

14. KLINKER, J. E. A modification of the Warburg respirometer to measure the respiration rate of tomato leaf discs. *Plant Physiol.* 25: 354-355. 1950.
15. LATIES, G. G. The role of pyruvate in the aerobic respiration of barley roots. *Arch. Biochem.* 20: 284-299. 1949.
16. McNULTY, I. B. and NEWMAN, D. W. The effects of a lime spray on the respiration rate and chlorophyll content of leaves exposed to a fluoride atmosphere. *Proc. Utah Acad. Sci.* 33: 73-79. 1956.
17. McNULTY, I. B. and NEWMAN, D. W. Effects of atmospheric fluoride on the respiration rate of bush bean and gladiolus leaves. *Plant Physiol.* 32: 121-124. 1957.
18. MEYER, B. S. and ANDERSON, D. B. *Plant Physiology*. Pp. 462-464. D. Van Nostrand, New York 1952.
19. MILLER, G. W. Properties of enolase extracts from pea seed. *Plant Physiol.* 33: 199-206. 1958.
20. NIELSEN, H. M. Determination of microgram quantities of fluoride. *Anal. Chem.* 30: 1009-1011. 1958.
21. NIELSEN, J. P. and DANGERFIELD, A. D. Use of ion exchange resin for determination of atmospheric fluorides. *A. M. A. Arch. Ind. Health* 11: 61-65. 1955.
22. RECKENDORFER, P. Ein Beitrag zur Mikrochemie des Rauchs Schadens durch Fluor; Die Wanderung des Fluors im pflanzlichen Gewebe. I. Teil: Die unsichtbaren Schaden. *Pflanzenschutz-Berichte* 9: 33-55. 1952.
23. RICHARDS, H. M. The respiration of wounded plants. *Ann. Bot.* 10: 531-582. 1896.
24. THOMAS, M. D. The invisible injury theory of plant damage. *Jour. Air Pollution Control Assoc.* 5: 205-208. 1956.
25. UMBREIT, W. W., BURRIS, R. H., and STAUFFER, J. F. *Manometric Techniques and Tissue Metabolism*. Burgess, Minneapolis 1945.
26. WARBURG, O. and CHRISTIAN, W. Isolierung und Kristallisation des Gärungsferments Enolase. *Biochem. Zeits.* 310: 384-421. 1942.
27. WHITEMAN, T. M. and SCHOMER, H. A. Respiration and internal gas content of injured sweet-potato roots. *Plant Physiol.* 20: 171-182. 1945.
28. WILLARD, H. H. and WINTER, O. B. Volumetric method for determination of fluoride. *Ind. Eng. Chem., Anal. Ed.* 5: 7-10. 1933.

AN ANALYSIS OF AUXIN-GIBBERELLIN INTERACTION IN PEA STEM TISSUE^{1,2}

ARTHUR W. GALSTON AND HAVA WARBURG

JOSIAH WILLARD GIBBS RESEARCH LABORATORY, DEPARTMENT OF BOTANY, YALE UNIVERSITY, NEW HAVEN, CONN.

It has previously been reported from various laboratories (1, 8, 10, 14, 18) that etiolated pea epicotyl sections are promoted in their growth both by indoleacetic acid (IAA) and by gibberellic acid (GA) supplied separately. When GA and IAA are supplied together in optimal concentrations, the total growth increment never exceeds and usually does not equal the sum of the separate growth increments (14). This lack of interaction between GA- and IAA-mediated growth favors the view that these systems are metabolically distinct and possibly entirely unrelated. In contrast with this view are the results of experiments with green pea sections and decapitated etiolated pea plants (2, 17) from which it appears that GA-induced growth is synergistic with and possibly completely dependent on an IAA or auxin-induced growth.

The present work contributes to a resolution of this apparent discrepancy by demonstrating that, in etiolated peas, purely additive responses to the two growth factors are obtained when short (5 mm long) epicotyl sections are excised and treated, but that synergistic interactions are obtained when longer epicotyl pieces are exposed, at different loci, to appropriate concentrations of the two substances. The results are interpreted as supporting the "three-factor" hypothesis recently

advanced by Brian and Hemming (2) to explain the control of growth in stems.

MATERIALS AND METHODS

Alaska peas (*Pisum sativum* L.) were obtained from Associated Seed Growers, Inc., New Haven, Connecticut. They were permitted to imbibe for 4 hours in tap water in darkness, and were then sown in polyethylene trays containing water-saturated vermiculite (Mica-Gro Type B) which had previously been washed in running water to remove an inhibitor of growth. They were grown in a darkened cabinet in a dark room maintained at $27^{\circ} \pm 1^{\circ}$ C. The occasional illumination required for handling of the material was furnished by a dim green source found to be inactive both phototropically and photomorphogenically. This source consisted of a 15-watt Sylvania green fluorescent tube wrapped with 3 layers of green and 3 layers of amber duPont cellophane, and located about 30 cm from the working table area.

At the age of 7 days, the epicotyls were ready for harvest. The only seedlings selected for use in the growth experiments were those with recurved terminal buds and 3rd internodes between 20 and 40 mm long. Selected seedlings were severed slightly above the ground line with a razor, decapitated by a gentle stroking motion between thumb and forefinger, and trimmed at the base to a length of 100 mm. Such 100 mm long epicotyls were, in certain experiments, treat-

¹ Received June 23, 1958

² Research supported by the National Science Foundation under grant NSF G-2846

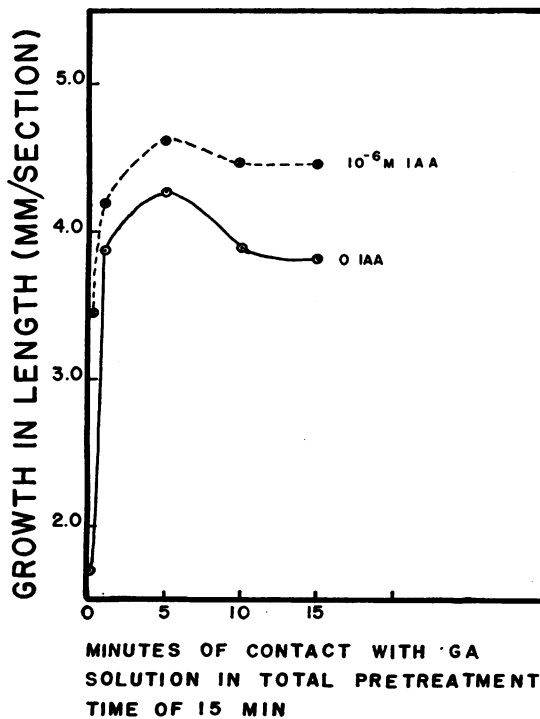
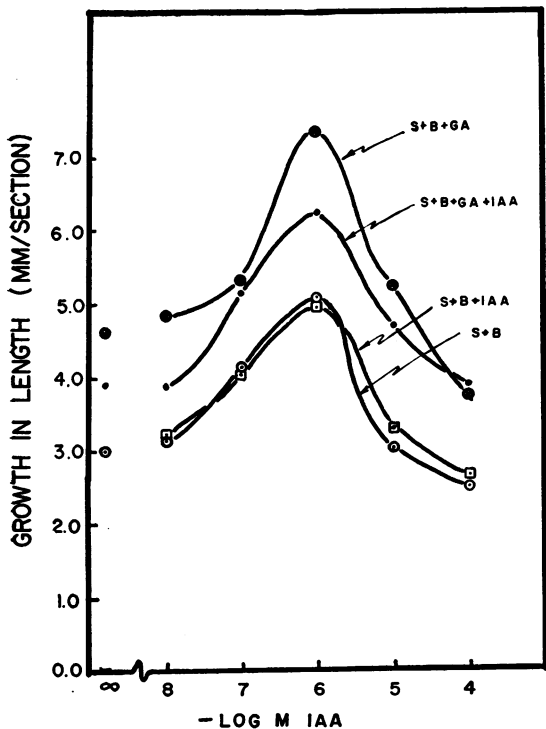
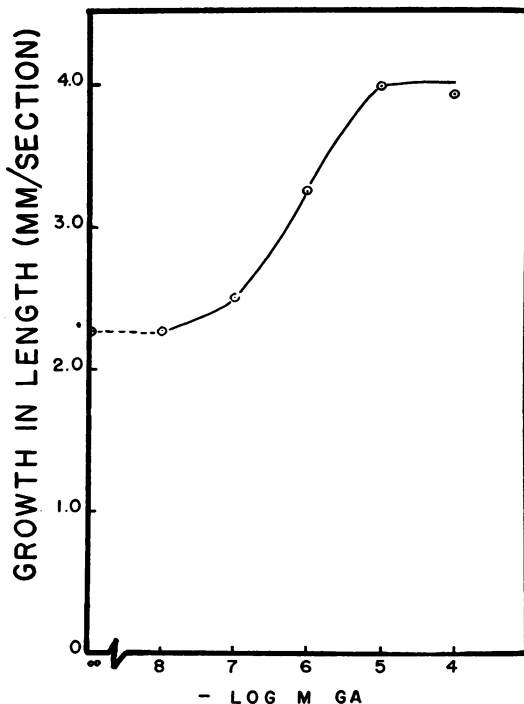
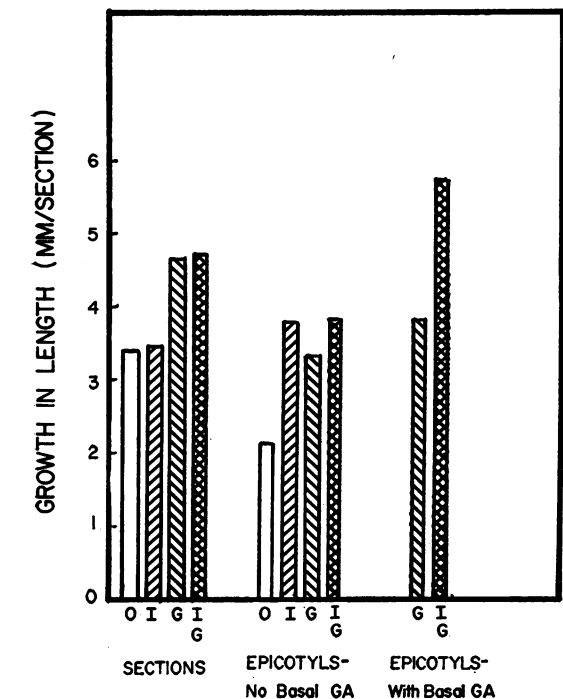


FIG. 1 (upper left). The effect of GA and IAA administered in various ways on the growth of excised pea epicotyl sections.

FIG. 2 (upper right). The relation between molarity of GA in the pretreatment solution and subsequent growth of excised sections.

FIG. 3 (lower left). Relation of the composition of the pretreatment medium to growth of sections in various concentrations of IAA. S + B = sucrose and buffer.

FIG. 4 (lower right). The effect of time of contact of epicotyls with GA on the subsequent growth of excised apical sections. Total pretreatment time 15 minutes.

ed basally with GA. Apical sections 5 mm long, equivalent to the S1 sections of Purves and Hillman (14), were obtained from the epicotyls by the use of a guillotine previously described (6). For the growth tests, 12 such sections were incubated in 10 ml of medium in 10 cm diameter Petri dishes for about 18 hours in the dark room. They were then measured to the nearest 0.1 mm under a dissecting microscope equipped with an ocular micrometer. Standard errors were computed for the means of all growth experiments. These values were almost uniformly below 5% of the mean growth increment and, in all experiments reported in this paper, did not exceed 8%. Occasional experiments in which the growth data were more variable than this were discounted entirely.

Fresh weights of the groups of sections were routinely obtained to the nearest milligram after gentle blotting. For certain critical experiments, weights of the individual groups were also obtained in the dark room prior to immersion in the growth medium. Although no weight data are presented in this paper, the results of such measurements confirm in all details the conclusions reached with length measurements.

The growth medium always contained 2% sucrose and .02 M pH 6.1 $\text{KH}_2\text{PO}_4\text{-Na}_2\text{HPO}_4$ buffer (Fisher certified reagents) unless otherwise stated. IAA, obtained from the Nutritional Biochemical Company, was made up as a 10^{-3} M stock solution in an equivalent of KHCO_3 , adjusted to pH 7.0 with KOH and stored in a refrigerator for no longer than 1 month. The GA, obtained from Dr. P. W. Brian of Imperial Chemical Industries, England, was similarly made up to a 10^{-3} M stock solution, and stored in the refrigerator for no longer than 1 month. The distilled water used in these experiments was drawn directly from the tap of the stainless steel delivery line. The conductivity of such line distilled water never exceeded 0.3 ppm NaCl equivalents, as measured with a Barnstead purity meter, model PM-2. The small quantities of chromium in such water were found not to influence the growth of the sections, since glass-redistilled water gave no improvement in growth.

RESULTS

GROWTH EFFECTS OF GA SUPPLIED DIRECTLY TO APICAL SECTIONS OR BASALLY TO EPICOTYLS: GA and IAA were supplied in various ways to subapical sections of peas and the effects on growth noted. The varying procedures were as follows:

1.) Sections were excised, placed directly in growth media containing 10^{-6} M IAA, 10^{-4} M GA, neither, or both, in addition to sucrose and buffer. 2) 100 mm long epicotyls were pretreated for 30 minutes with their bases immersed in 10 ml of sucrose and buffer medium in a 50 ml beaker; sections were then excised and placed either in basal medium or medium supplemented by 10^{-6} M IAA, 10^{-4} M GA or both. 3) Like 2), but the pretreatment solution contained 10^{-4} M GA in addition to sucrose and buffer. In effect, such a procedure permits the separate calculation of the growth effects of GA and/or IAA, administered either directly to excised sections or to the epicotyl

stick. Typical data from such an experiment are shown in figure 1.

The following points should be noted: (a) Sections excised and placed directly in the growth medium are practically insensitive to 10^{-6} M IAA, but are very responsive to GA. Their response to GA and IAA supplied together does not exceed the expected additivity. These results conform well with those previously reported by others in this laboratory (14). (b) Sections derived from epicotyls pretreated basally with sucrose-buffer show a greatly depressed endogenous growth, a greatly heightened sensitivity to IAA and a slightly depressed response to GA. Growth in response to GA and IAA supplied together is far less than the expected additivity. These results can probably be interpreted as being the result of depletion, during the pretreatment, of growth substances from the region of the epicotyl subsequently excised and used for the growth study. (c) Sections derived from epicotyls pretreated basally with GA-containing solutions show significantly greater growth, when supplied with IAA, than any other sections. The combined effect of the IAA and GA treatment far exceeds the expectation of simple additivity, and may thus be considered synergistic.

This synergism could be considered to result either from consequences of the passage of GA through the tissue on its way to the apex, or to the 30-minute time lag between the GA and IAA application. An experiment was thus performed in which the GA was supplied to excised sections for 30 minutes, after which time the sections were removed, thoroughly rinsed, and transferred to IAA-containing media. The growth of such sections was no greater than that of sections placed directly in GA and IAA.

An analogous experiment was also performed in which the apical end of the epicotyl was dipped into GA during the pretreatment period, and the apical sections ultimately excised and placed in IAA-containing solutions. The growth under such circumstances was *less* than the growth of excised sections, and showed no synergistic interaction of IAA and GA. The synergism is thus not due to the temporal lag between GA and IAA application, and hence appears to result from some effect of GA application at the base of the epicotyl, about 100 mm away.

RELATION OF GA CONCENTRATION IN THE PRE-TREATMENT SOLUTION TO SUBSEQUENT GROWTH: Groups of epicotyls were treated for 30 minutes with sucrose and buffer solutions containing varying molarities of GA. At the conclusion of the pretreatment, sections were excised and placed in solutions containing sucrose and buffer. The growth results are shown in figure 2. There is a slight response to 10^{-7} M GA, half maximal response to 10^{-6} M, and optimal response in the range 10^{-5} to 10^{-4} M.

In another series of experiments, the interrelation between condition of pretreatment of the epicotyl and subsequent response of the section to a range of IAA concentrations was studied. From figure 3, it can be seen that pretreatment with 10^{-4} M GA raises the subsequent growth of the sections without altering the

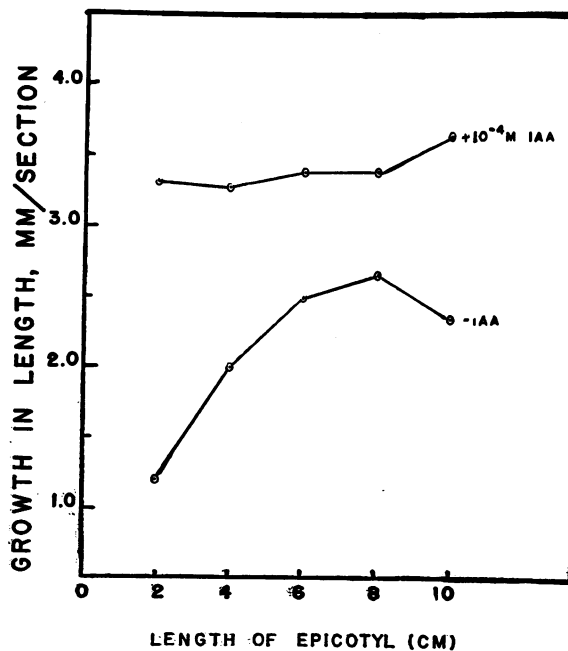
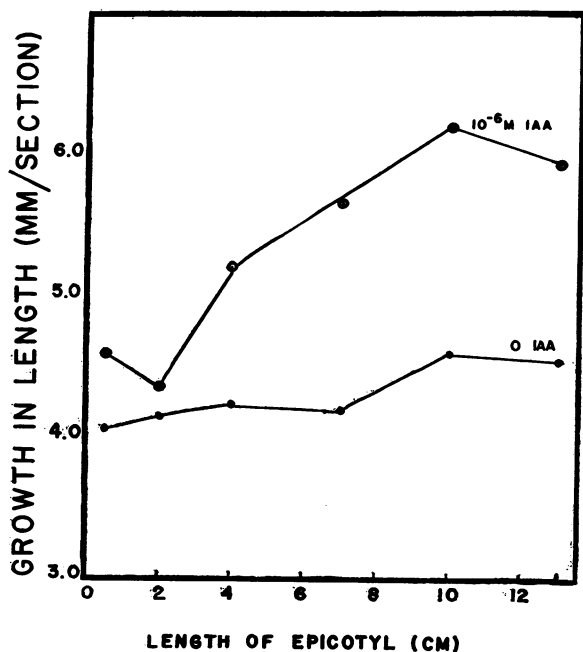
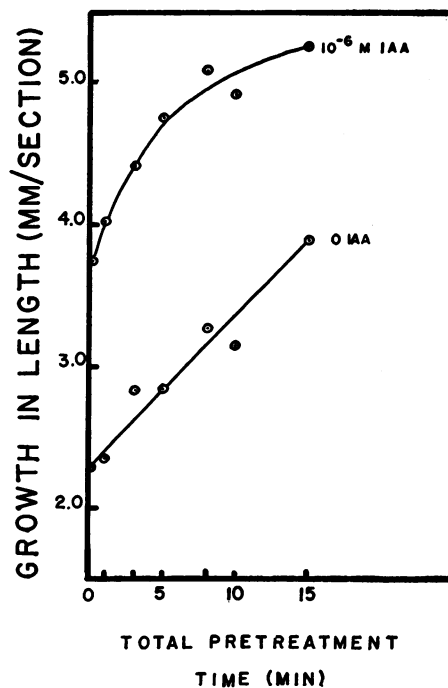
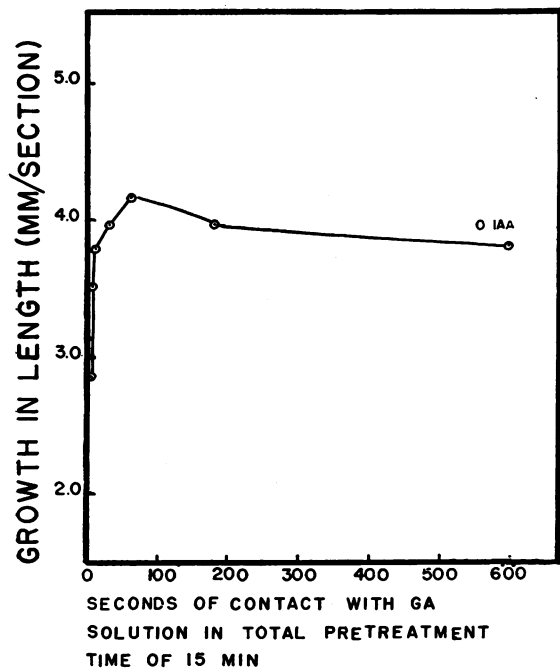


FIG. 5 (upper left). The effect of time of contact of epicotyls with GA on the subsequent growth of excised apical sections. Total pretreatment time 15 minutes.

FIG. 6 (upper right). Effect of total pretreatment time with GA on subsequent growth of excised sections.

FIG. 7 (lower left). The effect of length of epicotyl exposed to GA on subsequent growth of sections.

FIG. 8 (lower right). The effect of length of GA-treated green pea stems on the growth response of excised apical sections.

optimal IAA concentration; pretreatment with IAA produces a slight but significant depression of growth at some subsequent IAA levels; inclusion of IAA in the GA pretreatment medium results in a marked depression of the GA effect. Thus, GA and IAA appear to react synergistically when supplied at the different loci, but antagonistically when both are supplied basally. In another experiment, not presented here, it was found that the greater the GA concentration of the pretreatment solution, the greater is the growth of the sections at all IAA concentrations.

RELATION BETWEEN DURATION OF EPICOTYL PRE-TREATMENT WITH GA AND SUBSEQUENT GROWTH OF SECTIONS: It became apparent, during the various experiments, that the arbitrary pretreatment time of 30 minutes and the arbitrary pretreatment solution volume of 10 ml per 12 epicotyls were much greater than necessary. Figure 4 shows the result of an experiment in which 12 epicotyls were immersed in 1 ml of solution (sucrose + buffer + 10^{-4} M GA) in a 10 ml beaker for varying numbers of minutes. In all cases, the epicotyls were transferred, after exposure to GA, to another beaker containing sucrose and buffer only, and the apical sections uniformly excised after 15 minutes had elapsed since the 1st basal exposure to GA. Figure 5 shows a subsequent similar experiment in which the exposure time to GA was reduced to seconds.

From these graphs, it is clear that as little as 1 to 3 minutes of basal exposure to 10^{-4} M GA suffices to elicit the maximum growth response, if the apical 5 mm sections are excised from the 100 mm epicotyls a total of 15 minutes after their 1st exposure to GA. It also appears that as little as 3 seconds of exposure to GA produces a marked effect on subsequent growth.

To determine the apparent maximum rate of transport of the GA or its induced effect up the epicotyl, an additional experiment was performed in which the epicotyls were immersed for varying periods of time in 10^{-4} M GA and the sections excised without further delay. From figure 6 it is clear that a significant effect of basally-applied GA is apparent at the apex after 3 to 5 minutes, and that more and more effect is apparent at the apex as the total time of exposure increases, with some evidence of a plateau between 10 to 15 minutes in the + IAA cultures. This implies a translocation rate of GA or a GA-induced change as rapid as 20 to 33 mm/min.

RELATION BETWEEN LENGTH OF EPICOTYL TREATED WITH GA AND ITS SUBSEQUENT GROWTH EFFECT: The previous data indicate that GA or a GA-induced change, moving up the epicotyl, produces some effect which leads to greatly enhanced growth in the presence of IAA. In other experiments, it became apparent that the effect of GA is directly proportional to the length of epicotyl employed in the experiment. Epicotyls of various lengths from 5 to 100 mm were placed with their basal ends in a solution of 10^{-4} M GA in sucrose-buffer. After a standard exposure time of 15 minutes, 5 mm sections were excised from the apex, and placed in 10^{-6} M IAA and sucrose-buffer. The results, shown in figure 7, demonstrate that the effect

of GA is greater the longer the epicotyl, provided the sections are grown in the presence of IAA. There is also a much smaller but significant effect of length of epicotyl on growth of sections in the absence of IAA.

GIBBERELLIN-AUXIN INTERACTIONS IN GREEN PEA STEMS: Brian and Hemming (2) have shown convincingly that sub-apical stem sections derived from light-grown peas react to GA only in the presence of an auxin. The GA-IAA interaction in green sections, unlike that in etiolated sections, is clearly synergistic. It occurred to us, therefore, to repeat our experiments on the relation of stem length to GA effect with green peas.

Alaska peas were grown in vermiculite in a controlled-condition room maintained at 17° C, with a 16 hour photoperiod (8 A.M. to 12 midnight), the light of about 1500 ft-c coming from a bank of mixed fluorescent and incandescent lights. They were automatically subirrigated twice daily with a nutrient solution composed of 120 g "Hyponex" mixture (Hydroponics Chemical Company, Copley, Ohio) per 100 L of tap water. At the age of 14 days, the plants were harvested and trimmed to leafless stems of varying lengths, terminating in an apical bud still enclosed within the stipules (for further details, see Galston and Baker, (4)). These stems were then immersed basally for 1 hour in 10 ml of 4 % sucrose and buffer and 10^{-4} M GA contained in a 50 ml beaker. At the end of this time, apical 5 mm sections were cut with a guillotine, and placed as usual in either 4 % sucrose and buffer, or in sucrose-buffer augmented by 10^{-4} M IAA. The results are shown in figure 8. From these data, it can be seen that growth of the sections is independent of stem length when they are supplied with auxin, but that growth is greater with increasing stem length in the cultures devoid of auxin. Thus, green peas differ in at least 2 ways from etiolated peas: 1) IAA-GA synergism may be observed in very short stem sections, and 2) the interaction of GA with stem tissue, resulting in enhanced growth, is independent of auxin supply. These results, taken together with those of Brian and Hemming (2) showing strict dependence of GA effects on auxin, imply some effect of acropetally-migrating GA on auxin content or activity of the apical green stem tissue.

DISCUSSION

There have recently been several reports of the synergistic interaction of auxins and gibberellins in various biological systems (2, 8, 11, 15, 17, 18), and the evidence now seems strong that GA can generally function only if some auxin or apically-produced growth factor is present. From the present paper it appears that in the etiolated pea epicotyl, this synergism depends on the prior interaction of GA with some other component of the tissue present in relatively short supply throughout the epicotyl. Such a "three factor" interpretation of growth regulation in the pea internode coincides very well with and supports a similar hypothesis recently advanced by Brian and Hemming (2). This hypothetical "third factor"

would seem to be more abundant in green pea stem tissue than in etiolated tissue, for GA-IAA synergism can be demonstrated in very short (5.0 mm) sections of green stem, while much longer pieces of etiolated epicotyl are needed to show the same effect. The fact that, in the absence of added auxin, the effect of GA on green tissue is similarly dependent on length of stem traversed, suggests that the third factor has something to do with auxin metabolism, possibly a "sparing" of auxin.

A sparing action of GA on auxin is suggested by the work of Galston (4) Pilet (13) and Stutz and Watanabe (16), all of whom found GA application to depress the activity of IAA oxidase in various tissues, by the work of Nitsch (12) who found GA to increase the level of auxin in various woody shoots and by the indirect evidence of Vlitos and Meudt (17, 18) with slightly decapitated peas. Galston (4) was able to show that the depression of IAA oxidase activity was due to enhanced levels of a substance, presumably phenolic, which acts as an inhibitor of auxin destruction. Gortner and colleagues (7) have recently reported that ferulic acid (3-methoxy-4-hydroxy-cinnamic acid), a phenolic substance, functions in this manner in the pineapple. The indication that this "third factor" is more abundant in green than in etiolated pea tissue also parallels the situation already reported for the inhibitor of IAA oxidase (4). The quantity of IAA oxidase inhibitor in etiolated peas is also known to be controlled by the red-far-red reversible photoreaction (9).

It should also be noted that certain growth effects of GA cited in the literature, such as promotion of germination of lettuce seeds, expansion of excised bean leaf discs and some responses of excised stem sections appear not to be easily explicable in terms of an interaction of GA with auxin metabolism. Brian and Hemming (2) have also adduced considerable evidence against auxin-sparing as a mode of action of GA, based on the fact that GA evokes responses which cannot be produced by any concentration of externally applied IAA. Their arguments, while cogent, are not completely convincing because of the difficulty of equating auxin concentration and localization in the cell with that of synthetic auxin applied to the exterior surface of a mass of tissue. In any event, we do not wish to advocate auxin-sparing as a universal mode of action of GA, but would like to indicate that, in the pea plant, there is good evidence that GA causes cells to produce a substance which acts, *in vitro*, like an auxin-sparing substance, and acts *in vivo* like a promoter of growth and of GA-IAA synergism.

Although it is tempting to ascribe all of the effects reported in the present paper to actual movement of GA up the epicotyl, such a transport has not been unequivocally demonstrated in these experiments. The possibility must still be entertained that basally-applied GA does not actually reach the apex, but rather sets in motion a chain of chemical events which move rapidly up the epicotyl to the region excised and used in the growth studies. We intend to investigate this situation by the use of tritium-labelled gibberellic acid.

SUMMARY

1. When GA and IAA are applied jointly to excised 5 mm-long epicotyl sections of etiolated peas, the growth effects produced are no greater than additive, and are frequently less than additive. If, however, GA is applied basally to an excised 100 mm-long epicotyl, and the IAA subsequently applied to the excised apical section, the combined growth effects are much more than additive (synergistic).

2. The epicotyls react to as little as 10^{-7} M GA, half maximally to 10^{-6} M GA and optimally to 10^{-5} and 10^{-4} M GA. They can thus be used to assay GA in this range. The volume of solution to be assayed per epicotyl need not exceed .08 ml, and can thus be used to detect down to .03 μ g of GA.

3. Appreciable effects of basally-applied GA are evident at the apex, 100 mm away, within 3 to 5 minutes after application, indicating a transport rate as rapid as 20 to 33 mm/min.

4. The effects of GA in such an etiolated epicotyl is directly proportional to the length of epicotyl between the base, which received the GA, and the apex, which received the IAA. In green stems, where GA-IAA synergism is clearly shown in excised 5 mm sections, GA effects are dependent on the length of stem traversed, even if no auxin is supplied to the excised section.

5. These results can be interpreted in terms of a "third factor" required for GA-IAA interaction. Such a factor, apparently limiting in etiolated pea stem tissue and abundant in green tissue, may operate through an auxin-sparing mechanism.

LITERATURE CITED

1. BRIAN, P. W. and HEMMING, H. G. A relation between the effects of gibberellic acid and indolyl-acetic acid on plant cell extension. *Nature* 179: 417. 1957.
2. BRIAN, P. W. and HEMMING, H. G. Complementary action of gibberellic acid and auxins in pea internode extension. *Ann. Bot. (N.S.)* 22: 1-17. 1958.
3. BRIAN, P. W., HEMMING, H. G. and RADLEY, M. A physiological comparison of gibberellic acid with some auxins. *Physiol. Plantarum* 8: 899-912. 1955.
4. GALSTON, A. W. Investigations on a substance whose level in tissue is controlled by the red-far-red reversible photoreaction. In: *Photoperiodism and Related Phenomena in Plants and Animals*. An international symposium held at Gatlinburg, Tenn., Oct. 1957. (In press, 1958.)
5. GALSTON, A. W. and BAKER, R. S. Studies on the physiology of light action. IV. Light enhancement of auxin-induced growth in green peas. *Plant Physiol.* 26: 311-317. 1951.
6. GALSTON, A. W. and HAND, M. E. Studies on the physiology of light action. I. Auxin and the light inhibition of growth. *Amer. Jour. Bot.* 36: 85-94. 1949.
7. GORTNER, W. A., KENT, M. J. and SUTHERLAND, G. K. Ferulic and *p*-coumaric acids in pineapple tissue as modifiers of pineapple indoleacetic acid oxidase. *Nature* 181: 630-631. 1958.

8. HAYASHI, T. and MURAKAMI, Y. Studies on the physiological action of gibberellins (Part I). Bull. Natl. Inst. Agr. Sci. D (Japan): 159-197. 1958.
9. HILLMAN, W. A. and GALSTON, A. W. Inductive control of indoleacetic acid oxidase activity by red and near infrared light. Plant Physiol. 32: 129-135. 1957.
10. KATO, J. Studies on the physiological effect of gibberellin. I. On the differential activity between gibberellin and auxin. Mem. Coll. Sci. Univ. Kyoto Ser. B. 20: 189-193. 1955.
11. LUCKWILL, L. C. Fruit growth in relation to internal and external chemical stimuli. Paper presented at Mt. Holyoke College, June 1958. Seventeenth Growth Symposium (In press.)
12. NITSCH, J. P. Growth responses of woody plants to photoperiodic stimuli. Proc. Amer. Soc. Hort. Sci. 70: 512-525. 1957.
13. PILET, P.-E. Action des gibberellines sur l'activit  auxin-oxydasique de tissus cultiv  in vitro. Compt. rend. acad. sci., (France) 245: 1327-1328. 1957.
14. PURVES, W. K. and HILLMAN, W. S. Response of pea stem sections to indoleacetic acid, gibberellic acid and sucrose as affected by length and distance from apex. Physiol. Plantarum 11: 29-35. 1958.
15. SCHROEDER, C. A. and SPECTOR, C. Effect of gibberellic acid and indoleacetic acid on growth of excised fruit tissue. Science 126: 701-702. 1957.
16. STUTZ, R. E. and WATANABE, R. The gibberellins II. The effect of gibberellic acid and photoperiod on indoleacetic acid oxidase in *Lupinus albus* L. Argonne Natl. Lab., Biol., and Med. Research Div., Semiannual Report Jan.-June 1957, 107-109.
17. VLITOS, A. J. and MEUDT, W. Relationship between shoot apex and effect of gibberellic acid on elongation of pea stems. Nature 180: 284. 1957.
18. VLITOS, A. J. and MEUDT, W. The effect of light and of the shoot apex on the action of gibberellic acid. Contrib. Boyce Thompson Inst. 19: 55-62. 1957.

FOLIAR UPTAKE OF SALT CONSTITUENTS OF WATER BY CITRUS PLANTS DURING INTERMITTENT SPRINKLING AND IMMERSION^{1,2}

FRANK M. EATON AND R. B. HARDING

DEPARTMENT OF SOILS AND PLANT NUTRITION, UNIVERSITY OF CALIFORNIA CITRUS EXPERIMENT STATION,
RIVERSIDE, CALIFORNIA

On the basis of diverse methods of application and appraisal, the now rather extensive literature on foliar uptake gives one the impression that almost any substance in soluble or gaseous form may be absorbed by plant leaves. In some measure, the materials are translocated from the point of application to surrounding or other tissues. Boynton's review (1) places emphasis on the value and limitations of foliar application of plant nutrients. Bukovac and Wittwer (3), with a short review of pertinent literature, present new data on the uptake of 14 elements studied by means of radioactive isotopes. Van Overbeek (9) has reviewed papers dealing with the foliar absorption and translocation of plant regulators. He introduces his review with a critical analysis of mechanisms of solute entry into leaves in the light of cuticular compositions and structures. The foliar uptake of herbicides, fungicides, sulfur dioxide, fluoride, and smog constituents have all received recurrent attention.

The present paper has its background in two somewhat distinct fields of interest: 1) the accumulation of the salt constituents of natural waters by citrus leaves under sprinkler irrigation, and 2) the selective absorption and constancy of foliar cation accumulations.

As regards sprinkler irrigation, Harding et al (4) have shown that under some conditions there is an excessive accumulation of sodium and chloride in citrus leaves when orchards are irrigated with sprinklers. The sprinklers customarily used are the type

which make a full circle every 2 to 4 minutes. Between successive wettings there is opportunity for evaporation from the film left on the leaves. This latter fact gave rise to a question of whether the salts in the original irrigation waters were sufficiently concentrated to have caused the observed accumulations. Evaporation from the film remaining on leaves between successive wettings would result in high salt concentrations on the leaf surfaces.

Comparisons between day versus night sprinkling and intermittent versus continuous sprinkling are reported in this paper. Absorption was measured when the tops of small, rooted lemon cuttings and orange seedlings in potting soil were inverted for successive overnight periods in various single-salt solutions. The foregoing studies gave opportunity for appraising the constancy of cation absorption by leaves for comparison with absorption through roots as studied by others. This latter subject, as recently developed by Kretschmer et al (5), led to their statement that "increase in the absorption of any one cation results in reduction in absorption of some other cation or cations or increase in uptake of one or more anions."

MATERIALS AND METHODS

Budded Valencia orange trees growing in 5-gallon cans of soil were used for the sprinkling experiments. Rooted Eureka lemon cuttings and seedling sweet orange trees, both 6 to 8 inches tall and growing in 1-quart containers of potting soil were inverted over 3-liter jars of aerated solution and tops immersed for 6 periods of 18 hours each, between 3:00 P.M. and 9:00 A.M.

¹ Received June 27, 1958.

² Paper no. 1050, University of California Citrus Experiment Station, Riverside, California.