

to the question of the validity of our postulates regarding the equivalence of the physical boundary conditions to the s.p.b.c. and the existence and range of the interval G . These points must be investigated separately for each individual case, using primarily the standard methods for the study of the behavior of solutions of a differential equation in the neighborhood of a singular point.

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¹ Weyl, Hermann, *Math. Ann.*, **68**, 220 (1910).

² Bolza, O., *Lectures on the Calculus of Variations*, Chicago, p. 96 (1904).

³ Kuen Sen Hu, Thesis, Theorem 10.3 [*Contributions to the Calculus of Variations*, Univ. of Chicago Press, 1933].

⁴ Courant, R., and Hilbert, D., *Methoden der Math. Physik*, Berlin, 1931, Kap. 6, § 3.

*STUDIES ON THE GROWTH HORMONE OF PLANTS. III.
THE INHIBITING ACTION OF THE GROWTH SUBSTANCE
ON BUD DEVELOPMENT*

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It has long been known that when the growing point of a young dicotyledonous plant is removed, the axillary buds on the stem below it begin to develop. As long as the terminal bud is present, the development of the axillary buds is inhibited. A lateral bud may also be inhibited by the rapid growth of another lateral above it, as we have found in our experiments, or opposite it, as in those of Dostál (1926). Furthermore, Snow (1929a) has shown that the inhibition, in *Pisum*, is principally due to the young leaves in the developing bud. The evidence indicates that this inhibition is probably caused by a special substance (see Snow, 1929b). There was reason to believe that this inhibiting substance is of the same nature as the growth-promoting substance of *Avena* coleoptiles, and the experiments to be described here confirm this belief.

1. *Methods*.—Young plants of *Vicia faba*, 4 to 6 weeks old, grown in the light, were used. The lowest lateral buds of these plants grow with great regularity. The plants selected were of approximately equal height and with as nearly as possible equal numbers of buds and leaves. The

growth substance used was obtained from the growth of *Rhizopus suinus* (Thimann and Dolk, 1933) and had an activity of about 2.10^{-6} mg. per plant unit. The activity of this growth substance and of that obtained from the *Vicia* plants was tested on *Avena* coleoptiles under the standard conditions described by Went (1928), using the definition of units as given by Dolk and Thimann (1932).

2. *Production of Growth Substance by Vicia faba.*—It was first found that the terminal bud produces growth substance in rather large quantities. From terminal buds of young plants 12 cm. high, 30 to 40 plant units diffused out into agar blocks in an hour. From the buds of older plants the amount obtainable was less. The undeveloped lateral buds produce practically no growth substance. When, however, the plant is decapitated and the lateral buds are undergoing rapid development, each bud produces almost one-half as much growth substance as the terminal bud of an intact plant. Small amounts of growth substance are also produced by the leaves, less than one plant unit per hour being obtainable from the oldest leaves, and about 5 plant units per hour from the youngest leaves under the conditions of the experiment. It is therefore clear that growth substance production is associated with the actively developing parts of the plants, and that rather large quantities of the substance are regularly passing into the stem.

3. *Inhibition of Bud Development by Growth Substance.*—In order to make quantitative determinations of the effect of applying growth substance to the plant, it was necessary first to determine the time required for growth substance to enter the plant from an agar block. By plotting the amount of growth substance remaining in agar blocks after different periods of application to the stem, it was found that 6 hours were necessary for a complete transference of growth substance into the stem.

Agar blocks containing growth substance were therefore applied to the tops of decapitated plants every 6 hours. Intact plants, and also plants to which blocks of plain agar were being applied, were used as controls. Measurements of the length of the lateral buds, and also of the main stem, were made daily. When the amount of growth substance applied was of the same order as that diffusing from the terminal bud into agar (160 plant units every 6 hours), a slight but definite inhibition of the development of the lateral buds was observed. When, however, the amount of growth substance applied was larger than that diffusing from the terminal bud (1400–1700 plant units every 6 hours), the development of lateral buds was completely inhibited. Thus, in one experiment, the mean increase in length of the lateral buds in 8 days was 3.4 ± 0.5 mm. in intact plants, 16.0 ± 2.7 mm. in decapitated controls and 1.8 ± 0.6 mm. in plants to which 1670 units of growth substance had been applied. Several such experiments were carried out, each comprising thirty to forty

buds, and the amount of inhibition was similar in each case. The inhibition also takes place in the dark.

The necessity for applying larger amounts of growth substance than can be obtained from the terminal bud is fully justified on the ground that the application is generalized over the whole stem surface, while the normal supply from the tip is localized in the conducting tissue and therefore more effective in its action. Furthermore, there is evidence that wound substances may inactivate a part of the applied growth substance (Kisser, *et al.*, 1931). The inhibition is not to be ascribed to any damage, since the plants remained in good condition throughout the experiment, as was shown by the rapid development of the lateral buds as soon as the application of growth substance was stopped. While it is possible that the inhibition is due, not to the growth substance, but to another compound of similar nature present in the active concentrates, the present experiments make it probable that it is the growth substance itself, produced in the terminal bud, which inhibits lateral bud development.

Although it seems paradoxical that a substance promoting cell extension can also act as an inhibitor, this fact provides an explanation for much of the earlier work on inhibition, such as the experiments of Dostál, Snow (1929a) and Weiskopf (1927). The probable mechanism of the effect, together with a more detailed account of these experiments, will be published elsewhere.

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