AN EFFECT OF GIBBERELLIC ACID ON CIRCUMNUTATION

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(With 2 figures in the text)

Summary

Gibberellic acid causes a marked increase in the amplitude of circumnutation in dwarf pea seedlings. The effect may be detected within 12 hours from the time of treatment. The relation was investigated between the time at which this effect occurred and the time at which increased growth of the shoot was detected.

Introduction

The spontaneous movements executed by the apex of a growing plant presumably reflect differences in the rate of elongation of cells in various parts of the young stem. These movements, named 'revolving nutations' by Sachs (1875) and 'circumnutation' by Darwin (1880), have received little attention from plant physiologists during the last 60 years or so, even though cell elongation has been extensively studied. Sachs (1875) suggested a close relationship between straight growth and circumnutation, and the following experiments were carried out to discover whether the growth substance gibberellic acid (GA), known to promote the rates of stem elongation in many plants, will also bring about an increase in the rate of circumnutation.

Brian and Hemming (1955) demonstrated that GA stimulates markedly shoot elongation in pea seedlings belonging to certain genetically dwarfed varieties. Seedlings belonging to one of these varieties were chosen for the following investigation. Brian and Hemming found that doses of GA in the range 0.01 to 10.24 μg per plant produced similar initial effects upon elongation, but the effect of the larger doses was more prolonged.

Materials and methods

Seeds of the commercial dwarf-pea variety 'Meteor' were sown in John Innes No. 2 compost held in six-inch-diameter pots, five seeds per pot. Seedlings were raised in a greenhouse under natural day-length until the leaves at node 5 were almost fully expanded, some 16 days after sowing. (The node of the cotyledons is counted as node 1.) The plants were selected for uniformity, reduced in number to one per pot, and transferred to the laboratory. There they remained for the duration of the experiment under a régime of continuous light provided by a bank of four 'warm-white' fluorescent tubes supported 35 cm above the pots.

GA was obtained from L. Light and Co., Ltd.

The method used to observe the circumnutation of each plant was essentially that described by Darwin (1880). A piece of glass capillary 3 to 4 cm long was threaded through a small triangle of paper and slipped between the apical region of the plant and the enclosing stipule of a very young leaf. A glass plate was supported several centimetres above the plant, and the position of the apex was recorded from time to time by sighting down the length of the capillary against the piece of paper and placing a mark with a grease pencil where the line of sight passed through the glass. Successive dots, linked by lines, gave an indication of the movements of the apex, magnified by a factor which depended on the distance between the plant and glass plate. The lights were removed from above the plants while records were being taken.

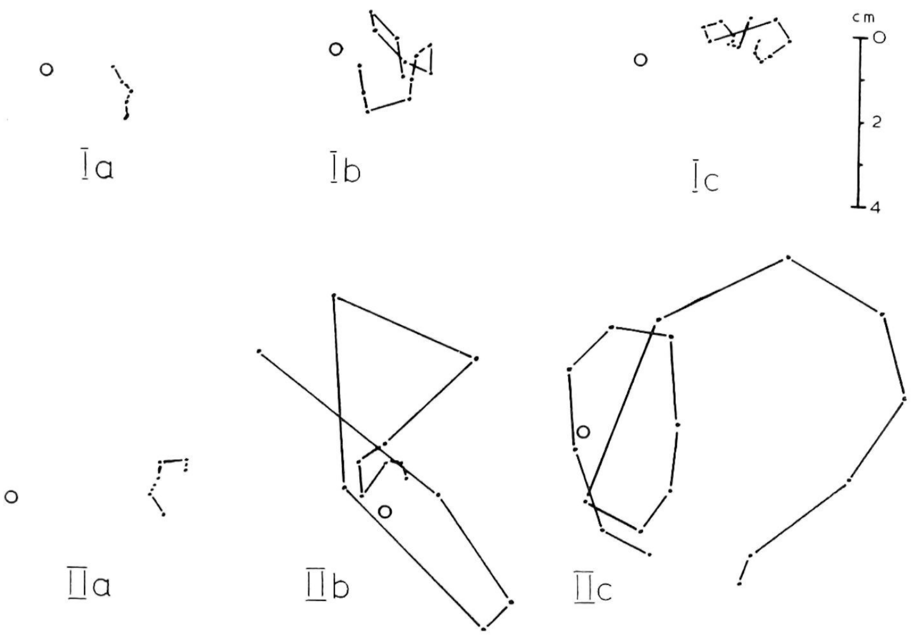

Fig. 1. The circumnutation of the apices of two pea seedlings, drawn upon a glass plate supported 6 cm above the apices. I. Untreated plant. II. Plant treated with 20 μg GA. Movements recorded (*a*) during 3.5 hours preceding treatment, (*b*) 17.5 to 24 hours after treatment, and (*c*) 41.5 to 47.25 hours after treatment. In each case the small circle indicates a point directly above the axis of the plant.

The straight growth of other plants was measured with the aid of a lever and a revolving smoked paper cylinder. A thin wire was looped around a very young internode below the apex of a plant and attached to the lever. The lever was supported by a knife edge, positioned for most experiments 8 cm from the point of attachment to the plant, and 40 cm from the other end of the lever, which was sharpened so as to scratch the smoked paper. A weight was attached to the lever in such a position that the sharpened end would fall gently if unsupported. The smoked cylinder was turned by an electric motor once every 20 minutes, so that the growth of the plant was recorded as a spiral line of very low pitch. After an experiment the paper cylinder was cut down one side, dipped in varnish, and the distances between the start and successive turns of the spiral measured with a travelling microscope.

GA was applied in 4 μl droplets of either absolute or 50% ethanol to a leaflet at node 5. Control plants were treated with a similar volume of solvent, but no GA.

Results

In one experiment the circumnutation of eight untreated plants was observed for several hours, and then four of the plants were treated with 20 µg of GA each. Observations were made during the next 2 days, and a marked increase in the circumnutation of the GA-treated plants could be detected (Fig. 1). On other occasions plants were treated with 5 µg of GA each, and similar increases in circumnutation were observed. The effect was in all cases one of increased amplitude of movement, without any obvious change in the number of revolutions. In all cases the GA-treated plants were found to be circumnutating more rapidly than the controls 12 hours after GA treatment, but because of the erratic nature of circumnutation it was not possible to estimate the onset of the effect accurately.

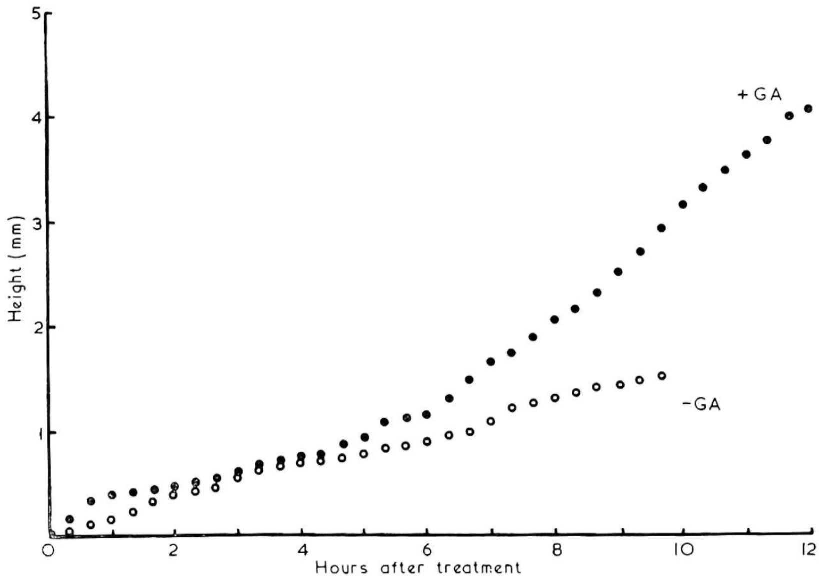

Fig. 2. Increases in the heights of two pea seedlings, one untreated, and the other treated with 5 µg of GA. Note the change in slope of the curve for the GA-treated seedling 5 to 6.5 hours after treatment.

In contrast, the time of the initial effect of GA on straight growth could be detected with some precision, as treatment brought about a change in the slope of a curve showing increase in stem length plotted against time (Fig. 2). Similar curves for the control plants did not show this discontinuity. The time intervals which elapsed between the time of treatment and the discontinuity were found to differ from 3 to 17 hours in different experiments. (The factors affecting this time interval are under investigation.) It is clear, however, that increases in straight growth and circumnutation take place about the same time after GA treatment.

Discussion

The increased amplitude of circumnutation observed after GA treatment is presumably merely an exaggeration of normal circumnutation. This strongly suggests that the GA brings about more rapid cell elongation in the expanding internodes, but does not determine which cells are to expand. It is conceivable that the pattern of circumnutation is defined by a control of the transport of endogenous and applied GA, but it is difficult to imagine how such a control could be imposed. As the stem does not bend to one side and remain there after GA treatment, it seems unlikely that there is a barrier to the lateral transport of gibberellin; and as a new growth rate is established within 1-2 hours after an effect upon straight growth has been initiated by applied GA, it seems that the GA invades fully its site of action within this time. Growth substances other than gibberellins are undoubtedly necessary for cell expansion, and it is possible that another substance arrives spasmodically in the elongating tissue. But again, it is difficult to envisage a mechanism for this. On the whole, it seems more satisfactory to suggest that the pattern of circumnutation is determined by endogenous differences between groups of cells, while the magnitude and rate of cell expansion is controlled by growth-regulating substances, including the gibberellins, which may derive from other regions of the plant.

After this paper had been accepted for publication, it was pointed out to the author that the effect of GA on the circumnutation of *Zinnia*, *Phaseolus* and *Lactuca* has been studied in France. Increased amplitude of movement was one of the effects observed in each case (Tronchet, 1960; Tronchet, Tronchet and Perney, 1960; Tronchet and Marchal, 1960; and Baillaud and Monnier, 1960). Darwin (1875, 1880) pointed out that circumnutation takes place with greater amplitude in climbing plants than in none-climbers, and so these observations form a further link between gibberellin and the climbing habit (Brian, Elson, Hemming and Radley, 1954; Lona, Bocchi, Borghi and Peri, 1956; Bukovac and Wittwer, 1956; and Brian and Grove, 1957).

Acknowledgment

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