# Effect of Relative Hormone Concentration on Auxin-Gibberellin Interaction in Correlative Inhibition of Axillary Buds

## I. D. J. Phillips

Department of Biological Sciences, Exeter University, Exeter Devon, U.K.

Received August 22, 1970

Summary. Indole-3-acetic acid (IAA) applied to the fully elongated second internode of decapitated *Phaseolus multiflorus* plants always inhibited axillary bud elongation at concentrations down to 100 µg/g lanolin, whereas gibberellic acid (GA<sub>3</sub>) enhanced bud elongation at concentrations down to 1000 µg/g lanolin. Lower concentrations than these of either IAA or GA<sub>3</sub> were without significant effect. All possible combinations of IAA and GA<sub>3</sub> within the concentration range 10<sup>1</sup> to 10<sup>5</sup> µg/g lanolin were antagonistic; IAA tending to inhibit, and GA<sub>3</sub> promote, axillary bud elongation growth. Treatment of an elongating internode with the hormones resulted in an increase in inhibition of bud growth by IAA in the presence of GA<sub>3</sub>.

#### Introduction

Application of auxin to the stem top in decapitated plants usually delays the outgrowth of axillary buds which normally occurs following excision of the apical bud. It has, nevertheless, been frequently observed that even relatively high concentrations of exogenous auxin do not completely substitute for the inhibitory influence of the apical bud over the axillaries (see Phillips, 1969a). Because the apical bud is a principal site of synthesis of gibberellins (Jones and Phillips, 1966) as well as auxin (Jacobs, 1962), the possibility that gibberellins in addition to auxin may participate in maintenance of correlative bud inhibition has already been explored. Apparently contradictory results have, however, been obtained in separate studies. For example, some workers have observed that the simultaneous addition of gibberellic acid (GA<sub>3</sub>) along with indole-3-acetic acid (IAA) resulted in a reduction of the inhibitory effect of IAA (Kato, 1958; Wickson and Thimann, 1958; Nakamura, 1965; Phillips, 1969b; Hillman, 1970), whereas others found that  $GA_3$  enhanced the inhibitory influence of IAA (Jacobs and Case, 1965; Scott, Case and Jacobs, 1967; Catalano and Hill, 1969).

Several possible reasons for these contrasting results may be seen, including variations in cultural conditions, species studied, age of treated plants, level of decapitation below the apical bud, and concentrations of applied hormones. The experiments reported in this paper investigated the interaction between IAA and  $GA_3$ , using all possible combinations of the two at widely varying concentrations, when the substances were applied in hydrous lanolin to the cut surface of a mature internode in runner bean plants grown in a glasshouse under conditions of full mineral nutrition. Runner bean was chosen as it has been found previously that in this species IAA alone is less able to control axillary bud elongation than is the case in several other species (Phillips, 1969b). The effect of changing the relative concentrations of exogenous IAA and  $GA_3$  in apical dominance phenomena have not been adequately studied previously. Scott *et al.* (1967) did examine the effects of a limited range of concentrations, but varied only the IAA concentration between 0.1 and 10 per cent with a constant 1 per cent  $GA_3$ .

The selection of a point of decapitation in a mature internode was made to remove the possible complication of differential elongation of the internode in the various treatments. It is recognised, however, that compensatory growth relationships between decapitated internode and axillary buds may be of particular significance in correlative bud inhibition (Jacobs and Bullwinkel, 1953; Scott *et al.*, 1967; Phillips, 1968), but the complex relationships between hormone treatment, internode age, and growth in internodes and in axillary buds of *Phaseolus multiflorus* will be reported elsewhere (Phillips, in preparation).

## **Materials and Methods**

Phaseolus multiflorus c.v. Scarlet Emperor plants were grown for 14 days in a glasshouse in pots of John Innes compost No. 2. At this time plants were selected which had attained a second internode length, above the primary leaf pair, of at least 15 cm. Decapitation was carried out at a point approximately 3 cm above the first node bearing the primary leaves.

Weighed quantities of IAA and  $GA_3$  were dissolved in a small volume of methanol, and the solution then rigorously dispersed by beating into a known weight of hydrous lanolin. Lanolin preparations were injected into gelatine half-capsules, and these were then used to cap the cut ends of stems. Decapitated plants not treated with hormone were capped with half-capsules containing plain hydrous lanolin (P.L.).

The two axillary buds of the primary leaves were measured to the nearest millimetre at the start of each experiment, and each day for four subsequent days. Sixteen plants were used in each treatment, and mean bud length for the thirty-two axillary buds was determined each day. Analyses of variance were carried out on the fourth day measurements, and treatment means compared by the Q test method (Snedecor, 1962).

#### Results

The independent effects of a range of concentrations of IAA (Fig. 1) and of  $GA_3$  (Fig. 2) on bud elongation in decapitated plants were tested. A satisfactory quantitative response to IAA was seen after two days



Fig. 1. Effect of IAA concentration on degree of inhibition of axillary bud elongation. IAA applied to cut stem of mature internode 3 cm above buds. Results expressed both in relation to decapitated plants treated with plain lanolin (A) and to intact control plants (B)



Fig. 2. Effect of decapitation and  $GA_3$  treatment of mature decapitated internode on axillary bud elongation over four days. Results expressed as percentage of mean bud length in intact control plants. All treatments significantly greater than intact control after 2 days.  $GA_3$  at 10<sup>5</sup> and 10<sup>4</sup> µg/g significantly greater than plain lanolin decapitated control (*PL*) after 3 days

where bud elongation in the IAA treatment was compared with that in decapitated P. L. controls (Fig. 1, lines A). Up to two days it was still apparent that the lower IAA concentrations had less inhibitory effect



Fig. 3. Effect of  $GA_3$  treatment of mature decapitated internode on axillary bud elongation in the presence of  $10^5 \ \mu g/g$  IAA. (*P.L.* bud length in decapitated plants treated with plain lanolin. IAA bud length in decapitated plants treated with  $10^5 \ \mu g/g$  IAA in the absence of any  $GA_3$ ).



Fig. 4. As Fig. 3, except IAA at  $10^4\,\mu\text{g/g}$ 

than did the higher concentrations. When the comparison was made with buds on intact control plants (Fig. 1, lines B), less linearity of response to IAA concentration was seen but, nevertheless, the lower IAA concentrations were less effective than the higher in maintaining buds in an inhibited condition. No indication was seen of stimulated bud elongation by even very low concentrations of IAA. This contrasts with the findings of Šebánek (1966) but agrees with those of Scott and Pritchard (1968).

The response to  $GA_3$  was, essentially, the opposite to that elicited by IAA. Higher concentrations of  $GA_3$  (10<sup>3</sup> to 10<sup>5</sup>  $\mu$ g/g) enhanced axillary



Fig. 5. As Fig. 3, except IAA at  $10^3 \mu g/g$ 



Fig. 6. As Fig. 3, except IAA at  $10^2 \,\mu g/g$ 

bud elongation to a level greater than that seen in the P.L. controls, and the lower concentrations (10<sup>1</sup> and 10<sup>2</sup>  $\mu$ g/g) had no significant influence on bud elongation (Fig. 2). Thus, a valid basis existed for a study of the interaction between concentrations of IAA and GA<sub>3</sub> over the range 10<sup>5</sup> to 10<sup>1</sup>  $\mu$ g/g.

Owing to the large numbers of plants involved and individual measurements necessary, the interaction between IAA and  $GA_3$  was studied



Fig. 7. As Fig. 3, except IAA at  $10^1 \,\mu\text{g/g}$ 

in separate experiments at weekly intervals over a total period of six weeks. Despite this, good consistency of results was obtained (Figs. 3 to 7). The inhibitory effect of even the highest IAA concentration  $(10^5 \,\mu g/g)$  was largely overcome by the simultaneous addition of  $10^5 \,\mu g/g$ GA<sub>3</sub>, but GA<sub>3</sub> concentrations of  $10^3 \,\mu g/g$  and below did not significantly affect the action of  $10^5 \,\mu g/g$  IAA (Fig. 3). Decreasing the IAA concentration to  $10^4 \,\mu g/g$  resulted in the stimulatory effect of GA<sub>3</sub> becoming more apparent, for the buds on decapitated plants treated with  $10^5 \,\mu g/g$  GA<sub>3</sub> in addition to  $10^4 \,\mu g/g$  IAA elongated more than buds of the P. L. controls (Fig. 4). The antagonistic effects of IAA and GA<sub>3</sub> on bud elongation became even more obvious when the IAA concentration was reduced progressively to  $10^3$ ,  $10^2$  and  $10^1 \,\mu g/g$  (Figs. 5 to 7), and at these lower concentrations of IAA the pattern of response to GA<sub>3</sub> concentrations was almost identical to that produced by the same GA<sub>3</sub> concentrations in the absence of IAA (compare Figs. 5 to 7 with Fig. 2).

### Discussion

These results show clearly that regardless of relative concentration,  $GA_3$  always antagonises the inhibitory effect of IAA on axillary bud elongation when both hormones are applied to the cut surface of a region of internode which has finished elongating. This confirms results for two tall and two dwarf species presented earlier, but which were obtained using only one concentration of IAA and  $GA_3$  (Phillips, 1969b). Superficially, therefore, these results are contradictory to the demonstration

that GA<sub>3</sub> increases the inhibitory effect of IAA (Jacobs and Case, 1965; Scott et al., 1967; Catalano and Hill, 1969). However, I have found in other experiments (Phillips, in preparation) that GA<sub>3</sub> can indeed enhance, rather than antagonise, IAA-induced inhibition of axillary bud growth in runner bean, but only when the treated internode has not completed its phase of elongation growth. This observation is in accord with the results of Scott et al. (1967), who noted a negative correlation between internode and bud extension growth in Pisum sativum. On the other hand, Jacobs and Case (1965) found that GA<sub>2</sub> enhanced the inhibitory influence of IAA in experiments where the treated internode did not elongate in any of the treatments, and also that GA<sub>3</sub> caused more IAA-<sup>14</sup>C to be distributed down the stem. These workers consequently concluded that enhanced auxin-induced bud inhibition in the presence of  $GA_3$  is due to an effect on auxin uptake and/or transport down the stem. If this is the case, then it is difficult to understand why similar results were not obtained in the experiments reported in the present paper or in those of Phillips (1969b), for one may have expected that the lower concentrations of IAA would have become more inhibitory, and not less, by the addition of GA<sub>a</sub>.

It is clear that a more detailed analysis of the effects of exogenous IAA and  $GA_3$  on both internode and bud growth is required before conclusions can be drawn as to the role of apically-synthesised gibberellin in in correlative bud inhibition. This will be presented later (Phillips, in preparation).

The author is grateful to Mr. John Havell for technical assistance.

## References

- Catalano, M., Hill, T. A.: Interaction between gibberellic acid and kinetin in overcoming apical dominance, natural and induced by 1 AA, in tomato (*Lycopersicum esculentum* Mill. Cultivar Potentate). Nature (Lond.) 222, 985–986 (1969).
- Hillman, J.: The hormonal regulation of bud outgrowth in *Phaseolus vulgaris* L. Planta (Berl.) **90**, 222-229 (1970).
- Jacobs, W. P.: Longevity of plant organs: Internal factors controlling abscission. Ann. Rev. Plant Physiol. 13, 403-436 (1962).
- Bullwinkel, B.: Compensatory growth in *Coleus* shoots. Amer. J. Bot. 40,385–392 (1953).
- Case, D. B.: Auxin transport, gibberellin and apical dominance. Science 148, 1729-1731 (1965).
- Jones, R. L., Phillips, I. D. J.: Organs of gibberellin synthesis in light-grown sunflower plants. Plant Physiol. 41, 1381–1386 (1966).
- Kato, J.: Studies on the physiological effect of gibberellin: II. On the interaction of gibberellin with auxins and growth inhibitors. Physiol. Plantarum (Cph.) 11, 10–15 (1958).
- Nakamura, E.: Studies on the branching in *Pisum sativum* L. Special Report of the Laboratory of Horticulture, Shiga Agric. Coll., Japan (1965).

3 Planta (Berl.), Bd. 96

- Phillips, I. D. J.: Nitrogen, phosphorus and potassium distribution in relation to apical dominance in dwarf bean (*Phaseolus vulgaris* c.v. Canadian Wonder). J. exp. Bot. 19, 617-627 (1968).
- Apical dominance. In: The physiology of plant growth and development, p. 163-202 (M. B. Wilkins, ed.). London: McGraw-Hill 1969a.
- Auxin-gibberellin interaction in apical dominance: Experiments with tall and dwarf varieties of pea and bean. Planta (Berl.) 86, 315-323 (1969b).
- Factors influencing the distribution of growth between stem and axillary buds in decapitated bean plants (in preparation).
- Scott, T. K., Case, D. B., Jacobs, W. P.: Auxin-gibberellin interaction in apical dominance. Plant Physiol. 42, 1329–1333 (1967).
- Pritchard, J. B.: The control of apical dominance in the Alaska pea. In: transport of plant hormones, p. 309–319. Amsterdam: North-Holland Publ. Comp. 1968.
- Šebánek, J.: Investigation of apical dominance in pea seedlings by means of <sup>32</sup>P transport. Acta Univ. Agr. (Brno) A. 4, 587–596 (1966).

Snedecor, G. W.: Statistical methods. Iowa: State Univ. Press 1962.

Wickson, M. E., Thimann, K. V.: The antagonism of auxin and kinetin in apical dominance. Physiol. Plantarum (Cph.) 11, 62-74 (1958).

Dr. I. D. J. Phillips Department Biological Sciences Perry Road Exeter EX4 4QG, England