphotographs, the percentage distribution of amyloplasts was determined between apical and basal cell halves (longitudinal distribution) and between the half of the cell uppermost and lowermost during geostimulation (transverse distribution). These percentage distributions were determined for 2 representative cells from each of 2 coleoptiles from each of the 100 discrete treatments; thus, in all, 400 cells were examined in 200 different coleoptiles.

The influence of quantitative nullification of the gravitational stimulus on oat seedling growth was assessed in parallel experiments. Following about 72 hours of growth on tilted axis clinostats imposing gravitational stimuli of 0.00, 0.01, 0.02, 0.03, 0.04, 0.05, 0.10, 0.15, 0.20, 0.25, 0.50, 0.75, or 1.00 × g, seedlings were harvested and shadowgraphed between 2 glass plates. Lengths of organs were subsequently determined, using a cartographer's wheel. Number of roots per plant and percent germination were also noted. In this experiment, as in all others involving growth measurements, plants were randomly harvested across gravity treatments, negating possible bias introduced by consistently harvesting any gravity treatment earlier or later than others.

The effect of partial gravity stimulus on geotropic curvature was also assessed. In these experiments, 72-hour-old oat seedlings grown on clinostats imposing 0.00, 0.05, 0.10, 0.20, 0.25, 0.50, 0.75, or 1.00 × g unidirectional gravity stimulus were subjected to 20 or 40 minutes stationary transverse geostimulation. For 1 hour following geostimulation, plants were returned to the clinostats on which they were grown. Curvatures were measured from shadowgraphs prepared immediately after the 1 hour post-stimulation period.

Respiration Studies. Oat seedlings were grown in clinostats modified to serve as the chamber components of continuous flow respirometers. Seedlings were sequentially exposed to horizontal or vertical clinostat rotation (table III, Regimes HV and VH).

Respiration as CO_2 evolution into the metered air stream passing over the plants within the clinostats was assayed hourly by infrared gas spectrophotometry. The weight of the growing tissue at the time of measurement of respiratory activity was determined on the basis of the weight of tissue when the experiment was terminated (5).

The influence of sequential reorientation of clinostat axes on growth of seedlings was directly assessed, using periods of horizontal and vertical rotation identical to those used in the respiration study (table III, Regimes HV and VH). In these growth experiments, plants were also maintained with continuous horizontal or vertical rotation assessing growth under these conditions (table III, Regimes H and V). Prior to each reorientation of rotational axes, 7 beakers containing about 20 plants were removed from each of the gravity treatment regimes, harvested, separated as to roots and tops, and weighed. Mean weights of plant roots and tops in each beaker were used in the statistical analyses.

Convenience of experimental manipulation predicated the use of length measurements in some experiments and weight measurements in others. To validate the interchangeable use of weight and length data, the relationship of weight to length in roots and tops of seedlings was established. This relationship further served as a gross indication of morphological characteristics of organs.

Three-day-old seedlings grown as in the other experiments were harvested, separated as to roots and tops, weighed, and shadowgraphed between 2 glass plates. Lengths determined from these shadowgraphs with a cartographer's wheel were then collated with the weight at harvest and the degree of this relationship tested. Data used in the statistical analyses were the mean weights and lengths of plant roots and tops harvested from each beaker.

Data obtained from all experiments were subjected to analysis of variance when applicable. If data interpretation and presentation were facilitated by their use, regression methods were incorporated into these analyses. When discrete differences among means rather than trends have been presented, these differences were delineated by appropriate multiple comparison methods (7, 10). Relationships between length and weight measurements, as well as observed and calculated particle distribution within cells by quadrants, were tested by correlation methods.

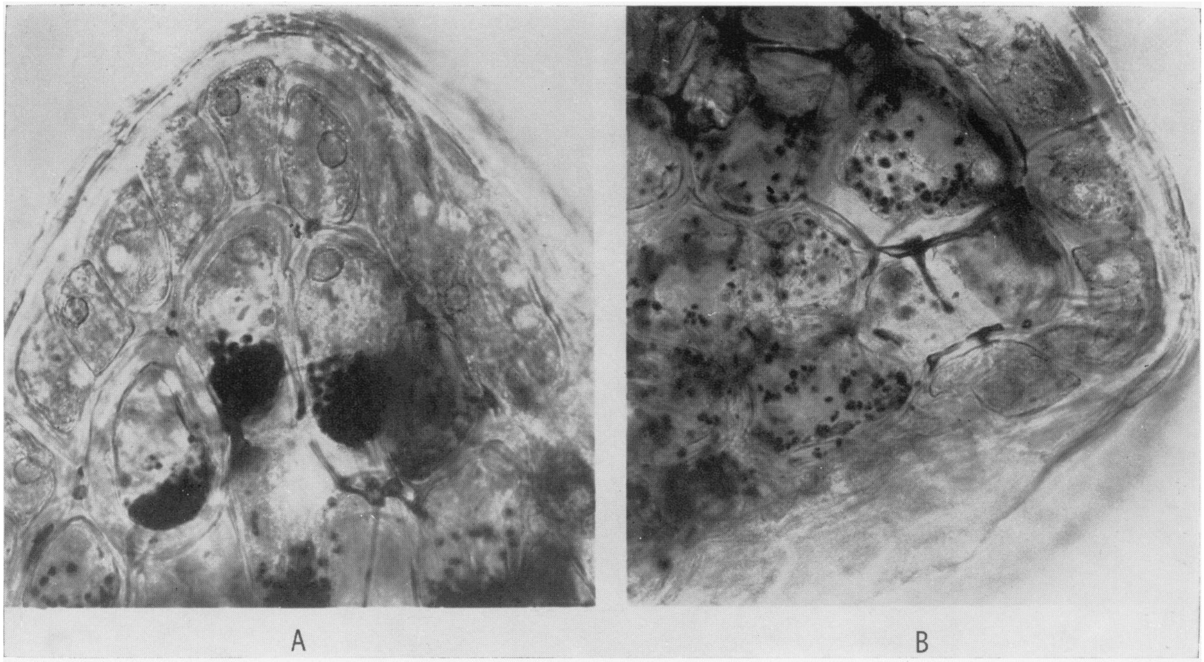

Fig. 1. Distribution of amyloplasts in cells of *Avena* coleoptiles grown (A) on a vertical-axis clinostat (plant vertical) or (B) on a horizontal-axis clinostat (plant horizontal), both rotating at 2 rpm.

Results and Discussion

Microphotographs of oat coleoptile sections showed that amyloplasts were concentrated in the basal halves of coleoptile cells when plants were grown on a vertical-axis clinostat which rotates the plants, but did not nullify the directional component of the gravitational stimulus (fig 1A). Conversely, amyloplasts in the cells of coleoptiles grown on horizontal-axis clinostats effecting nullification of the directional component of the gravitational stimulus were more uniformly distributed throughout the protoplasm (fig 1B). Similar microphotographs of coleoptile sections of plants subjected to intermediate levels of nullification and various transverse geostimulation periods have been diagrammatically depicted (fig 3).

Transverse geostimulation induced amyloplasts to settle to the side of the cells lowermost during this treatment (table I). The degree of this settlement was little effected by the 5, 10, 15 and 20-minute period of geostimulation used. This is not unexpected, for the minimum stimulation time used exceeded the calculated time necessary for an amyloplast to fall completely across a cell of this size (2). The degree of transverse particle sedimentation was not materially affected by the level of longitudinal gravitational force under which the plants were grown.

When geostimulated plants were returned to the gravity treatment under which they were grown for 1 additional hour, uniform transverse distribution of amyloplasts was reestablished (table I).

Longitudinal sedimentation of amyloplasts in non-geostimulated plants progressively increased with the level of gravity force imposed from 0.00 to 0.14 × g range (fig 2A). When the longitudinal gravity

Table I. *Percent of Amyloplasts in Halves of Oat Coleoptile Cells Lowermost during Geostimulation Immediately after Geostimulation and 1 Hour after the end of the Stimulation Period*

Hrs after end of geostimulation treatment	Min transverse geostimulation was applied 0	5–20
0	49.8b*	60.2a
1	48.8b	52.3b

* Means followed by the same letter do not differ significantly at the 5 % level; means not followed by the same letter differ significantly at the 1 % level. n = 40 for 0 minutes stimulation; 120 for 5 through 20 minutes stimulation. Error mean square = 18.2. Differences required 1 %: 60.2 vs. 52.3, 49.8, 48.8; 5.2, 8.6, 8.9, respectively; 5 %: 52.3 vs. 49.8, 48.8, 6.3, 6.6, respectively; 49.8 vs. 48.8: 6.6 (see 10).

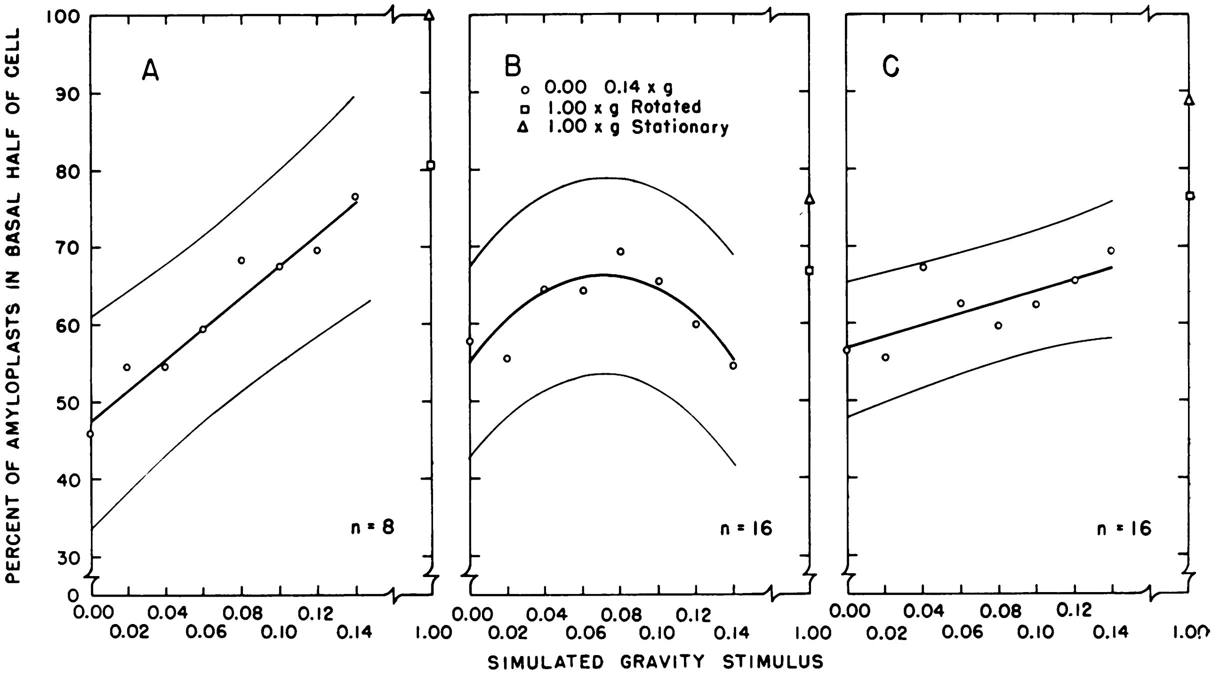

FIG. 2. The percentage of amyloplasts in basal halves of cells of oat coleoptiles grown with various levels of unidirectional gravitational stimulus (A) before 5 through 20 minutes geostimulation, (B) immediately after 5 through 20 minutes geostimulation and (C) 1 hour after geostimulated plants were returned to the gravity condition of their growth. Lines above and below fitted curves are 95 % confidence intervals on a new mean observation in 0.00 to 0.14 × g range. Equations of the regressions presented are A) $P = 47.9\ (\pm 13.4) + 200.30\ (\pm 91.00)\ g$; B) $P = 54.8\ (\pm 2.9) + 332.83\ (\pm 179.05)\ g - 2344.680\ (\pm 1243.947) g^2$; C) $P = 57.3\ (\pm 8.5) + 71.45\ (\pm 57.60)\ g$. Where P = percent of amyloplasts in basal half of cell and g = the operative unidirectional gravity force. The values in parentheses following regression coefficients are the 95 % confidence limits of the coefficient. n = Number of cells used to establish each mean.

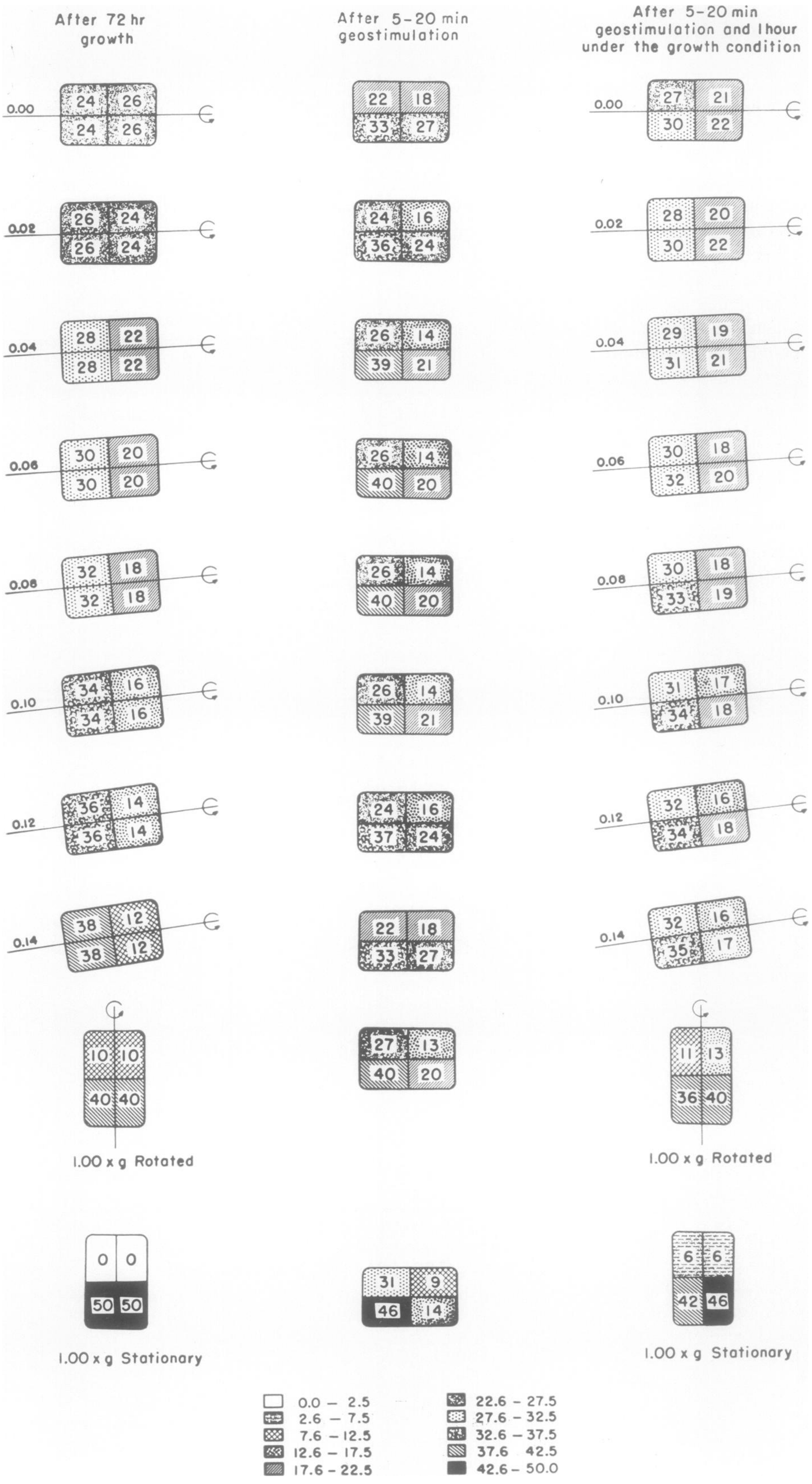

FIG. 3. Average amyloplast distribution in oat coleoptile cells by quadrants as calculated by collation of significant transverse and longitudinal distribution trends.

force tended to markedly concentrate the amyloplasts into the basal halves of the cells (i.e., forces in excess of 0.08 × *g*), geostimulation modified the longitudinal distribution of the amyloplasts. Under these conditions, transverse geostimulation induced amyloplasts to move out of the basal half of the cells into the apical half (fig 2B).

Amyloplasts in geostimulated plants which were returned for 1 hour to the longitudinal gravity force under which they were grown tended to redistribute to a pattern similar to that in nongeostimulated plants (fig 2C).

Cells of plants grown without nullification but with rotation showed a lesser concentration of amyloplasts in their basal halves than did stationary controls (1.00 × *g* rotated vs. stationary, fig 2A, B, and C and table II). As with the plants grown with longitudinal gravity forces in the 0.08 through 0.14 × *g* range and for the same reasons, geostimulation induced amyloplasts to move from the basal to apical cell halves. These geostimulus-induced asymmetries in longitudinal distribution of amyloplast tended to be negated by 1 hour in their vertical growth condition.

Table II. *The Influence of Vertical Rotation and Geostimulation on the Percentage of Amyloplasts in the Basal Half of Cells*

Condition during growth and in the post-stimulation period	Hr following geostimulation	0	1
	Min of transverse geostimulation 0	5–20	5–20
Rotated about a vertical axis at 2 rpm	80.6bc*	66.9d	76.0c
Stationary	100.0a	76.9c	88.8b

* Means not followed by the same letter differ significantly at the 5 % level. n = 8 for 0 minute stimulation; 16 for 5 through 20 minute stimulation. Error mean square = 11.54. Differences required 5 %: 100 vs. 66.9, 76.0, 76.9, 80.6, 88.8; 11.3, 11.1, 10.9, 8.6, 10.0, respectively; 88.8 vs. 66.9, 76.0, 76.9, 80.6; 9.1, 8.9, 10.5, 10.0, respectively; 80.6 vs. 66.9, 76.0, 76.9; 10.8, 10.5, 10.0, respectively; 76.9 vs. 66.9, 76.0; 8.6, 8.2, respectively; 76.0 vs. 66.9; 8.2 (see 10).

A pictorial description of the overall modifications of amyloplast distribution effected by the various treatments employed is obtained when data on longitudinal distribution trends (fig 2A, B, C and table II) are collated with the data describing transverse distribution (table I). The description obtained (fig 3) expectedly correlates highly with observed distribution patterns (correlation coefficients of observed and calculated percentages are, respectively, 0.907, 0.925 and 0.937, for cells depicted in columns 1, 2 and 3 of fig 3). This circuitous approach to the joint effects of longitudinal and transverse forces on particle distribution patterns circumvents statistical difficulties inherent in analysis of this type of data on whole cell basis.

Growth responses to nullification of the gravitational stimulus and concomitant increases in intracellular particle distribution and respiration must be interpreted on bases consonant with considerations of growth control by auxin level. Roots generally possess auxin contents at or near supraoptimal levels for growth (1). Conversely, coleoptiles generally possess auxin levels which are suboptimal for growth. The increase of auxin in the side of a coleoptile lowermost during geostimulation results in increased growth by that side of the organ and consequent curvature.

The supraoptimal auxin level in the roots permits the direct expression as growth of respiration increases caused by gravity nullification. Increases in coleoptile respiration in the presence of adequate auxin levels are expressed as growth when growth is measured as increased curvature in response to geostimulation.

Root growth (fig 4) and coleoptile curvature in response to 20 or 40 minutes of geostimulation (fig 5) increased as the simulated gravity force imposed during seedling growth was decreased from roughly 0.10 to 0.00 × *g*. It is evident that as uniformity of particle distribution increases, growth of both roots and coleoptiles correspondingly increases if auxin supply is adequate (compare figs 2A and 3 with 4 and 5).

Neither the percent germination (avg. 69.8) nor the number of roots per plant (avg. 4.2) was affected by gravity nullification.

The data trends in the 0.10 to 1.00 × *g* range of figures 4 and 5 are inconsequential because of the great variability of *Avena* curvature and overall

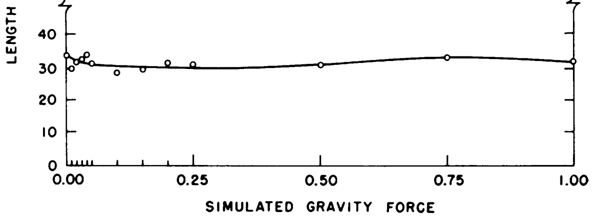

FIG. 4. The influence of varying gravity forces on root □ and coleoptile ○ lengths. Regression equations for these curves are: $R = 162(\pm 5) - 132.7(\pm 64.2)\,g + 257.98(\pm 171.16)g^2 - 153.813(\pm 118.248)g^3$; $C = 33(\pm 1) - 19.7(\pm 13.8)\,g + 52.34(\pm 36.81)g^2 - 32.926(\pm 25.432)g^3$. Where R and C = root and coleoptile lengths, respectively, and g = the operative unidirectional gravity force. The values in parentheses following regression coefficients are the 95 % confidence limits of the coefficients. Regressions are based on measurements of 1872 plants.

growth data (see confidence intervals on regression coefficients of equations in both figures).

Respiration rates prior to the first reorientation of clinostat axes 61 hours after planting were similar to those already published (5). As before, seedlings rotated on horizontal-axis clinostats showed consistently higher respiration than those rotated on vertical-axis clinostats. The magnitude of this difference decreased with increasing age of the seedling. Within 1 hour following the reorientation of clinostat axes, respiration rates of seedlings grown with vertical rotation which were then subjected to horizontal rotation had attained levels consonant with those expected from horizontally rotated seedlings. Conversely, during this same period, respiration rates of plants grown with horizontal rotation but then subjected to vertical rotation decreased to levels consonant with those expected from vertically rotated plants. Subsequent periodic reorientation of clinostat axes resulted in corresponding changes in rates of respiration of the plants they contained (fig 6A).

When the time trend in respiration rates (primarily the effect of seedling weight increase with age) is removed, the effect of the gravity nullification on respiration rate more clearly emerges (fig 6B).

Analyses of these respiration rates disclosed that differences between hourly readings made within the sequential periods of orientation were wholly due to effects of orientation and the time trend in respiration (fig 6A) or to orientation alone when the time trend in respiration was negated (fig 6B). Since no difference was found due to the time within an orientation period when measurement was made, it is evident that the 1-hour period between reorientation and the first respiration measurement in the new orientation was adequate to repress completely or impart the stimulatory effects of gravity nullification.

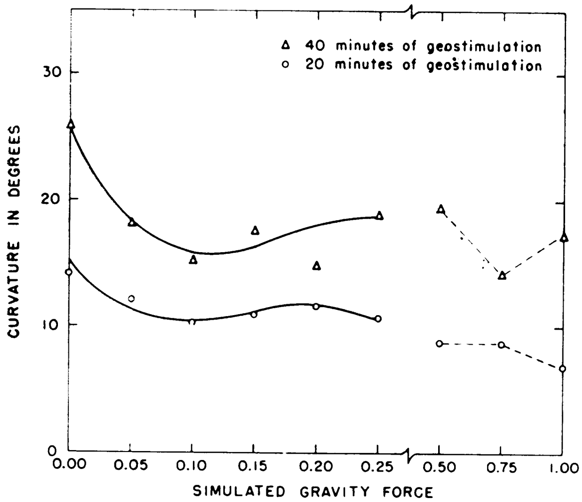

FIG. 5. The effect of varying gravitational forces on the geotropic curvature response of *Avena* coleoptiles. Regression equations for these curves are: $C_{40} = 25.8 (\pm 2.4) - 209.68 (\pm 86.70) g + 1341.095 (\pm 838.270) g^2 - 2454.9473 (\pm 2156.2601) g^3$; $C_{20} = 15.3 (\pm 1.8) - 120.95 (\pm 64.74) g + 929.201 (\pm 621.296) g^2 - 2088.2617 (\pm 1599.5288) g^3$. Where C_{40} and C_{20} = degrees curvature following 40 and 20 minutes geostimulation, respectively, and g = the operative unidirectional gravity force in the 0.00 through 0.25 range. The values in parentheses following the regression coefficients are their 95 % confidence limits. Regressions are based on responses of 240 coleoptiles subjected to each period of geostimulation.

Table III. *Treatment Regime Followed in Studying the Effects of Intermittent Horizontal and Vertical Clinostat Rotation on Respiration (HV and VH) and Seedling Growth (all Regimes)*

Regimes*	Time periods in hrs			
	Planting-61**	61–65	65–69	69–73
H	H	H	H	H
V	V	V	V	V
HV	H	V	H	V
VH	V	H	V	H

* H = rotated on a horizontal-axis clinostat at 2 rpm; V = rotated on a vertical-axis clinostat at 2 rpm.

** Planting of seeds took place approximately 3 hours after the 2-hour soaking period commencing at time 0.

Once induced, respiration enhancement by gravity nullification is maintained as long as the gravitational stimulus is nullified. Respiratory enhancement may, however, be successively reinduced by returning tissues which have been subjected to a unidirectional gravitational stimulus of sufficient magnitude and duration to conditions nullifying the gravitational stimulus.

Seedlings rotated on vertical-axis clinostats either intermittently or continuously grew less than those continuously exposed to horizontal rotation (table IV). These growth data clearly show that plants initially removed from the gravitational stimulus through rotation on a horizontal-axis clinostat but subsequently intermittently subjected to this stimulus through rotation on a vertical-axis clinostat grew less than those maintained without this stimulus (table IV, compare H and HV). These data likewise show, albeit without meaningful magnitude or statistical inference, that growth of plants initially subjected to the gravitational

Table IV. *The Influence of Intermittent Horizontal and Vertical Clinostat Rotation on the Weight of 61 to 73-Hour-old Oat Seedlings*

	Treatment*			
	H	HV	V	VH
Mean fr wt in mg/plant	102.6a**	92.2b	87.8b	89.8b

* Treatment code defined in table III.

** Means followed by different letters differ significantly at the 1 % level; means followed by the same letter do not differ significantly at the 5 % level. n = 28. Standard error mean = 1.83. Differences required 1 %: 102.6 vs. 92.2, 89.8, 87.8; 6.7, 7.0, 7.1, respectively; 92.2 vs. 89.8, 87.8; 6.7, 7.0, respectively; 89.8 vs. 87.8; 6.7; 5 %: 92.2 vs. 89.8, 87.8; 5.1, 5.3, respectively (see 6).

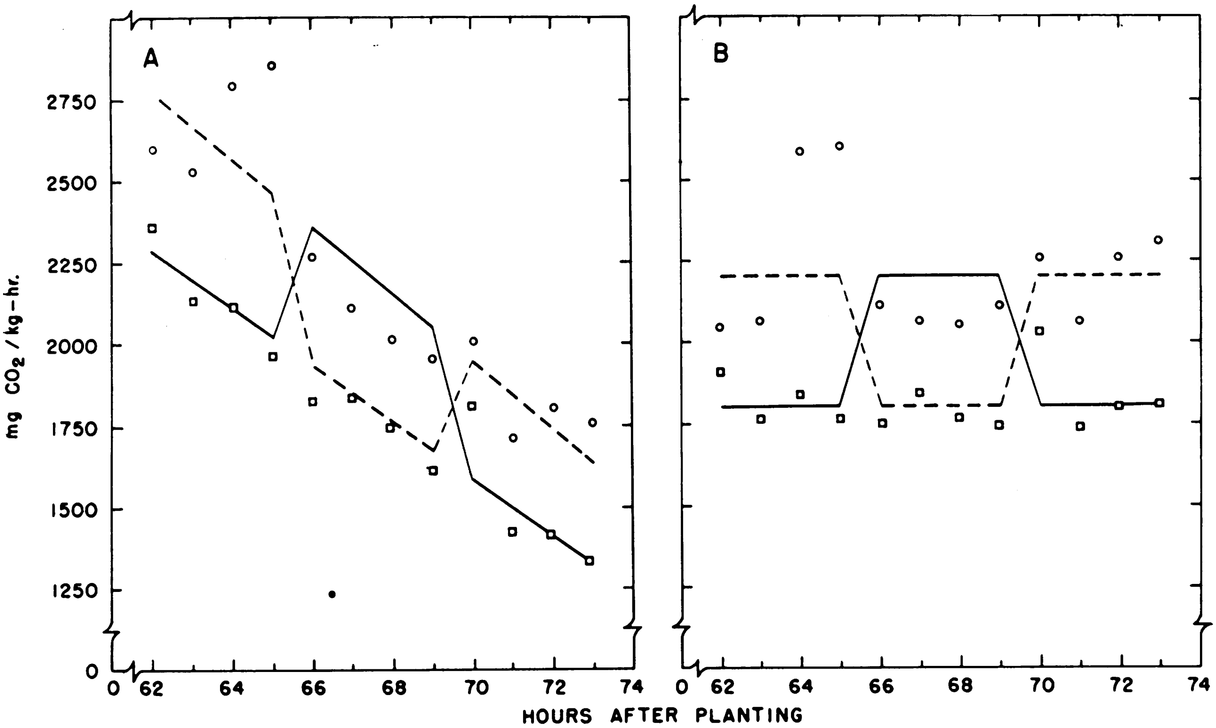

FIG. 6. Respiration rates of plants sequentially subjected to rotation on a horizontal-axis clinostat (0 × g) ○. or vertical-axis clinostat (1 × g) □. (A) With existent time trend of respiration and (B) with time trend of respiration removed. Symbolically, ----0---0---- represents VH in H; ----□---□----, VH in V; ——0——0——, HV in H; ——□——□——, HV in V; regimes HV and VH of table III. Data are mean respiration rates from 3 successive experiments.

stimulus but subsequently intermittently removed from this stimulus displayed modest increases in growth (table IV, compare V and HV). Roots of seedlings, regardless of gravity treatment or time of harvest, were on the average greater in weight than the tops (56 mg vs. 37 mg, avg., respectively). Though both tops and roots increased in size with time of harvest, no measurable joint effect of gravity treatment and plant part could be inferred in a probability sense. This was likely due to the relatively small sample size employed, about 20 plants per time of harvest at each gravity treatment, coupled with the high variability associated with oat seedling growth.

Fresh weights and lengths of roots per plant were highly correlated regardless of gravity treatment, as were lengths and weights of coleoptiles (table V). Previously and presently reported enhancement of seedling growth (primarily of roots) attributable to nullification of the gravitational stimulus was again well-evinced in these data. The ratio of weight to length of these organs was not materially altered. These data thus quantitatively document the observation that gravity stimulus nullification does not modify the seedlings in any way not directly explicable on bases of growth phenomena attendant upon modified rates of respiratory metabolism.

It is clearly evident from the data at hand that enhancement of respiratory metabolism may be "turned on" or "turned off" quickly and at will. The respiratory enhancement imparted by clinostat rotation depends solely on the angle of inclination of the clinostat axis on which the plants are growing. It

Table V. *The Relationship of Organ Lengths and Weights in 3-Day-old Oat Seedlings Grown on Horizontal or Vertical Axis Clinostats Rotating at 2 rpm*

	Orientation of rotational axis	
	Horizontal	Vertical
Plant tops		
Fr wt in mg	28.7a*	26.9a
Length in mm	24.7a	24.8a
Correlation coefficient (r)	0.979	0.972
Wt/length	1.16a	1.08a
Plant roots		
Fr wt in mg	52.5a	47.4b
Length in mm	161.3a	127.9b
Correlation coefficient (r)	0.934	0.984
Wt/length	0.33a	0.37a

* Means within a row which are followed by a different letter differ at the 1 % level; means within a row which are followed by the same letter do not differ at the 5 % level. Correlation coefficient required for significance at the 1 % level is 0.418. n = 37. Standard error mean = 1.08, 1.35, 0.09, 1.39, 1.73, 0.05 for rows 1, 2, 4, 5, 6, and 8, respectively.

is similarly apparent that asymmetries in intracellular particle distribution are governed and may be imparted or negated by the same alterations of the angles of inclination of clinostat axes.

Increased growth and coleoptile curvature responses associated with nullification of the gravitational stimulus have been shown explicable on bases of enhanced respiratory metabolism (5). Data presented in this manuscript show that intracellular particle distribution is effected in a specific and defined manner by the same treatments which alter the rates of respiratory metabolism. Further, the effects are imparted in corresponding periods of time and at corresponding magnitudes of unidirectional gravitational stimulation.

Physicochemically, plant respiration involves reactions between particles of sufficient mass to be graviprecipitated in cell sap and particles which are so low in mass that they are distributed by thermal energy. When cells are grown with a unidirectional gravitational stimulus, the heavier particles tend to accumulate in their lower halves. The reaction alteration of the particles distributed by thermal energy in the region of higher concentration of the gravity precipitated particles (or the precipitation of the larger particles if they are altered) creates reaction rate-limiting concentration gradients.

This physically imposed reaction-rate limitation is negated when the gradient is eliminated by uniform distribution of the graviprecipitable entity throughout the protoplasm.

Appropriate clinostat rotation imparts distribution to graviprecipitable particulate cell inclusions. This distribution enhances respiratory metabolism. The enhanced respiratory metabolism, in turn, promotes greater coleoptile curvature in response to auxin asymmetry (4, 5) and increases overall growth of roots where auxin levels are supraoptimal.

This empirically based explanation of plant responses to nullification of the directional component of the gravitational stimulus serves well in explaining some historical findings.

The observed transitory increase in respiratory activity following geostimulation of vertically grown plants (12) would be expected. Tipping plants results in a transitory partial elimination of concentration gradients in the respiratory reactants. Precipitated reactants are redistributed across the concentration gradient of the reactants distributed by thermal energy. Reaction-created concentration gradients are only transitorily negated by this redistribution of the graviprecipitated reactants, for geotropic stimulation imparts only a transient disruption of these concentration gradients. The rate of reestablishment is conditioned by the rate of respiration.

Inversion of plants for a short time prior to transverse geostimulation increases subsequent curvature response as compared to plants which had not been inverted before geostimulation (11). The observed increase in geocurvature may be tentatively ascribed to enhanced respiratory metabolism resulting from more uniform particle distribution imparted by the short period of inversion.

Because the developed relationship between particle distribution, respiration, and growth phenomena affords explanation of results for so many past studies involving the gravitational stimulus, as well as the data at hand, one is driven to accept the following causal sequence: nullification of the gravitational stimulus or reorientation in the force field imparts a more uniform distribution to graviprecipitable metabolically active particles. This increases respiratory metabolism which, in turn, as governed by auxin economy (5), promotes observed growth phenomena of which curvature is but a special case.

Recently, a quasi-rigorous proof that starch amyloplasts are not necessary for geotropic response has been advanced (13). The absence of amyloplasts in wheat coleoptiles which display slight geocurvature responses after many hours of geostimulation does not consider likely geostimulus-induced modifications of distribution patterns of other metabolically active graviprecipitable intracellular entities. Though amyloplasts were assuredly used in this study to index particle distribution, the role of starch in gravity-induced phenomena is readily acceded to be not truly necessary.

The relationship here defined of gravitational stimulus, particle distribution, and associated respiratory and growth phenomena imply that gravity sensing by plants does not involve any complex sensing device as has so often been hypothesized. On the contrary, it is broadly based on the defined physicochemical relationship between particle distribution and respiratory metabolism.

The data clearly show that tilting the axis of a single-axis clinostat results in quantitative nullification of the gravitational stimuli. This leads inescapably to the ancillary conclusion that highly complex machines used in rotating plants about multiple axes (9) are, at best, questionably virtuous.

The data support contentions that discrete thresholds of graviperception in plants do not exist (6). Since the mass of protoplasmic particles involved in metabolism is virtually a continuum, any level of unidirectional gravitational force will result in some degree of nonuniformity of distribution of these particles. If one accepts that graviperception results from the nonuniform distribution of metabolically active graviprecipitable particles, one is then logically bound to deny the existence of discrete thresholds of gravity perception by plants. It is readily acceded that small degrees of nonuniformity in distribution of metabolically active particles would likely escape detection or be obscured by random variability when gross reactions to gravity stimulation are employed as indices of thresholds of gravity perception.

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