

# GROWTH HORMONES IN PLANTS

AUTHORIZED ENGLISH TRANSLATION OF  
DIE WUCHSSTOFFTHEORIE  
UND IHRE BEDEUTUNG FÜR DIE ANALYSE DES WACHSTUMS  
UND DER WACHSTUMSBEWEGUNGEN DER PFLANZEN

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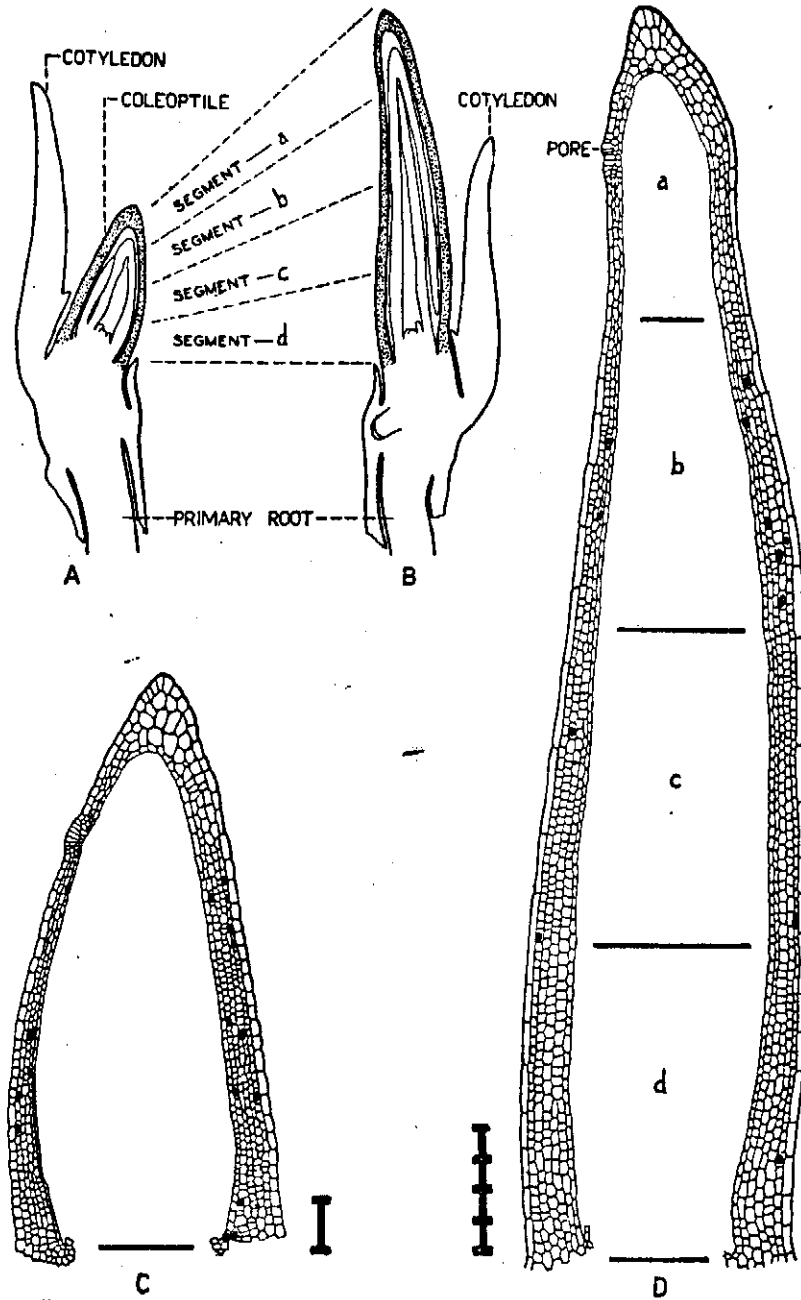


FIG. 23.—Median longitudinal sections of *Avena* coleoptiles at different stages of development. A and B, diagrams through germinating embryos,  $\times 11$ . C and D, detailed drawings of coleoptiles, 1.62 mm. and 4 mm. in length, respectively,  $\times 40$ . Mitoses are evident throughout. From D to maturity, the 1 mm. segments a, b, c, and d elongate to the dimensions indicated by the diagram in Fig. 24. The heavy line beside C and D indicates the relative length of the coleoptile, to be compared with the heavy line in Fig. 24. (After Avery and Burkholder, 1936.)

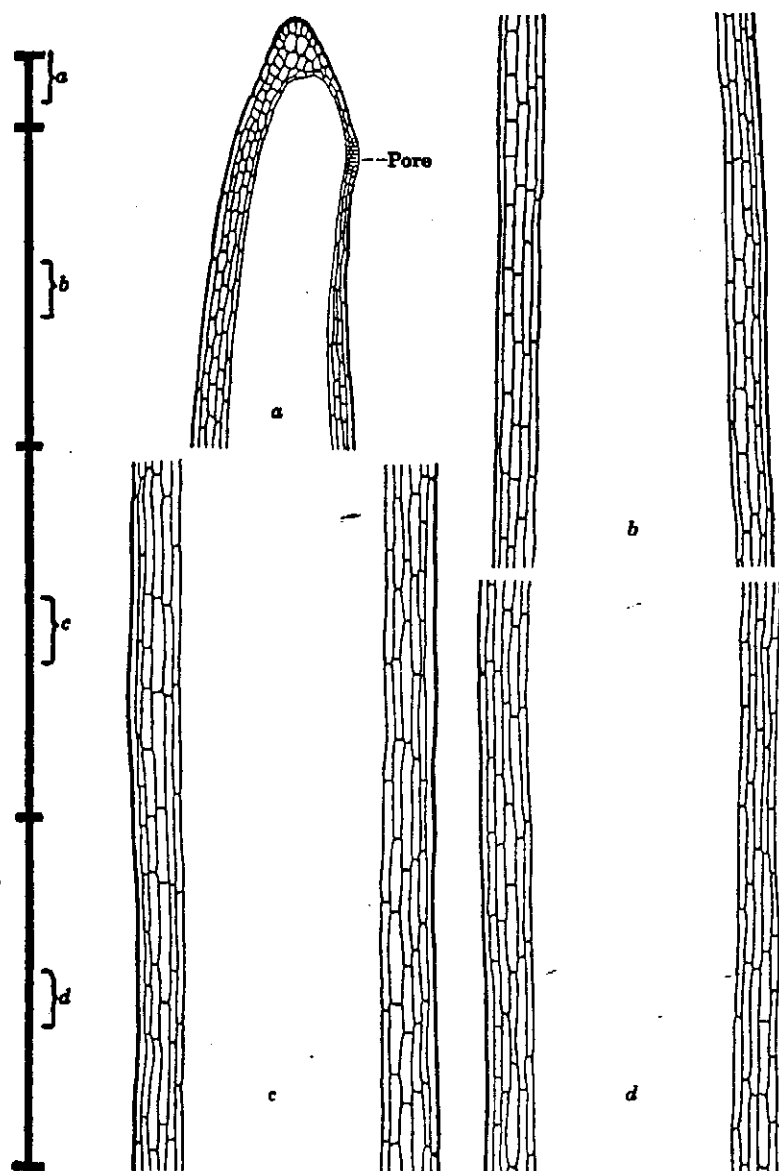


FIG. 24.—Detailed drawings of cells in longitudinal sections from different levels of a mature *Avena* coleoptile. The heavy line at the left indicates the relative length of the marked segments designated *a*, *b*, *c*, and *d* in proportion to the over-all length of the coleoptile. Compare with Fig. 23. The drawings represent part of the apical end of segment *a* and small portions from the middle of segments *b*, *c*, and *d*. Compare the small size of the cells near the apex with the elongated cells in the lower portions. Note the extreme length of the epidermal cells. (Adapted after Avery and Burkholder, 1936.)

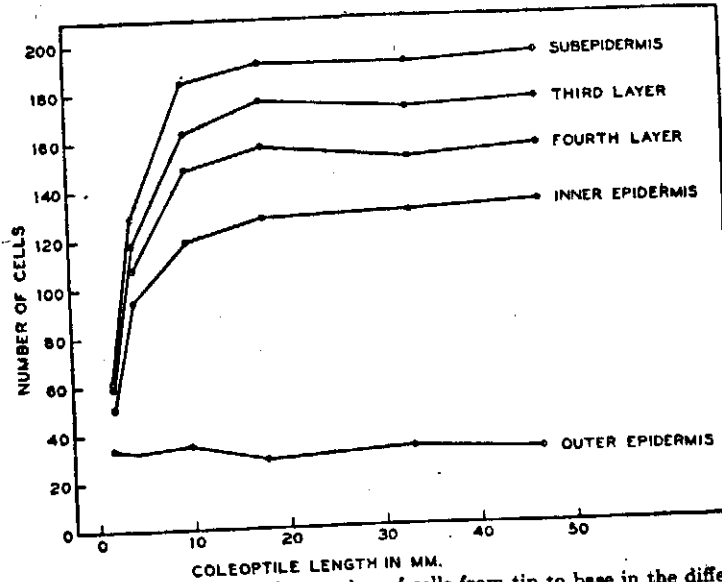


FIG. 25.—Graph showing the number of cells from tip to base in the different layers of the *Avena* coleoptile, at six stages in its growth. The outer epidermal cells do not increase in number, while the cells of the other layers multiply rapidly in the early period of development and then remain about constant in number. A definite gradient of cell-division intensity, decreasing inward from the subepidermis to the inner epidermis, is apparent for the first quarter of the growth period. During the last three quarters of its growth period, the increase in length of the coleoptile is proportional to the elongation of its constituent cells. (From Avery and Burkholder, 1936.)

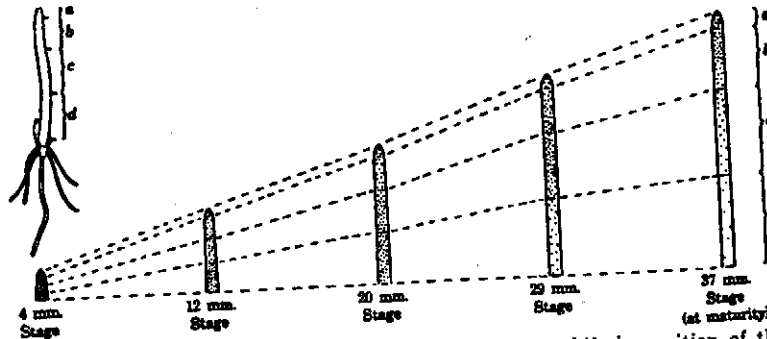


FIG. 26.—Diagrams of the *Avena* coleoptile to show shift in position of the zone of maximum growth intensity at different stages of development. Coleoptiles 4 mm. in length were marked into four 1 mm. segments (a, b, c, d) and the length of each was measured in several later stages of growth. The density of the dots indicates relative growth intensity. Note that the region of maximum growth shifts from the base in the young coleoptile (12 mm. stage) to the apical region in a maturing coleoptile. (Adapted after Avery and Burkholder, 1936.)

rapidly throughout most of the coleoptile while it is young, the region of greatest elongation is basal (Fig. 26). As the coleoptile nears maturity, growth slows down throughout its length, ceases at its base, and becomes relatively greater near its apex. At the time the foliage leaf bursts through, all basal growth has ceased, but a localized region of slow elongation at the tip below the pore may persist for as much as two or three days after the leaf bursts through the coleoptile. These same facts apply, in general, to the coleoptile of *Triticum*, on which similar observations were made.

*Light-growth Reaction.*—The inhibiting effect of light upon the rate of growth in plants was recognized in the older plant phys-

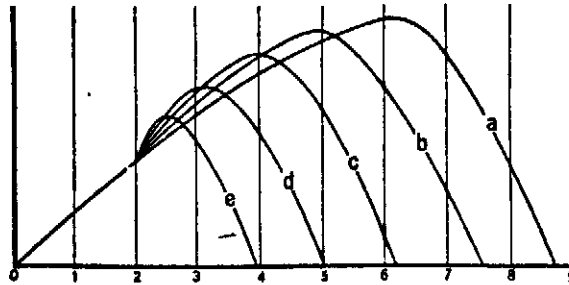


FIG. 27.—The course of growth in the *Avena* coleoptile in different intensities of light. Ordinate: growth; abscissa: 12-hour periods. *a*, growth of coleoptiles in weak light for  $4\frac{1}{2}$  days; *b*–*e*, growth of other coleoptiles kept for 1 day in the same weak light as in *a*, and then transferred to different intensities of light, increasing successively from *b* to *e*. Greater light intensity shortens the period of growth and causes the size of coleoptiles to be smaller at maturity. (After Sierp, 1918.)

iology literature (deCandolle, 1832; Sachs, 1874). Since the time when Blaauw (1914) attempted to use light-growth reactions as the foundation for a theory of phototropic curvatures, the role of light in growth has been the subject of many investigations.

Although Blaauw did not perform any experiments on the light-growth reactions in the *Avena* coleoptile, such investigations were carried out by Vogt (1915), Sierp (1921), Lundegardh (1921, 1922), Koningsberger (1922), Renner (1922), Brauner (1922), Erman (1923, 1930), Went (1926, 1928*a*), Dillewijn (1925, 1927*a*, *b*), Pisek (1926), Beyer (1926, 1927*a*, *c*, 1928*b*), Priestley (1926*c*), Gradmann (1930), Bergann (1930), Nuernbergk and duBuy (1930), Cholodny, (1931*d*, 1932*b*, 1933*a*), and duBuy (1933). Sierp (1918) studied the development of the *Avena*

coleoptile in darkness and when subjected to varying amounts of light. As may be seen in Fig. 27, he found that the rate of growth of the coleoptile is temporarily increased with increasing amounts of light. The point of maximum growth is reached sooner, and the final size of the coleoptile is not so great under conditions of increasing light.

Van Dillewijn (1927a) illuminated the *Avena* coleoptile by placing a lamp vertically over the plant; the light was reflected horizontally on to the experimental object by three oblique mirrors. He noted the influence upon the rate of growth of continued illumination as well as short periods of illumination with differing amounts of light. In some experiments only the tip was illuminated, in others, the subapical zones; or the entire coleoptile was supplied with light. Light-growth reactions appeared in all cases. The reactions were sharply defined when definite zones, near the tip, were illuminated for a short time with a definitely determined amount of light. After a latent period there occurred a depression of growth during the course of which two types of response could be distinguished, one of short, the other of long duration (Sierp, 1921). In the short reaction, the maximum depression of the growth rate was reached after  $\frac{1}{2}$  hour; in the long reaction, on the other hand, after  $1\frac{1}{2}$  hours. The long reaction could be observed only when the tip was illuminated (Went, 1928a: *tip response*); the short reaction, when the basal zones were illuminated (Went: *base response*). Growth was accelerated again after this retardation. When the entire coleoptile was illuminated, these effects were summated. When illuminated plants were darkened, Sierp (1918) found that a dark-growth reaction took place also.

*Geo-growth Reaction.*—The question whether gravity can produce fluctuations in the growth of the *Avena* coleoptile in a manner similar to that brought about by light has been investigated with contradictory results. Zollikofer (1921) reported continually changing rates of growth in response to stimulation by gravity; while Koningsberger (1922) observed no geo-growth reaction during continued rotation on the clinostat, but a growth-promoting effect was produced by gravity in both erect and inverted coleoptiles. The dorsiventrality curvatures, however, mentioned elsewhere, can easily disguise growth changes when the *Avena* coleoptile is clinostated. With this source of error

removed, Bremekamp (1925) and Dolk (1929a) showed that no geo-growth reactions appear in the *Avena* coleoptile. Navez and Robinson (1932b) came to the same conclusion.

*Growth Substances and Normal Growth.*—As has been mentioned previously, Paál (1918) showed that growth substance is being formed continuously in the nonilluminated coleoptile tip, whence it migrates into the more proximal portions of the coleoptile and promotes growth.

Rothert (1894) and Stark (1917) showed that the removal of the coleoptile tip produces a retardation of growth in the coleoptile stump, a fact that Söding confirmed when he investigated this same question (1924, 1925, 1929). The rate of growth (Table 3)

TABLE 3.—GROWTH IN LENGTH OF NORMAL AND DECAPITATED AVENA COLEOPTILES

The figures in the table are average values from Tables I to III of Söding, 1925 (p. 589)

Treatment	Increase in the first 5 hr.	Increase in the following 13 hr.
A. Decapitated.....	0.63	2.57
B. Decapitated, the tip replaced, and again removed after 5 hr.....	0.94	1.65
C. Intact control plants.....	1.49	3.40

in the first 5 hours after decapitation was only 42 per cent of that in normal seedlings. Furthermore, the rate of growth of the coleoptile stump was increased about 49 per cent in the first 5 hours when the removed tip was again replaced. Söding's experiments showed that the rate of growth of normal plants is not reached in decapitated plants in the first few hours, even with their tips replaced, probably because the transport of growth substance is retarded by the wound. After 10 to 14 hours, even without replacing the tip, the rate of growth of decapitated coleoptiles became about the same as that of normal seedlings. This increase in growth was brought about by "physiological regeneration" of the tip, which produced about the same amount of growth substance as the normal.

It is clear from this that a substance is dispersed from the tip which promotes growth in the basal region. If, instead of replac-

ing the tip after decapitation, one covers the wound with agar containing growth substance, the rate of growth can be increased far beyond the normal (Fig. 1) (Went). It has been found that when the growth-substance content of the agar amounts to 100 WAE (Boysen Jensen, 1933a), the coleoptile stump surpasses the enclosed leaf in growth, which normally never occurs. Söding (1929) investigated different portions of the coleoptile for growth substance and found that the amount decreased greatly from tip to base. This observation has been confirmed by the work of Thimann (1934).

From these and other experiments, it has been concluded in the past that growth substance is formed exclusively in the tip under normal conditions and that it migrates from there into the more proximal portions of the coleoptile where it stimulates growth. In view of the upward movement of growth substance which has been demonstrated in certain plants by Zimmerman and Wilcoxon (1935), it appears equally probable that the hormone or its precursor is being formed in the endosperm (Cholodny, 1935b) and moved upward in the vascular system to the tip, from which point it is dispersed downward. In fact, Pohl (1935) concludes from a series of important experiments that the coleoptile tip does not produce growth substance but can only activate the reserve stored in the endosperm. The phenomenon of "physiological regeneration" apparently could be explained by this interpretation. Further confirmatory evidence is found in the observation that physiological regeneration (Söding, 1929) takes place just as vigorously whether the coleoptile is decapitated at the tip or several millimeters below and Heyn (1935) has found that physiological regeneration does not take place when the coleoptile is separated from the food stored in the seed.

The hypothesis that the decrease in rate of growth after decapitation may be caused by lack of growth substance has been disputed by Priestley (1926d) and by Tetley and Priestley (1927). When the coleoptile is decapitated, water exudes from the cut surface; this loss of water is, according to Priestley, the essential reason for the retardation of growth, and he contended that retardation must persist until the supply of water is rendered normal again by healing of the wound. The promotion of growth by replacement of the tip was explained by partial closing of the wound. It may be said here that Priestley's explanations

are no longer tenable in the light of the more recent discoveries concerning the role of growth substance.

A question of importance is whether growth takes place in the *Avena* coleoptile when growth substance is completely absent. As shown by Söding's experiments, some growth takes place in the first 5 hours after decapitation, but Dolk (1930) showed that this occurs only because of the growth substance still

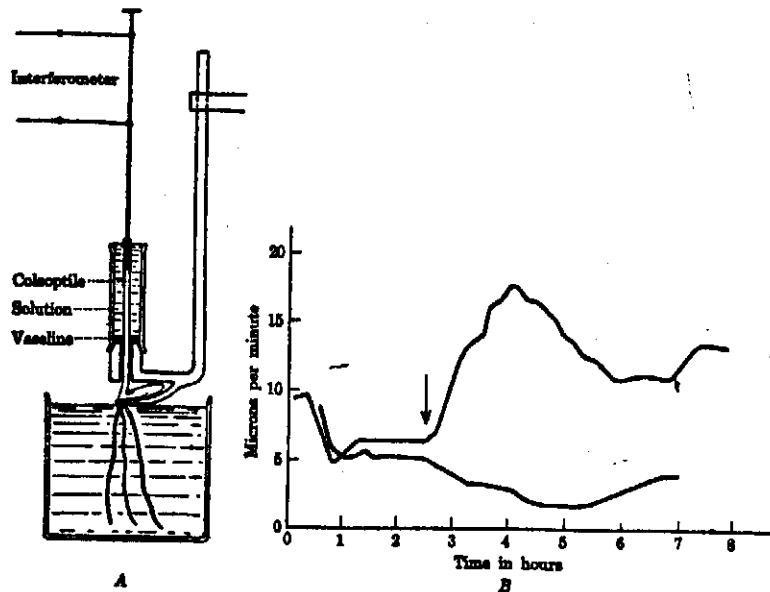


FIG. 28.—Stimulating effect of growth hormone (acidulated pollen extract) upon growth of a decapitated *Avena* coleoptile. A, diagram showing culture chamber in which coleoptile is grown immersed in solution. B, graph showing the increased rate of growth of a coleoptile treated with growth-hormone solution at the time indicated by arrow, as compared with a control plant (lower curve) which continues its growth in water. Growth was measured interferometrically. (After Laibach and Kornmann, 1933a.)

present in the coleoptile stump. If the coleoptile is decapitated again 2 hours after the first decapitation, its growth ceases almost completely but can be renewed by supplying growth substance. From these experiments it may be concluded that normally no growth substance is formed below the tip of the coleoptile and that the growth substance present in the stump at the time of decapitation is gradually used up. In any case, without growth substance there is no growth.

An interesting technique was developed by Laibach and Kornmann (1933a) to demonstrate the accelerating effect of growth substance (extracted from pollen) upon growth in length of the decapitated *Avena* coleoptile (Fig. 28).

Went (1928a) suggested reasons for the distribution of growth in the *Avena* coleoptile, stating that the rate of growth in the

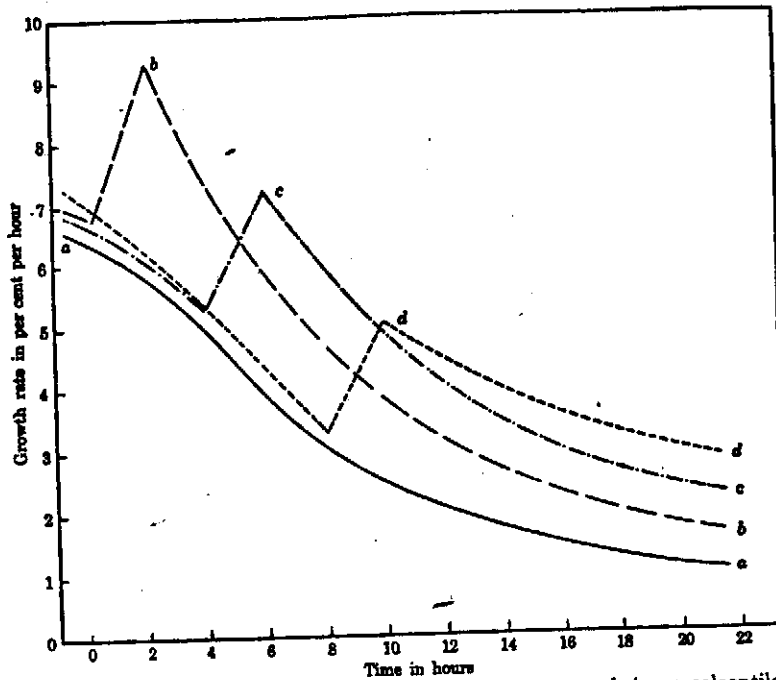


FIG. 29.—Growth rate of the upper 10 to 15 mm. zones of *Avena* coleoptiles with different amounts of growth hormone. a, the normal course of growth; b, growth of a group of coleoptiles to which auxin paste was added at an early stage; c and d, other groups of coleoptiles to which auxin was applied at later stages in growth. (After Went, 1935c.)

basal portion is limited by the failing supply of growth substance; on the other hand, growth in the tip is limited by the lack of organic material (supplied by the seed) which is necessary for cell elongation. The rate of growth reaches a maximum at that point where both food and growth substance are present in sufficient amount, and the water supply is adequate. DuBuy showed (1933) that growth in the coleoptile is gradually retarded when the endosperm is removed; aging is also mentioned as one

of the factor complexes significant in its growth. Went has discussed the subject in a later paper (1935c) and concluded that growth substance is a limiting factor in the elongation of the coleoptile during its later stages of development. Artificially increasing the auxin supply in a coleoptile accelerates the growth rate either directly by promoting growth or indirectly by preventing senescence (Fig. 29). With a supply of food available, the addition of auxin brought about a revival of growth in the basal portion which had ceased to elongate; on the other hand, when the food supply was removed, further additions of auxin showed no growth-promoting effect.

From the foregoing observations it seems clear that the rate and distribution of growth in the normally developing coleoptile are regulated by the supply of growth substance.

*Growth Substances and the Light-growth Reaction.*—Went (1926) and van Dillewijn (1927a) conjectured that the growth reactions produced by complete illumination of the tip zone are the result of changes in the amount of growth substance given off, and Went (1928a) actually found a decrease of about 18 per cent in the amount of auxin given off when the tip was illuminated with 1,000 meter-candle seconds. According to duBuy (1933), weak blue light produces no change in growth-substance supply, and even strong white light (with heat and some of the red removed) may have no effect; on the other hand, white light plus the heat radiation decreases the supply of growth substance.

General illumination of the lower zones of the coleoptile also produces light-growth reactions, as mentioned earlier, but it is not possible at this time to offer a satisfactory explanation of the phenomenon. Further data are discussed under light-growth reaction in the stems of seedlings. That the influence of light on growth depends upon the kind of growth substance present has been shown by van Overbeek (1936a). When auxin *a* is applied unilaterally in agar blocks to *Avena* coleoptiles, curvature is less under illumination with white light, than in darkness; when 3-indole acetic acid is similarly applied, no difference in growth is observed in darkness or in light.

*Foliage Leaves.*—The presence of growth substance has been demonstrated in buds and foliage leaves of several species of dicotyledons (see chapter on the occurrence of growth substances), and in *Nicotiana* (Avery, 1935) it has been shown that

## GROWTH HORMONES IN PLANTS

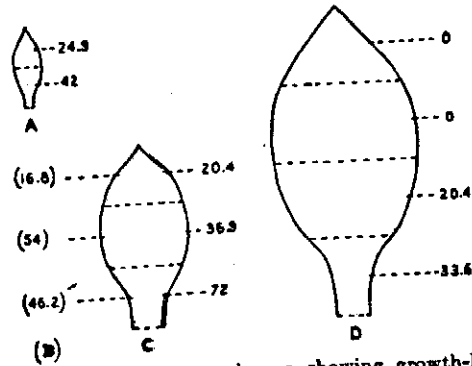


FIG. 30.—Diagrams of *Nicotiana* leaves showing growth-hormone content (expressed in plant units) at different ages and in different portions. A, young leaf. C and D, older leaves from plants grown in a greenhouse. B, leaf of same age as C, but kept in dark for 10 days, followed by 1 day in the light. The auxin concentration gradient shown in A and C is due to accumulation in the midrib and movement toward the base of the leaf. In contrast, leaf B shows less accumulation at the base (data in parentheses). Note disappearance of growth hormone at the distal end of the older leaf, D. (After Avery, 1935.)

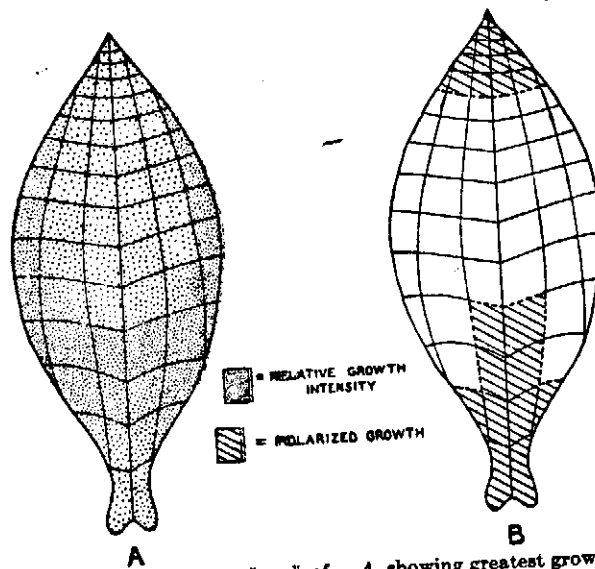


FIG. 31.—Growth of the *Nicotiana* leaf. A, showing greatest growth intensity (localized growth) in marginal and basal regions, as indicated by the density of stippling. B, the segments increased in length more than in width. While this polarized growth is not pronounced at the apex toward the end of the growth period, it is very striking at the basal end of the leaf, where it is correlated with higher concentrations of growth hormone. (After Avery, 1935.)

the concentration is greater in young leaves, tending to decrease as the leaves mature. It has been shown, also, that there is a definite concentration gradient from the tip to the base of a leaf, the concentration being low at the distal end and increasing toward the base (Fig. 30). The increase toward the base is due to the accumulation of growth substance in the proximal end of the midrib and is correlated with greater longitudinal growth ("polarized growth") of the midrib in this region. Inasmuch as the application of growth-substance paste (lanolin method, Laibach, 1933b) to large veins brings about a bending (differential growth) response, it may be assumed that it is the agent responsible for promoting the normal growth in length of the midrib and larger lateral veins in the leaf; hence, growth substance is responsible, at least in part, for the normal growth pattern exhibited by the leaf (*cf.* Figs. 30 and 31).

**Axial Parts: Hypocotyls, Internodes, and Flower Stalks.**  
*Distribution of Growth.*—Rothert (1894) investigated the distribution of growth in the hypocotyls and epicotyls of dicotyledonous seedlings. In seedlings with epigeal cotyledons the hypocotyl usually elongates first. Enlargement of the growing point above the cotyledons begins only after the growth in length of the hypocotyledonary axis is completed. As long as the hypocotyl is very short, it grows throughout its entire length; later the basal portion ceases growing, and a growth zone of a rather constant length (1 to 4 cm.) is established in its upper portion. Following cessation of growth in this region the epicotyl begins to develop. The distribution of growth in the epicotyl of *Phaseolus* is shown in Fig. 32.

The distribution of growth in stems with several elongating internodes is often quite complicated. It would not be of value to discuss this question at length here, since the significance of growth substance for these growth processes has not been investigated.

Very obvious light-growth reactions are exhibited by many seedling axes. According to Blaauw (1915), a decided retardation of growth appears in *Helianthus* after brief illumination; this is followed later by an increase in growth enduring for a short period. According to van Overbeek (1933), the rate of growth in the hypocotyl of *Raphanus* is decreased to about one-half by illumination.