schen by E. KRETSCHMER 1931, of the philologists in Illustrierte Litteraturgeschichte der vornehmsten Kulturvölker, Boele van Hensbroek, of the members of the Royal Academy of Sciences in its collection of portraits, of the Rectores Magnifici in the students' almanacs of recent years.

From this table it appears that with the gifted the forehead is higher, the upper jaw not so long, that the whole jaw system is less developed than with the adults. Similarly the proportions of upper jaw to the forehead and of the forehead to the whole jaw system point to a stronger development of the forehead and a slighter development of the jaw system with the gifted.

The results of the somato-psychological inquiry [1]) also point to a greater intellectual power in persons with a high forehead, to a lower one in persons with a low forehead. Concerning the 415 biograms it was stated that of 245 persons = 59.0 % the forehead was called high, of 59 persons = 14.2 % low, 111 cases = 26.7 % being doubtful. The distinction in intellectual power was judged in the first place by the differences mentioned by the reporters with regard to mental grasp (easily understand something new, quickly see the point), good sense (accurate knowledge of what one has read, capacity to explain something clearly) and level-mindedness (judging on loose grounds, repeated contradictions) and in the second place by the distinction observed with respect to broad-mindedness (free from prejudices of class or circle, not clinging to trifles and conventions) and narrow-mindedness (attached to conventions, fussy).

	High foreheads	Low foreheads	Doubtful cases	Averagely
Intelligent	74.3 %	59.3 %	68.5 %	67.4 %
Sensible	60.6 %	50.9 %	50.4 %	59.9 %
Level-minded	3.6 %	18.6 %	9.9 %	14.0 %
Broad-minded	79.2 %	76.3 %	79.2 %	78.2 %
Narrow-minded	8.6 %	11.8 %	6.3 %	9.1 %

In intelligence, good sense and broad-mindedness the persons with high foreheads are above the persons with low foreheads, in level-mindedness and narrowness on the other hand below them.

[1]) E. D. WIERSMA, Capita psychopathologica 1931, pp. 87 ff.
,, Lectures on Psychiatry 1932, pp. 78 ff.

Botany. — *Analysis and Integration of various auxin effects.* II. By F. W. WENT. (California Institute of Technology.)

(Communicated at the meeting of September 30, 1939.)

9. *The molar activity of different substances in the growth reaction.*

The arguments in favor of the theory that auxin takes part in a specific chemical reaction which leads to growth (THIMANN 1935, WENT 1936, WENT and THIMANN 1937, KOEPFLI, THIMANN and WENT 1938, D. BONNER 1938) have either not been understood, or overlooked in discussions on the mode of action of growth promoting substances, as certain publications show (HITCHCOCK and ZIMMERMAN 1938). For this reason they may be stated again with the help of a figure (fig. 1).

If a substance is able to take part in a given reaction, it will do so only if and when it comes in contact with the other components of that reaction. This seems an obvious statement, but its importance in biological reactions was not realized before THIMANN in 1935 indicated that a substance such as coumaryl acetic acid, may be a perfectly good growth promoting substance, but still fail to produce growth activity in the Avena test because it is hardly transportable. Therefore after diffusion out of the agar block it does not reach the cells which are growing and consequently the Avena test is negative. Recently WENT and WHITE (1939) have measured the transport rates of a number of substances active in the Avena test, and found that there is a very close parallelism between their transport rate and growth activity, as measured in the Avena test. This fully substantiates THIMANN's hypothesis, that the apparent growth activity of a substance in the Avena test is a function of its transportability.

Transportability is of course only one of the properties which affect the quantitative side of the physiological response to growth substances. Permeability of the cells, destruction of the substance before it reaches the reactive system, rate of the growth reaction, rate of movement of the substance inside the cell all will affect its activity. If growth promoting substances are tested by means of the Avena test, then a very wide range of specific molar activity is found, as represented with crosses in fig. 1. There are hardly any two substances which have the same activity. The extremes lie still further apart than the figure indicates, since some substances have activities well below 0.1 % of indole acetic acid. These data on activity in the Avena test do not give, of course, the slightest indication of a distinct chemical reaction, leading towards growth in which these substances are involved. Still the stoichiometric relationship between growth and the concentration of a given growth promoting substance, indicate such a chemical growth reaction.

When these growth substances are applied by submerging short (5 mm) sections of Avena coleoptiles in the solutions, then the molar activities of the substances do not lie as far apart as in the Avena test, and for a few substances the activities are practically the same (solid dots in fig. 1). Various authors pointed out that in the pea test a much more uniform molar activity of different substances is found. This is shown graphically with the circles in fig. 1. A number of substances show a molar activity of 100 %

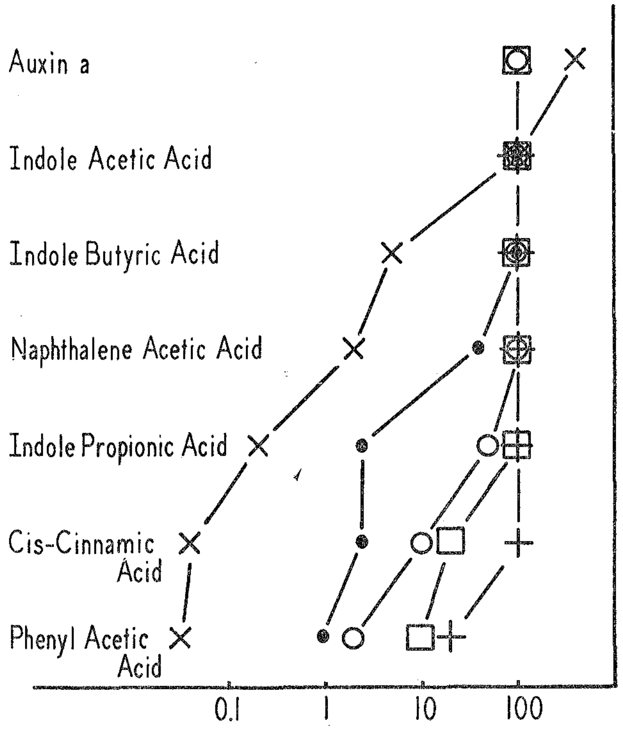


Fig. 1. Relative activities (abscissa) of various growth promoting substances. Activity of indole acetic is always taken as 100.

× Activity in standard Avena test.

● ,, when tested on Avena coleoptile sections.

○ ,, in standard pea test.

□ ,, in pea test when peas have been pre-treated for 2 hours with γ phenyl butyric acid 100 mg./1. (activity in growth reaction proper).

+ ,, in pretreated peas, but corrected for undissociated free acid molecules.

compared with indole acetic acid. Other substances are slightly less (indole propionic, indole valeric acid) or somewhat more active (naphthalene acetic acid in a few experiments). But a number of others are quite far below the 100 % activity (cis-cinnamic acid and a number of other acids with the benzole nucleus). In section 3 we have already seen that the pea test

reaction is a complex of at least 2 reactions, of which the second or growth reaction proper requires a very low auxin concentration. Therefore in general the pea test curvatures are limited by the preparatory activity of the growth promoting substances. To measure the molar activities of substances in the growth reaction proper, D. BONNER (1938) pretreated split stems of peas with γ phenyl butyric acid, so that the preparatory reaction was completed before the peas were placed in the different substances to be compared for growth activity. Of course, lower concentrations of the auxins were effective. As will be seen from the squares in fig. 1 the relative molar activity clearly increased for those substances which were less active than indole acetic acid while the relative activity of the others remained the same. Thus by narrowing down the test to one single reaction, a remarkably close 1 : 1 ratio for molar activity was found for most substances. Are the exceptions still subject to further explanation? Two other factors influencing activity may be considered as bearing on this question. One is the acid strength of the growth promoting substance.

BONNER (1934) had shown that only the undissociated auxin molecules were able to induce growth. This was confirmed by THIMANN (1935), D. BONNER (1938) and VAN SANTEN (1938). Therefore the pH of the cell sap in the same concentration a stronger acid (lower pK) will be more dissociated, i.e. less active, than a weaker growth promoting acid of higher pK. Now all the indole acids reproduced in fig. 1 have approximately the same pK (4.8, see ALBAUM and KAISER 1937), and the pK of auxin *a* is of the same order of magnitude (VAN SANTEN's (1938) statement, that the pK of auxin *a* is significantly different from that of indole acetic acid does not find any support in the literature, since the only published determination of the pK of auxin *a* is only a rough approximation and close enough to 4.8 to consider it the same as that of indole acetic acid). But phenyl acetic acid (pK 4.2) and ciscinnamic acid (pK 3.8) are decidedly stronger so that considerably fewer molecules at the same molarity will be available for growth. D. BONNER (1938) also made this correction, which is shown in the + signs of fig. 1. This leaves only phenyl acetic acid and other phenyl compounds of a lower molar activity than indole acetic acid.

Without further quantitative data it can be said that the rate of the growth reaction is much slower with phenyl acetic acid than with substances with the indole nucleus. This can be seen by watching the progress of the pea test curvatures, which start rather soon in indole acetic acid, and are completed in about 6 hours, but which start some hours later with phenyl compounds, and correspondingly continue much longer. Since we know that the sensitivity of the pea test decreases from 4 hours on after splitting, phenyl compounds will seem to have a lower molar growth activity, since they react after a considerable part of the sensitivity of the test plants has been lost. As soon as quantitative data on the rate of the growth reaction are available, this correction, which tends to bring the molar activity of phenyl acetic acid up, will be made.

If we review the evidence discussed in this section, and consider fig. 1 again, then the conclusion is inevitable, that if corrections are made for secondary properties or reactions which influence the quantitative response, all active substances have the same molar activity in the growth reaction proper. Or in other words, one molecule of indole acetic acid combines in the same way as a molecule of e.g. cis-cinnamic acid with the substrate to give a definite amount of growth. For this phenomenon not a stimulation, but a chemical reaction gives the proper mental picture.

Only if after an intensive study, in which all primary and secondary factors contributing to physiological activity have been studied and evaluated, still a major discrepancy between the molar activities of various substances exists, the conclusion that no stroichiometrical relationship between applied substance and reaction can be drawn, although it is still not binding. Concerning such a stoichiometrical relationship, the statement that "activity in green tissues indicates no such relationship, since at the minimum active concentrations we have found great differences in the molar equivalents of different substances" (HITCHCOCK and ZIMMERMAN 1938 p. 473) has of course no bearing on our problem, since not even an elementary attempt has been made to eliminate complicating factors affecting activity.

From the data in this section it becomes not only clear, why the activities of various substances may greatly differ in one and the same test object, but also why in different objects the same substances may have either a high or a low activity. For in different plants either the growth reaction, or the preparatory reaction, or the penetration, or the dissociation, or the destruction or the transport or any number of other factors may be limiting the growth response.

10. *General consideration of growth and differentiation.*

Since for no other group of developmental processes in organisms an equally detailed analysis has been carried out, a few more general remarks may conclude this paper. Some of the following points have been discussed already by WENT and THIMANN (1937) in their concluding chapter, but a few points seem worth restating.

The biological system which is best understood is respiration. But as we now know, this is a straight forward chemical process, of which the initial, intermediary and end products are chemically definable, and of which many reaction-systems can be built up outside the cell. In growth and development the endproducts of the biological system are not definable in chemical terms as yet. Also this system is more closely associated with the living cell, so that at present we seem to be very far removed from having part of the growth reactions take place in test tubes. But the same thing could be said of respiration 50 years ago. Still plant growth and root formation seem to belong to the least evasive amongst developmental processes of living organisms. Each one of the following points may have

been analyzed to some extent for other processes, but the combination of all recent advances in the field of auxin action may offer clues for the solution of other developmental problems so that an enumeration seems worth while.

1. Through the development of different test methods first the chemical nature of the growth substance was established.
2. By elimination of non-essentials affecting activity it was concluded that the auxins take part in a definite chemical reaction leading to growth.
3. Therefore a logical basis was created for an analysis of the relation between chemical structure and growth activity. It was found that growth activity is due to only a small portion of the active molecule. The complexity of the latter is probably connected with other functions it performs in the organism (see point 6).
4. The interlocking actions of auxin and a number of other growth factors such as sugars, biotin and calines was established.
5. It has been shown that a whole chain of reactions, in which the other growth factors mentioned in 4 take a part, lies between the first auxin action and its ultimate effect on the physical and physiological properties of the cell.
6. As discussed above auxin takes part in at least two of the earlier reactions in this chain: it is a component of the growth reaction proper and at the same time conditions the cells to respond.
7. In many cases the auxin concentration inside the plant is not sufficient for a given response, as e.g. rooting. If, however, its concentration is high enough to induce the root forming reaction proper, such a plant will root when treated with either auxins or hemi-auxins. If this possibility is not borne in mind, the specificity of the growth or root forming reactions may seem almost lacking.
8. The polarity of morphogenetic processes such as root formation or bud growth is connected with the polar transport of auxin, which polarity is, according to WENT and WHITE (1939), far more pronounced than generally concluded from experiments, in which leakage occurs. The polarity also accounts for the fact that the auxin may be present everywhere in the plant, but still it becomes effective only at the points predetermined through the polar structure of the organism.
9. The anatomical investigations have also adduced evidence, that the action of the auxins is complex and has to be broken down into a number of simpler effects before a general picture can be obtained.

When these and similar points are kept in mind, the great variety of factors inducing e.g. root formation becomes less puzzling. For now we know that such a physiological phenomenon is the result of a whole chain of interacting factors and reactions, which means that influencing almost any one of these factors will affect the final result. Thus the following treatments have been reported to lead to, or increase, root formation on stems:

1. Incision of stems. Results in initiation of root primordia just above incision, due to downward transport and accumulation of root forming factors.

2. Bending a stem downwards. Roots form along the lower side, due to lateral transport of auxin towards lower side.

3. Tightly wrapping a brass wire around a growing branch. This will automatically cause ringing, so that condition 1 is realised.

4. Inverting cuttings before planting. Prevents leakage of root growth factors from the basal cut surface.

5. Applying peptone to cuttings. Effective when amino acids are limiting root formation.

6. Treating cuttings with various salts, especially manganese compounds.

7. Treating cuttings with sugar, when carbohydrates are low.

8. Application of vitamin B_1. This induces elongation of root primordia, which before were invisible.

9. Placing plants in air containing ethylene. This only works when the stems have an adequate auxin supply.

10. The same provision has to be made for the effectiveness of hemi-auxins.

11. Application of auxins, both natural and synthetic, to stems.

12. Sticking a germinating grain in the split end of a cutting. This supplies auxin.

It will be obvious, that without differentiating between all these different agents, root formation would seem to be just as unspecific as e.g., differentiation in the animal embryo is being considered by many embryologists. This enumeration, which might as well have been substituted with one of the factors influencing growth, shows sufficiently, how we are not lacking facts, but that our greatest need is intelligent interpretation, which can be made on the basis of the 9 points mentioned in the first part of this section. We must also realize that growth is a very complex phenomenon, which has to be analyzed into its most simple components, before a synthesis of the phenomenon itself can be attempted. In a recent paper Hitchcock and Zimmerman (1938) claim "that explanations for growth promotion and root formation in special test objects such as the Avena coleoptile, and hypocotyls of the pea, bean, sunflower, etc., fall far short of explaining what occurs in normal plant tissue" (why are the above mentioned tissues not normal?). Undoubtedly growth and root formation in full grown plants will be more complex than in seedlings, which is the reason why the growth analysis was started in seedlings. If Hitchcock and Zimmerman had found discrepancies between the established basic phenomena and their own observations, it is up to them to analyze the reasons for these discrepancies, and not only "compare the results reported for special test objects with those obtained with normal plant tissue treated under natural conditions". A *comparison* between the pea test and the Avena test would indicate that

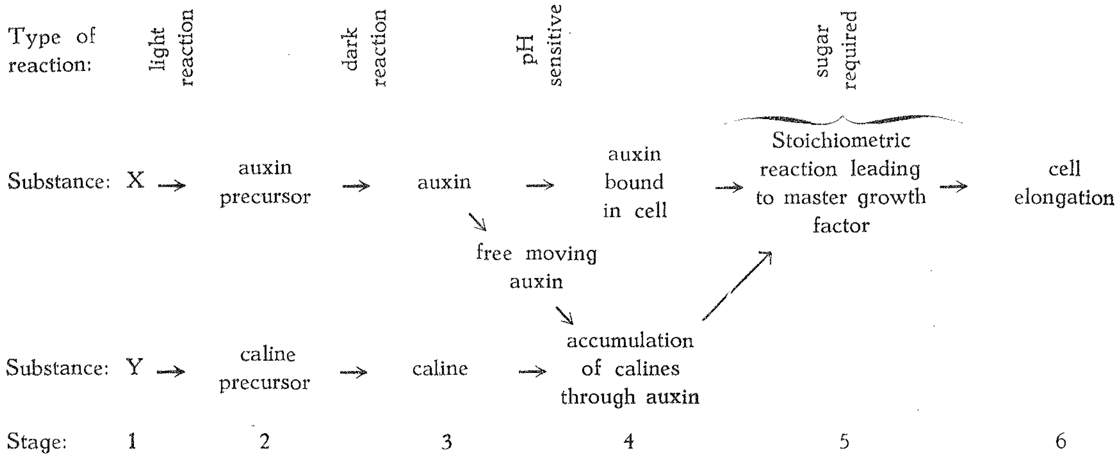
the one gives little support for the facts found with the other, but an *analysis* reveals the reasons for these differences, and shows that the facts are in complete agreement. It is surprising that Hitchcock and Zimmerman do not adhere more to the basic principles of research as outlined by their director: "it is now generally conceded not only by scientists but by thinking practical men that the quickest and surest way of solving practical problems is to establish basic principles that underlie practical problems" (Crocker 1938, p. 394), for repeatedly they claim that through their efforts "it has been possible to change the trend of growth substance research from a highly theoretical plane to one in which the principal interest is centered in dealing with facts in relation to normal tissue". It seems to the writer that here the words of Berle (1938) are pertinent (although bearing on social science, the editors of the Journal of Heredity quoted them, indicating that in their opinion they apply to biological sciences as well): "In recent years 'fact finding' has been an academic fetish. Refusal to relate facts to theoretical organization of the subject, and to draw tangible conclusions, has been recently carried to the point of sheer cowardice."

To conclude this discussion, we might say, that although neither the actual growth reaction, nor the carrier or substrate with which auxin combines are known as yet, still through auxin our knowledge of the growth and developmental processes, that is, those most closely connected with life, is steadily increasing. Again through the preceding analysis the similarity between the processes of growth and root formation already stressed by Thimann (1935) has been confirmed and extended. This is of importance, since the growth phenomena induced by auxin are more easily open to experimental attack than root formation. Thus by testing the results of the growth studies for their applicability to typical developmental processes, much is found about the latter with relatively little superfluous experimental effort. Such an introduction of the efficiency principle in scientific work is desirable, although it cannot be made compulsory, for the same reason that artistic efforts are difficult to rationalise.

Summary.

In reviewing a number of recent publications it was shown, that in any of 4 auxin-induced phenomena (growth in length, pea test, bud inhibition and root formation) the effect of auxin is dual; a preparatory reaction, pH insensitive, precedes the actual growth or root forming reaction proper. Many substances which are unable to cause growth or root formation, are effective in the preparatory reaction. They have been named hemi-auxins, to indicate that they have only part of the activities of the auxins. In table 1 the activities of five different groups of substances have been summarised, which leads to the conclusion, that we have to distinguish between substances, taking part in one or a combination of the following reactions: growth reaction proper, root forming reaction proper, preparatory reaction

for growth, pea test, or bud inhibition, preparatory reaction for root formation. In three out of four cases the preparatory reaction could be identified with a redistribution of other growth factors within the plant. The evidence for the existence of these other growth factors (calines) has also been discussed (section 1). As far as the growth reaction proper is concerned, the evidence that this is a chemical reaction, in which per molecule of active growth promoting substance a constant amount of growth occurs, again has been presented. Figure 1 is an eloquent example of how all growth substances tend to come up to the same molar activity if an increasing number of secondary properties indirectly influencing the growth reaction proper are eliminated. By first analysing growth in its component parts, we can now synthesize these into the following scheme:



In germination of the seedling the processes from 2 on take place, in the growing plant from 1 on. The steps between 5 and 6 are to be found in WENT and THIMANN (1937).

The writer gratefully acknowledges the help of the Rockefeller Foundation in furthering the work summarized in this article. For the help of the Works Progress Administration, acknowledgement has been made in the individual papers, but should be repeated here.

LITERATURE CITED.

ADDICOTT, F. T. and J. BONNER, Science **88**, 577—578 (1938).
ALEXANDER, T. R., Plant Physiol. **13**, 845—858 (1938).
ALBAUM, H. G. and S. KAISER, Am. J. Bot. **24**, 7, 420—422 (1937).
AVERY, G. S., Etudes et Recherches sur les Phytohormones, Paris, 49—54 (1938).
BERLE, A. A., The Annals, Amer. Acad. Pol. Soc. Sc. **196**, 230—231 (1938).
BONNER, D. M., Bot. Gaz. **100**, 200—214 (1938).
BONNER, D. M. and A. J. HAAGEN-SMIT, Proc. Nat. Acad. Sc. **25**, 184—188 (1939).
BONNER, D. M., A. J. HAAGEN-SMIT and F. W. WENT, Bot. Gaz. In press. (1939).
BONNER, J., Protoplasma **21**, 406—423 (1934).
BONNER, J. and G. AXTMAN, Proc. Nat. Ac. Sc. **23**, 453—457 (1937).

BOUILLENNE, R. and M., Bull. Soc. Roy. Bot. Belgique **71**, 43—66 (1938).
BOYSEN-JENSEN, P., Etudes et Recherches sur les Phytohormones, Paris, 71—84 and 115—125 (1938).
COOPER, W. C., Bot. Gaz. **99**, 600—614 (1938).
CROCKER, W., Science **88**, 387—394 (1938).
CZAJA, A. T., Planta **28**, 354—358 (1938).
FERMAN, J. H. G., Rec. trav. bot. néerl. **35**, 177—287 (1938).
FITTING, H., Biol. Zentralbl. **56**, 69—86 (1936).
HAMNER, C. L. and J. W. MITCHELL, Bot. Gaz. **99**, 569—583 (1938).
HITCHCOCK, A. E. and P. W. ZIMMERMAN, Contr. Boyce Thompson Inst. **9**, 463—518 (1938).
KOEPFLI, J. B., K. V. THIMANN and F. W. WENT, J. Biol. Chem. **122**, 763—780 (1938).
KONINGSBERGER, V. J. and B. VERKAAIK, Rec. trav. bot. néerl. **35**, 1—13 (1938).
MICHENER, H. D., Science **82**, 551 (1935).
MICHENER, H. D., Am. J. Bot. **25**, 711—720 (1938).
MITCHELL, J. W., and W. E. MARTIN, Bot. Gaz. **99**, 171—183 (1937).
MITCHELL, J. W., and N. W. STUART, Bot. Gaz. **100**, 627—650 (1939).
OVERBEEK, J. VAN, Proc. Nat. Ac. Sc. **22**, 187—190 (1936).
OVERBEEK, J. VAN, Bot. Gaz. **100**, 133—166 (1938).
ROBBINS, W. J. and M. B. SCHMIDT, Am. J. Bot. **26**, 149—159 (1939).
SANTEN, A. M. A. VAN, Proc. Kon. Ned. Akad. v. Wetensch., Amsterdam, **41**, 513—523 (1938).
STUART, N. W., Bot. Gaz. **100**, 298—311 (1938).
THIMANN, K. V., Proc. Kon. Akad. v. Wetensch., Amsterdam, **38**, 896—912 (1935).
THIMANN, K. V., Am. J. Bot. **24**, 407—412 (1937).
TRAUB, H. P., Proc. Am. Soc. Hort. Sc. (1938).
WENT, F. W., Proc. Kon. Akad. v. Wetensch., Amsterdam, **38**, 752—767 (1935).
WENT, F. W., Biol. Zentr.bl., **56**, 449—463 (1936).
WENT, F. W., Plant Physiol. **13**, 55—80 (1938).
WENT, F. W., Am. J. Bot. **25**, 44—55 (1938*a*).
WENT, F. W., Chronica Botanica **4**, 503—505 (1938*b*).
WENT, F. W., Am. J. Bot. **26**, 24—29 (1939).
WENT, F. W., Am. J. Bot. **26**, 109—117 (1939*a*).
WENT, F. W., Bull. Torrey Bot. Club. In press (1939*b*).
WENT, F. W., Am. J. Bot. **26**, In press (1939c).
WENT, F. W. and K. V. THIMANN, Phytohormones. MacMillan, New York (1937).
WENT, F. W. and R. WHITE, Bot. Gaz. **100**, 465—484 (1939).