ON GRAVITY AND GROWTH

The Dynamic Response to Gravity by Growing Plants

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(Summary)

Living creatures, unlike inanimate objects, tend to respond actively rather than passively to the pull of gravity. Experiments with wheat seedlings are described to show that upward growth is a dynamic, quantitative response to gravity rather than merely a directional orientation to a field, as previously thought. This response has been measured experimentally in terms of work accomplished during growth; and certain adaptive, qualitative changes are described. The relation of this research to underlying concepts of the form of organisms is mentioned, and two practical applications suggested.

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Inanimate objects move against the earth's gravitational field only when propelled by forces external to themselves. In nature, the ejectae of volcanoes, the water of artesian springs, and mountains uplifted by crustal movements are the more obvious examples. Living creatures have found other means of overcoming this ubiquitous force. Birds fly; men can throw stones or shoot arrows. Such activities have been analysed, and put to man's use in extremely sophisticated ways.

Another, more widespread, method for overcoming gravity displayed by living things has passed nearly unnoticed and completely unstudied until very recently. So common is it, we rarely observe that the great majority of higher plants and animals actively resist the pull of gravity by the application of forces within their own bodies. Most striking are examples in the plant kingdom where great trees witness that tons of material have been lifted scores of feet above the earth.

This overcoming of gravity is the result of growth forces. Growth requires energy for many processes, some only poorly understood; but we can measure, quite exactly, that energy used in overcoming gravity. If a wheat seedling sprouts and grows four centimeters in four days, and has then a weight of 0.05 grams, it has accomplished $0.05 \text{ gm} \times 1 \text{ G} \times \frac{4 \text{ cm}}{2}$ or 0.1 gram centimeters of work in four days. Since at least half of this growth is accomplished on the third day, the work rate reaches more than 0.05 gram-centimeters in twenty-four hours.

This is neither the greatest nor the smallest work output among plants. Bamboo grows far faster and many creeping plants grow upward very little. The

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wheat seedling is, however, a convenient research object. Its first shoot, called the coleoptile, has a four day life span and a simple structure. Nearly all of its growth is upward and can thus be evaluated by a single measurement.

We have long known that the growing plant orients itself with respect to gravity due to the downward diffusion of growth stimulating substances (auxins) from the tip. We have not understood that there is a quantitative growth response to gravity as well as a qualitative one. If the only dynamic response were orientation, we might expect a plant grown in an environment of twice the earth's normal gravity to be half as high.

By growing wheat seedlings in a centrifuge in the dark (to use respiratory energy free from photosynthesis), it is easy to vary the gravitational forces exerted on the plant. The very simplest experiment will show that growth is not readily depressed by increasing the work load. At two times gravity there is no observable difference in the height attained by the mature coloptile. If we increase the gravitational field sufficiently, we find that we are finally growing shorter seedlings, but, by the time we have reduced their height to one-half of normal, we are imposing a force of 500 times earth's gravity. Beyond this we cannot go. Growth does not yet fail, but the structure has reached its mechanical limit, and the hollow, oval coleoptile buckles and breaks.

The structure does not fail without an adaptive response, which, although inadequate in the long run, is not insignificant. In the increased gravitational field, the young shoot increases its diameter and hence its cross-section area. At 150 times gravity this increase amounts to 37.9% in cross-section, 54.6% in moment of bending and 16% in actual resistance to bending forces at right angles to the long axis.

In addition, while the dry weight of control plants is 9.35% of wet weight; at 150 times gravity, the percentage has become 10.72. More solid material has entered into the construction.

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These factors must be taken into account in considering the work response. If actual weight raised to actual height be calculated as gram centimeters of work done, we find that the increase in work in relation to the force of the gravitational field of the plant's environment is linear and proportional for all forces up to nearly 100 times normal gravity. That is, the growing plant compensates almost perfectly for the increased force. (figure 1)

Beyond this point, compensation fails to keep up with further increase in the force of the field, but work output continues to increase at a lower rate. At 500 times gravity plants are doing about twice the work of those centrifuged at 100 times gravity.

The work done against gravity over the whole four days does not bring out the entire picture. More work is done during the later half than the earlier for exactly the same reason that work is expended laying brick at the third storey of a building than at the second, and more at the second than at the first, because the bricks must always start from the ground. The following table will show the relation between growth and work done in an average of 650 normal wheat seedlings.

(Insert TABLE)

About 95% of the total work is accomplished in the last half of the period but only 77% of the growth takes place. During the first day, when growth is starting, the percentage of work done is nearly negligible. Increasing the gravitational field to fifty times normal during this first day results in a work load of 357.5 mg mm (50 x 7.15 mg mm). This is less than the 389.9 mg mm work load on the fourth day under normal gravitational conditions. It suggests that centrifugation at 50 times gravity during this period will not overtax the plant's resources.

Experiments to test this hypothesis show that growth is not inhibited under these circumstances, but is, on the contrary, stimulated. By the 60th hour, plants centrifuged for the first twenty-four hours are 3.64 mm or 19.4% taller

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than control plants of the same age. This effect is observable at lower forces; 10 times gravity produces 5.67 mm or 30.2% increase in height, and even at 500 times gravity there is a slight, but not statistically significant, increase of 0.32%.

Similar centrifugation performed on the second, third and fourth days of the coleoptile's life does not produce this stimulatory effect, but instead, inhibits growth during the period of centrifugation and for about twenty-four hours afterward. Rates for each of the four days are shown in figure 2.

It is reasonable to conclude that the increase in the gravitational field places little strain on the plant's work capacity during the first day, but later, when normal work output is greater, the strain becomes intolerable and decreased growth results.

There is another aspect of work done which has not been measured in these experiments. Height attained is the record of building blocks raised to their position and left there. Water of transpiration is also raised against the pull of gravity; the work involved in this process is likewise multiplied by the environmental force. This water, evaporating from the coleoptile, is not here considered, but must not be forgotten as it is involved in the growth process, just as is the work required for the brick-layer to lift himself to the upper stories of a building under construction, even though no brick-layers remain in the completed building.

One can reasonably imagine the means by which the increased gravitational field interferes with cell elongation. The compensatory mechanism, making more energy available to overcome gravity, is by no means so easily explained. At present, one can only take refuge in the doctrine of homeostasis, and observe that this response to changes in gravity is similar to the efforts of all organisms to maintain their integrity in the face of changing environment.

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Such a mechanism must also account for the increased growth observed in plants centrifuged during the first day of life. The homeostatic controls, having been adjusted for a gravitational field of a certain strength, do not respond at once to the reduction of the field to "normal" at the end of twenty-four hours, but continue, for some time, to demand the same output of energy which now produces greater growth in the weaker gravitational field.

The analysis of the response of living things to gravity has barely begun, and we have not yet had time to formulate hypotheses regarding the mechanics of the observed changes. When we have learned more, we may be in a position to apply our knowledge to problems of plant and animal growth.

To speculate, one might suggest that a way may be found to increase the relative dry weight and hence the strength of trees, thereby producing usable lumber from fast-growing but structurally weak species. In wheat itself, strength of mature stems is an important factor in minimizing wind and rain damage. Beyond these specific suggestions, it is hoped that work in this direction may shed light on the oldest, most inscrutable of biological problems, the control of the form of living organisms and especially the role of gravity in this control.

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TABLE

Comparison of Growth and Work Accomplished During

Maturation of the Normal Wheat Coleoptile

TIME	GROWTH	% GROWTH	WORK DONE	% WORK DONE
1st day	c 3.5 mm	8.65	7.15 mg mm.	0.75
2nd day	5.76 "	14.24	42.94 " "	4.49
3rd day	21.88 "	54.08	516.31 " "	53.97
4th day	9.32 "	23.03	389.86 " "	40.79
Total	40.46 mm	100.00	956.26 mg mm	100.00

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Figure 1

The work output response of wheat coleoptiles grown for four days under various gravitational forces. Control plants (1 x gravity) do 0.0956 gm cm work in growing 4.06 cms. The dotted line represents theoretically perfect compensatory response.

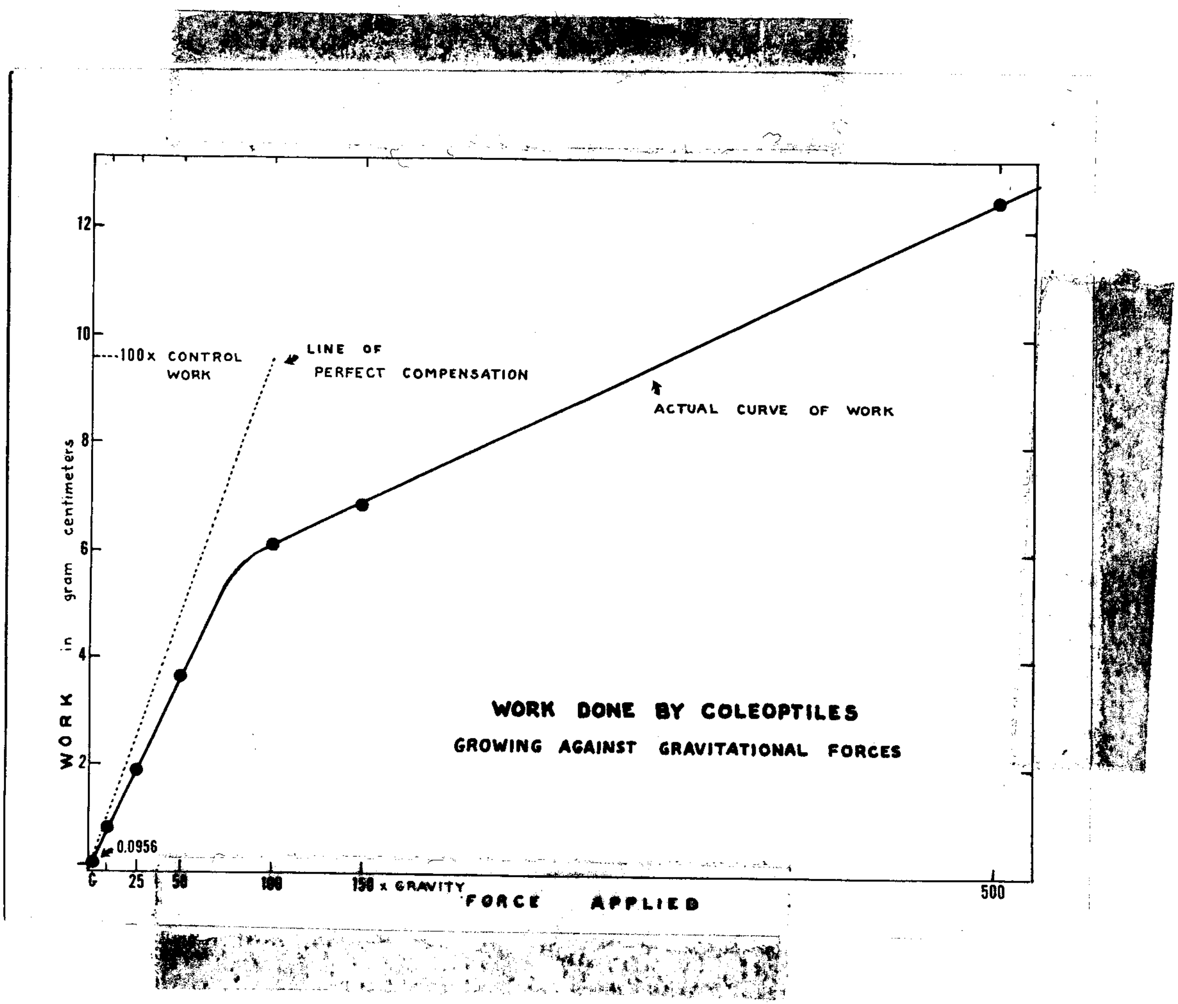

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Figure 2

Growth rates of wheat coleoptiles centrifuged at 50 x gravity on each of four different days. Shaded blocks indicate faster or slower growth than that of control plants indicated by heavy black horizontal line. Note that in A, normal height has been achieved earlier than in controls so growth from 72-96 hours is very small.