Light and Hormones in Plant Development

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There are a number of factors which are essential for plant growth. Some of the growth factors come from the environment in which the plant is growing. These will be called the external growth factors. Factors such as water, the mineral nutrients, light, CO_2, etc., are external growth factors. Many other growth factors are synthesized within the plant. Among these are the multitude of organic materials synthesized by the plant which make up the plant itself. Most of these factors are made in response to the requirements of the plant and do not normally limit growth.

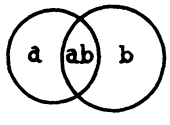
There are a few internal factors, however, which may often limit growth. These are factors, often hormones, which have developed to regulate and control growth. The levels of these factors, and thus the rate and form of growth, are often controlled by one or more environmental influences.

The overall influence of all growth factors cannot be readily described by conventional algebraic symbols. It can be described rather precisely, however, by the symbolization used in simple set theory. Thus, growth factors may be defined, and their relation to growth described by the simple formulation:

$$\text{growth} = f(a) \cap f(b) \cap \ldots \cap f(n)$$

where f(i) is a function of the i^{th} growth factor, of n growth factors.

The symbol $\cap$ is defined as the intersection of two sets. Here each set is a function of one of the n growth factors. An intersection may be visualized geometrically as the portions of two sets which overlap. Thus, ab is the intersection of sets a and b.



This definition of growth may be justified by two generalized observations which are true of all growth factors. First, when any one growth factor is completely absent no growth occurs (this is the definition of a growth factor). Second, when any one growth factor is provided in "infinite" amounts, growth does not approach an "infinite" rate but rather approaches a maximum. It can be readily verified that our formulation, above, has precisely these properties.

Using this principle we can design experiments to test whether a particular internal growth factor (often a growth hormone) mediates the response to a particular environmental or genetic factor. When we saturate with the hormone a particular growth factor should be saturated. Thus, any environmental factor which acts by modifying this growth factor should now be without effect. On the other hand, environmental factors acting through other steps should have maximum effectiveness.

Of course, the growth process is much more complex than this simple analysis would suggest. It is indeed surprising that a number of physiological analyses do show substantially complete interactions. Some of these analyses are described below.

Due to limitations of space and the recent rapid developments in this field the experiments described will be limited in two ways. First, I wish to emphasize so far as possible the light and hormonal responses of plants which determine the growth and form of plants as they may be observed in the field. Recent discoveries have substantially increased our understanding in this direction although we still have a long way to go. Second, the newer discoveries and results will be emphasized. Experiments demonstrating principles which have been understood for some time have been well worked out in the various laboratory manuals now available.

The relatively recent discovery of the importance of the plant growth hormone, gibberellin, and its various physiological effects have made the interpretation of many developmental phenomena much more straight-

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forward than was previously possible. So long as we tried to explain dwarf growth, light inhibition of stem elongation, and related phenomena through an auxin-mediated mechanism continuous problems arose. It is now quite clear that gibberellin rather than auxin is the controlling factor in many of these responses. Experiments demonstrating this relationship are generally straight forward and quite unambiguous. They will be emphasized here.

Influence of Light and Darkness on Plant Development

Materials:

Dwarf pea seed, variety Little Marvel, or Morse's Progress No. 9.
Darkroom equipped with a green light for observations and a separate room or an isolated area with a source of low intensity red light for light treatments.

The pea seeds should be germinated in vermiculite, in the dark, after soaking in water for two to four hours. Several seeds (10-20) should be sown in each pot.

When the seedlings are 3-4 cm tall about 5-6 uniform seedlings should be selected per pot and the rest discarded. The seedlings in one-half the pots should be treated with gibberellin (one drop of an ethanolic solution containing 1,000 ppm gibberellin). Following gibberellin treatment one-half of the treated seedlings and one-half of the untreated seedlings should be moved to continuous red light of low intensity, and the controls remain in the dark. Stem length of the selected plants should be measured at the time of treatment and on alternate days thereafter for about six days.

After five to six days all plants should be brought into the laboratory and their various characteristics immediately observed. The morphological characters to be observed are:

1. Total stem length
2. Number of expanded internodes
3. Presence or absence of the apical hook
4. Degree of expansion and development of the leaves

Note that gibberellin completely prevents light inhibition of stem elongation, but does not prevent other light effects.

The Influence of Red and Far-Red Radiation on Plant Development

Materials:

Bean seeds, variety Pinto, or other.
Two dark chambers: one with a fluorescent tube wrapped in red cellophane or cellulose acetate, the second with two small incandescent lights over which red and blue cellophane or cellulose acetate have been fastened. With incandescent bulbs the filters must not be touching the bulb.
An ethanolic solution of gibberellin at 1,000 ppm.

The bean plants should be grown in the greenhouse with one plant per pot until the second internode begins expansion (about 10 days). At that time plants are ready for treatment.

The experimental treatment consists of growing the plants in the greenhouse in bright sun during the day. Each evening one-third of the plants should be placed in each of the dark chambers and exposed to the lights in the chambers for two to four hours. The lights should be turned off either manually or with a time switch without exposing the plants to any outside light. The plants should remain in the boxes until morning when they will be returned to the greenhouse with the controls for the daily light period. At the beginning of the experiment one-half of each of the three sets of plants should be treated with two drops of the gibberellin solution.

The total stem length should be measured at the time the experiment begins and every two days thereafter for six to eight days. Note that the increase in total stem length is the proper measure of stem elongation. The rate of stem elongation is simply the product of the average rate of cell division (per column of cells) and the average rate of cell elongation. Compare measurements of stem growth with measurements of root growth.

Dwarfism in Plants

Materials:

Zea mays seeds, variety dwarf d-1. These seeds may be obtained from Turtox.
Gibberellic acid, 1,000 ppm in ethanol.

The seeds should be soaked overnight in water then planted 2-3 per pot in the greenhouse. After the plants germinate, dwarf and normal plants may be segregated by sight. Thin to one plant per pot. Select so that one-half of the pots are dwarfs and one-half of the pots are normals. After the seedlings are well started (about 7-10 days) one-half of the dwarfs and one-half of the normals should be treated with one drop of gibberellin solution.

In 1-2 weeks the results should be clear. Observe particularly the similarity between the dwarf and normal plants which have been treated with gibberellin. This demonstrates that the growth potential of the dwarf and normal plants are identical when the plants receive adequate amounts of gibberellin.

Site of Formation of Natural Gibberellin in Bean Plants

Greenhouse-grown pinto bean plants should be selected when the second internode is 8-12 mm long. One-half the plants should be decapitated immediately above the node distal to the second internode. The first trifoliolate leaf should also be removed. The cut surface of the stem should be immediately covered with lanolin. One-half of the decapitated and one-half of the intact plants should be treated with two drops of an ethanolic solution of gibberellin at 1,000 ppm. The length of the second internode should be measured daily for 6-7 days, or until all elongation for this internode has ceased.

Observe that decapitation of the plant results in a marked decrease in the growth of the second internode. Note also that when gibberellin is made saturating the growth of the second internode is substantially indentical whether the stem apex is present or not. This indicates that the influence of the stem apex on growth of the stem may be completely replaced by gibberellin treatments.

This experiment may be supplemented by applying indole-acetic acid instead of gibberellin to the stem. Little or no response will normally be observed.

Comparison of the Responses to Auxin and Gibberellin

Materials:

Dark-grown beans. Germinate beans in dark for 5 days (with necessary green light). Move to low intensity red light for 24-48 hours.

IAA @ 100 ppm in ethanol (or in lanolin).

GA @ 100 ppm in ethanol.

The 6-7 day old beans are decapitated immediately below the plumular hook. After about 2 hours one drop IAA is applied to one side of the stem about 5 mm below the cut tip. GA is applied in the same manner to another set. At the same time, intact plants are treated in the same manner. The heights of the intact plants are recorded.

Three to six hours after treatment the plants are observed for bending responses. Only the IAA-treated plants will show bending. In our experience only the decapitated plants bend. Presumably the intact plants are saturated with auxin. Gibberellin-treated plants show no bending response. However, they are not saturated with gibberellin, since they show a good growth response to gibberellin within 24 hours. This is demonstrated by measuring the plants the next day. Little or no growth response to IAA will be observed but gibberellin will promote elongation. It can be seen that IAA is not rapidly translocated across the stem. Thus, auxin can function in tropistic responses, while gibberellin moves so rapidly across the stem that it could hardly mediate bending responses.

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