5th Award

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PLANT FORM AND FUNCTION DEPEND GREATLY ON GRAVITY

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The action of gravitational force on the form of a leafy, branching plant can be neutralized and its effects essentially eliminated by rotating the plant and its soil slowly about its axis while holding it in a horizontal position. The resulting mess of folded leaves and bent stems provides a striking demonstration of the advantageous effect of gravity on the form of a typical plant and on the plant's effectiveness in capturing solar energy for subsequent use by mankind. Without gravity as we know it, life on this planet would be quite different and probably less abundant.

Most of us believe that life started in the oceans from whence the terrestrial forms evolved slowly long ago but the earth's mantle of characteristic vegetation consists primarily of a myriad of rooted, erect, green plants. They supply nourishment for the animals about them and provide for man's life and comfort on earth, but they grow as they do and function as they do only because the tissues of every plant are subject to the pull of gravity and develop to the advantage of the plants and their dependents. Without gravitational force, our source of energy and material for life would probably have been a relatively thin mantle of green.

The Clinostat. To demonstrate the formative and beneficial effect of gravity on a typical plant, it is only necessary to select one that is growing well in a flower pot, and to attach the pot to the rotating table of a clinostat whose axis is horizontally oriented. This instrument is a simple machine of no prescribed design, powered by electric or coiled-spring clockwork, and so arranged that the motor turns the table slowly and evenly. The rotation rate can be anything from about 4 times per minute to once or twice per hour.

The rate must be so slow that no centrifugal force is applied to the rotating plant but so rapid that no growth response can take place in one position before the plant is rotated into a new position. The instrument was developed in Europe in the 19th century for use in proving such facts about geotropism as the minimum presentation time for reception of the stimulus and the effects of various angles of inclination from the perpendicular. The idea is simple but effective and the instrument is a practical device for eliminating the effects of geotropism in plants.

When a growing plant is thus rotated by a clinostat in horizontal position and thereby freed from the formative effects of unidirectional gravity, there will be at least two and often three changes in the form and appearance of the plant. The more rapid the growth rate of the aerial organs, the more pronounced these changes will be. When they all occur at once the plant becomes a twisted system of leaves and branches, as illustrated by figure 1.

<u>Leaf epinasty</u>. The first of these changes, and an important one in relation to the function of a plant as a capturer of radiant energy, appears as a folding of the leaves down and often close against the stem to which they are attached at its nodes. Some leaves show this epinastic curvature by bending at a hinge close to the node but there are great variations among species as to the part of the leaf which grows faster on its upper surface and thus forces the leaf blade back toward the stem. Now instead of being held out in the air and light, with the blade nearly parallel to the surface of the soil and evenly illumined by direct and reflected sunlight, the leaves face out from the twig which bears them usually overlapping each other to a considerable degree and with their under surfaces close to those on the opposite side of the

[illegible] The leaves [illegible]

constant rotation because the growth hormone, called auxin, remains on the dorsal side of the leaf where it is formed in the light. Cell enlargement, an essential stage in the normal growth process, depends on the presence of auxin in the growing cell so the upper side of the petiole or blade grows much faster than the ventral side if the plant is rotating on a horizontal clinostat.

The existence of this hormone for cell growth has been known only since its discovery by Went in Holland in [illegible]. More than one substance may act as the hormone in different plants but the dominant and essentially universal compound is known to be indoleacetic acid, sometimes abbreviated to IAA. It is formed in the light from the amino acid tryptophane but never in more than such extremely small amounts that its presence can be detected only by delicate bioassay in which an extract of it is applied to one side of a test plant which then grows faster on that side. Leaves are only one place in which auxin is made but its synthesis there and accumulation in the dorsal tissues are the causes of the epinasty that bends the leaves when the effects of gravity are eliminated.

We are still uncertain of the exact mechanism by which gravity causes part of the auxin to move to the ventral side of the leaf where its presence causes growth on that side, thus balancing the growth of the dorsal tissues. The result is a leaf at right angles to the stem unless unequal light on the leaf blade causes a redistribution of the auxin and a more favorable placement of the leaf with respect to light. We think that most of the auxin crosses to the lower side through the petiole but it is too early to say this with complete confidence. We do know that it arrives as an effect of gravity and that the result is beneficial to the plant and to man.

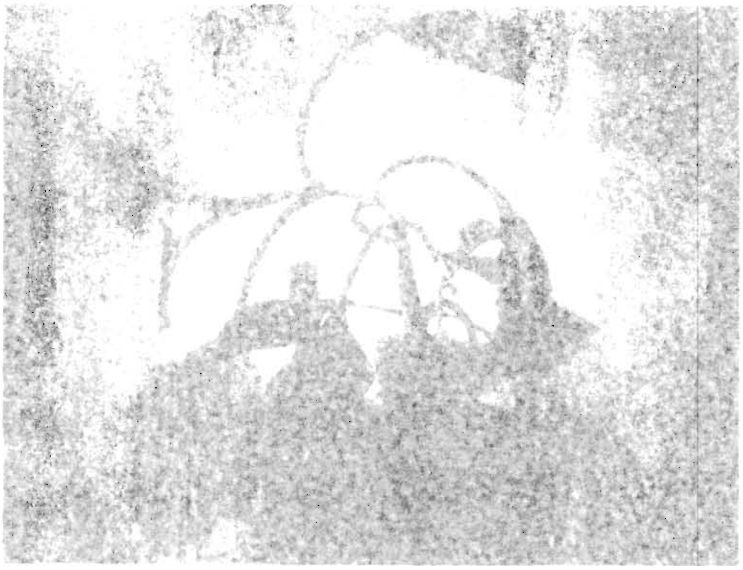

Fig. 1. Leaf and Branch Epinasty with a Bent Axis

Dahlia Seedling after 3 days on a Clinostat

Branch Epinasty. The second change in an upright plant when it is released from the formative effects of gravity, appears in its young branches. On the horizontal clinostat each growth zone produces such a sharp, backward bend in less than 24 hours that the tip of each branch is no longer in line with the lower part of the lateral branch. Instead of making a characteristic axillary angle that is commonly from about 30° to about 60°, the tip will be seen to make something close to a right angle with the axis of the plant. If the plant is a vigorous seedling such as that of a Cosmos or a dwarf Dahlia (see fig. 1 above), or if it is a Coleus with its actively growing branches from 1 to 4 inches long, the growing tips of all branches will be found to point toward the soil within a day or so. With the leaves all folding slowly back against the bending, curved branches, the result is a very inefficient arrangement of the plant's green tissues.

This change in the form of a lateral branch is another manifestation of the same epinastic potential that produces the bending of the leaves. The reason seems to be the same -- the delivery of excess auxin from the leaves to the dorsal side of the growing nodes and internodes of the stem. When the branched plant stands in the gravitational field, the result of the extra auxin on the dorsal side is good. Part of the auxin moves to the ventral side by an unknown mechanism that is activated by gravity. The upper and lower sides of the growing branch tip come to have about the same auxin supply and growth rates, so the branch continues to form its characteristic angle with the axis of the plant.

If there is only a slight excess of auxin supplied to the dorsal side, or if the auxin is moved relatively easily to the ventral side by gravity, the axillary angle will be small, as in trees and other plants with columnar form. Trees and herbs with branches more nearly horizontal either have more auxin on the dorsal side of the growth zone of each branch or more resistance to transverse movement of auxin by gravity. By such combinations of growth hormone and its transport within plants, the forms of erect plants are determined but no such variation and no such good results in spreading leaf blades in the sun and air could be obtained without gravitational force.

The physiological bases for these processes of auxin distribution in branches are as yet incompletely known. When epinasty of twigs was discovered in Germany in 1901, it could only be described. Very few people know any more about it to-day. The discovery of auxin in 1927 opened the way for analysis of epinasty but a rigorous proof of auxin distribution in branch tips, and of the mechanism for its transport to growing tissues there, has not yet been obtained. The one known factor is the force of gravity but we do not know quite how it effects the beneficial distribution of this essential growth hormone.

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..., we have tested 21 species of leafy plants for uneven growth of the axis on horizontal clinostats, turning 1 rpm. in most cases. Each one of the 110 tests resulted in a bend of at least 10°, with a 90° bend frequently observed overnight and a 180° turn of the growing tip a common occurrence for a few species. All plants started with their main axes straight but the curvatures began within a few hours. Except for plants of the genus Impatiens, which bend through many inches of the soft stem, the uneven growth appeared in 2 or 3 elongating internodes just below the youngest leaves. These internodes usually bend together in the same plane (as shown in fig. 1) but in a few plants a skewed bending

Table 1. Species Tested for Axial Bending.
The number of plants tested for each is shown at the left of the name

2	Browallia americana L.	6	Impatiens Sultanii Hook f.
17	Coleus Blumei Benth.	4	Lycopersicon esculentum Mill.
2	Cosmos bipinnatus Cav.	3	Matthiola incana annua Voss
2	Cucumis sativus L.	12	Mirabilis Jalapa L.
2	Cuphea ignea A.DC.	2	Nicotiana alata grandiflora Comes
	Dahlia pinnata Cav.	4	Pelargonium zonale Ait.
6	Fuchsia hybrida Voss	10	Phaseolus vulgaris humilis Alef.
3	Gynura aurantiaca DC.	2	Pisum sativum humile Poir.
	Helianthus annuus L.	2	Solanum tuberosum L.
2	Heliotropium arborescens L.	6	Torenia Fournieri Lind.
		4	Zinnia elegans Jacq.

has occurred, due to m[illegible] growth rates on different [illegible] of adjoining internodes [illegible] therefore bend in different directions. [illegible] all cases, the bending [illegible] never undone on the [illegible] though [illegible] or more

[illegible] (genus Phaseolus) [illegible] remarkable [illegible] [illegible] plants approaching the flower [illegible] stage, [illegible] [illegible] compound leaves above the pair of simple leaves, [illegible] a few days [illegible] so that the flower buds open [illegible]

[illegible] plants make this 180° turn by a localized curvature in each [illegible] internodes below [illegible] compound lea[illegible]

still [illegible] produces [illegible] curvature [illegible] it appears to come into the internode from the leaf just above it. With the plant erect in a gravity field, each internode grows at the same rate throughout its cross section; when the formative effects of gravity are cancelled out on the rotating clinostat, [illegible] means [illegible] resistance [illegible] tissues on one side of each internode to [illegible] the flow of auxin through them and [illegible] hence to that side [illegible] [illegible] induced by auxin on the other side. Something like this [illegible] occurs in the [illegible] of other species as they [illegible] to [illegible] on the clinostat [illegible] process shows more clearly in the long and fewer internodes of the garden bean

[illegible] tests with the horizontal clinostat [illegible] [illegible] apparent action of gravity [illegible] even lower [illegible] [illegible] through the main stem. [illegible] [illegible] a series of [illegible] turns [illegible] from the [illegible] its growing stem, the axis [illegible] straight unless [illegible] plant is rotated on a clinostat. Then it bends toward the defoliated side until the plant is returned to a normal field of gravity where the axis becomes straight again. The same effect can be demonstrated in a dahlia plant. Gravity somehow redistributes the uneven supply of auxin from the leaves.

Another way by which to demonstrate this balancing action of gravity is to rub a small amount of lanolin containing 1% by weight of TIBA (triiodobenzoic acid), on one side of the growth zone of the axis of a plant like Sunflower or Fuchsia. This chemical is known to interfere with downward transport of auxin within the stem. If only a small amount of it enters the stem the stem does not bend by growth toward the treated side <u>unless</u> the plant is rotated on the clinostat. Gravity seems to overcome some resistance through tissue that receives a little TIBA but even an erect stem bends when more TIBA is applied to one side of it.

Other experimental evidence has been obtained in support of this theory of a regulatory function of the pull of gravity. The curvatures in the plant's axis, induced by experiments or due to some differences in auxin transport tissues, appear only when the plant is on a horizontal clinostat. Logically the auxin should there be evenly distributed across the stem, with a brief pull of gravity continually exerted in all possible lateral directions within the stem. The bending comes only when the force is not exerted <u>down</u> the stem. Gravity seems to aid the downward transport by somehow overcoming a resistance that develops or has been introduced. Until we know more of the mechanism of non-gravitational transport, it is impossible to explain further an effect of gravity that is so easily demonstrated.

[illegible] The practical value of the force of gravity in keeping plants erect and symmetrical, with their foliage held in positions of maximum advantage, has probably been appreciated thus far by few people. Most of us think more about the action of gravity in tipping plants over. With the clinostat only an instrument for scientific research, we can have no earthly problem of plant inefficiency and malformation in well anchored, healthy plants but the prospect of space travel to the moon or longer has created a real problem for those who must plan the details of such trips by man. He cannot take enough oxygen with him so he must take along some plants to make it and to recycle his waste products. We are learning that the plants must be tall and leafy. The man will be only [illegible] possibly uncomfortable but the plants must retain their efficiency in a gravity-free state or the trip will be impossible.

Advance knowledge of gravit[illegible] the life of plants on earth has therefore become invaluable for the men who must leave the earth. These relatively simple experiments with clockwork toy have shown what knowledge must next be obtained an more accurate, quantitative assays of the [illegible] that is indicated by the abnormal forms of plants in the clinostats. [illegible] have confirmed our deductions [illegible] growth curvatures of leaves, branches and main stems, [illegible] on the connections [illegible] made in our thinking, [illegible] know how, where and [illegible] practical [illegible] upset the tiny [illegible] which the gravity [illegible] helps [illegible] automatically [illegible] plants [illegible]