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Effects of Light Quality on Apical Dominance in *Xanthium strumarium* and the Associated Changes in Endogenous Levels of Abscisic Acid and Cytokinins

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Summary. Apical dominance in *Xanthium strumarium* was influenced by the quality of illumination received at the end of the photoperiod. The involvement of the red/far-red regions of the spectrum was apparent. The persistence of the effects was partially dependent on the age of the individual buds concerned. Plants receiving 30 minutes of illumination from tungsten lamps after a 16-hour photoperiod from fluorescent tubes failed to branch, whereas plants given an identical photoperiod, both in terms of day-length and photosynthetically available light energy, but lacking the far-red from tungsten lamps, branched profusely.

The influence of the spectral distribution of illumination on the levels of cytokinins and abscisic acid in the plant, and the correlation with the degree of branching, is presented and discussed. The cytokinin content was much higher in inhibited than released buds. The cytokinins present were probably not able to participate in bud growth because of an accumulation of inhibitors resembling abscisic acid. The concentration of the inhibitors in inhibited buds was 50 to 250 times that occurring in all other plant parts examined.

Introduction

Apical dominance in the shoots of herbaceous plants is manifest by almost complete correlative inhibition of axillary bud outgrowth by the presence of an intact apex. The nature of the mechanism is still not fully understood, though there are several extant hypotheses which have been fully reviewed by Phillips (1969). The degree of uncertainty surrounding these is such that Shein and Jackson (1971) have recently expressed strong doubts about all of them.

Most of our knowledge of apical dominance has arisen from experiments involving either or both of two procedures: (i) some degree of surgery on the plant, the most frequent being removal of the apex, and (ii) exogenous application of natural or synthetic hormones, either singly or in combination. Much valuable information has come from studies of this kind, but cautious interpretation has been necessary in view of the uncertainty about complications resulting from surgery,

and doubts about which are the correct sites for exogenous application of hormones. In spite of these difficulties, the importance of at least four of the known groups of plant growth regulators has been indicated. Auxin has been known for some time to be involved, evidenced by the fact that decapitation usually releases some lateral buds from correlative inhibition, dominance being reimposed by auxin application to the cut stump (Thimann and Skoog, 1933). Application of kinetin to the meristems of axillary buds can release them from correlative inhibition (Sachs and Thimann, 1964, 1967). In all cases of bud release by kinetin, however, outgrowth was short-lived unless auxin was directly supplied to the outgrowing kinetin-treated buds. Gibberellic acid (GA_3) has been found in some cases to enhance lateral bud growth (Kato, 1958, Nakamura, 1965) and in other cases it enhances apical dominance (Brian *et al.*, 1959). Phillips (1971) has clarified the role of exogenously applied GA_3, showing that it can be a modifying factor in auxin-regulated apical dominance. He suggests that gibberellin synthesized in the apex normally stimulates growth in elongating internodes and may not reach the axillary buds. If, however, there is excess gibberellin it may reach the buds and enhance their growth.

The precise role of growth inhibitors is uncertain, though their involvement in apical dominance is indicated by recent work. Axillary buds subject to correlative inhibition have been shown to contain higher concentrations of growth inhibitors than those released from apical dominance (Dörffling, 1966). Arney and Mitchell (1969) found that abscisic acid (ABA) applied to decapitated pea plants could achieve inhibition of lateral bud outgrowth comparable to that produced by the intact apex, but Hillman (1970) found that ABA alone promoted bud outgrowth slightly in *Phaseolus*. He did, however, find that ABA interacted with auxin and GA_3 to give inhibition almost comparable to that of the apex itself. Shein and Jackson (1971) have supported the view that the mechanism of apical dominance depends on an interaction between hormones, but unfortunately ABA was not included in their investigation.

Our understanding of the mechanism of correlative inhibition might be improved if changes in the degree of apical dominance could be conveniently achieved without any degree of plant surgery or exogenous application of hormones. It would then be possible to follow the changes in endogenous hormone levels during release from correlative inhibition. A change in environmental conditions would be a possible way of altering the degree of apical dominance. Light intensity, supply of mineral nutrients, and water stress are among factors which are known to affect the growth of lateral shoots, but none of these would be entirely suitable for the present purpose since they are all likely to cause changes

in the supply of major metabolites such as carbohydrates and amino acids. Light quality has been noticed in the past to affect apical dominance in a few plants. If the degree of branching could be altered with a small change in light quality not involving any alteration in the amount of light available for photosynthesis, this would be a more acceptable approach. The first part of this paper describes how such a change in the photoenvironment can affect branching in *Xanthium strumarium*, and in the second part the associated changes in the levels of some hormones are presented and discussed.

Material and Methods

Plants of *Xanthium strumarium* L. were raised from seed and grown under strictly controlled conditions of lighting and temperature in growth cabinets. Two different illumination treatments were used throughout the investigation, both consisting of a photoperiod long enough to ensure that no flowering was induced. In the first treatment the plants received 16 hours of illumination from "daylight" fluorescent tubes (intensity 4.50×10^4 mJ cm^{-2} s^{-1}) followed by 30 minutes from tungsten filament lamps (intensity 7.09×10^3 mJ cm^{-2} s^{-1}). In the second treatment, illumination from daylight fluorescent tubes continued for the entire 16.5 hours of the photoperiod, the intensity being the same as in the first treatment apart from the final 30 minutes when it was adjusted so that the number of quanta received was the same. Light from tungsten lamps is rich in radiation of the far-red (FR) region (700–750 nm), whereas light from daylight fluorescent tubes contains virtually no FR. The two treatments are subsequently called + FR and − FR. Throughout the experiments the day temperature was 25° C and the night temperature 15° C. The relative humidity was 50–60 per cent.

From the plants in each treatment the axillary buds, leaves and apical buds (including the three youngest leaves) were extracted and analysed for the presence of cytokinins and abscisic acid. Cytokinins were extracted using the method outlined by Letham and Williams (1969) and assayed using the method of Kende (1964). This depends on the capacity of the extracts to retard chlorophyll degradation in sections of barley leaves, and is virtually specific to cytokinins (Letham, 1967). The results obtained using this assay were checked by means of the soybean callus assay (Miller, 1963). Inhibitors resembling ABA were extracted using the method of Mizrahi *et al.* (1970) and assayed using the method of Tucker and Mansfield (1971) which is not subject to interference from other growth hormones.

Results

There was a significant difference in mean bud length between plants grown under the two illumination treatments. A deficiency of far-red led to bud elongation and the formation of visible leaves, an effect being first evident after 21 days and becoming increasingly apparent with time (Fig. 1). The short period of far-red at the end of the photoperiod prevented any major expansion and the majority of the buds did not reach a length greater than 5 mm.

Experiments involving the transfer of plants from one illumination treatment to the other suggested that there was a critical age beyond

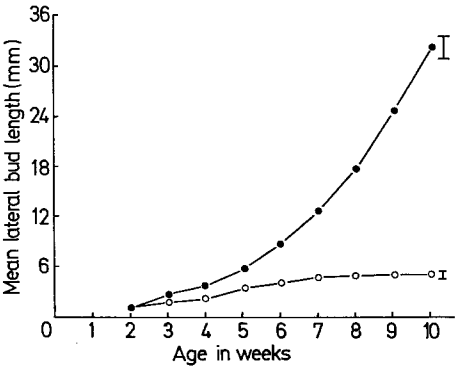

Fig. 1. Lateral bud length in *Xanthium strumarium* as influenced by light quality at the end of the day. Mean bud lengths from eight replicate plants. The vertical bars represent the standard errors of the means. • — FR treatment; ∘ + FR treatment

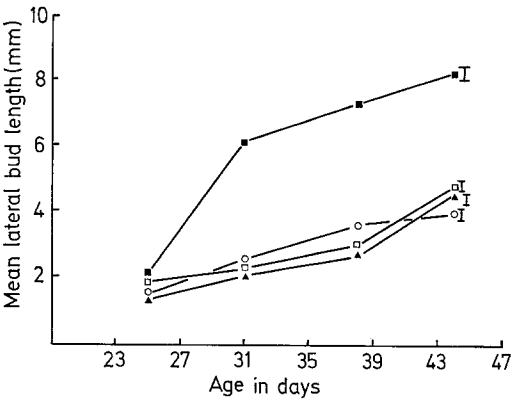

Fig. 2. Lateral bud length in *Xanthium strumarium* as influenced by light quality at the end of the day. Mean bud lengths from six replicate plants. All plants were grown initially in the +FR treatment. The vertical bars represent the standard errors of the means. ▪ plants transferred to —FR treatment after 25 days; ▫ plants transferred to —FR treatment after 31 days; ▲ plants transferred to —FR treatment after 39 days; ∘ +FR treatment throughout; ▪ differs significantly from all other treatments at $P < 0.05$

which bud growth could not be initiated by a deficiency of far-red light. A transfer from the +FR to the —FR treatment after 31 or more days was ineffective in causing bud elongation, whereas a similar transfer after 25 days led to a highly significant stimulation of bud growth (Fig. 2). Comparable experiments were performed with plants

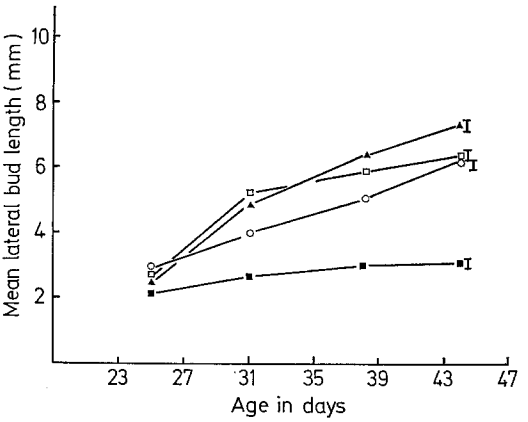

Fig. 3. Lateral bud length in *Xanthium strumarium* as influenced by light quality at the end of the day. Mean bud lengths from six replicate plants. All plants were grown initially in the −FR treatment. The vertical bars represent the standard errors of the means. ▪ plants transferred to +FR treatment after 25 days; ▫ plants transferred to +FR treatment after 31 days; ▲ plants transferred to +FR treatment after 39 days; ○ −FR treatment throughout; ▪ differs significantly from all other treatments at $P < 0.05$

grown in the −FR treatment initially and transferred to +FR at different times. Transfer on the 31st and 39th days failed to achieve any significant change in bud growth, but transfer on the 25th day was highly effective, further bud outgrowth being considerably reduced (Fig. 3). A repeat of these experiments, but with plants transferred at slightly earlier times, fully confirmed the results. Differences were, as might be anticipated, accentuated—for example, transfer from +FR to −FR after 23 days caused considerable elongation of axillary buds which soon formed expanded leaves, whereas plants grown in +FR throughout showed no signs of bud expansion.

The above results are based on measurements of the lengths of all the axillary buds on the plants, with the exception of those at the cotyledonary nodes. Additional information was provided by an examination of buds at individual nodes. Such an examination indicated that transfer from the +FR to the −FR treatment after 25 days or less led to a greater stimulation of bud outgrowth than a similar transfer made after 31 or 39 days. This difference was more pronounced at nodes 3–6 (nodes being numbered acropetally in sequence starting from the cotyledons), but nodes 7 and 8 which were barely initiated after 25 days did in fact respond to a change in light quality after 31 or more days. It thus appears that the stage of development of the individual

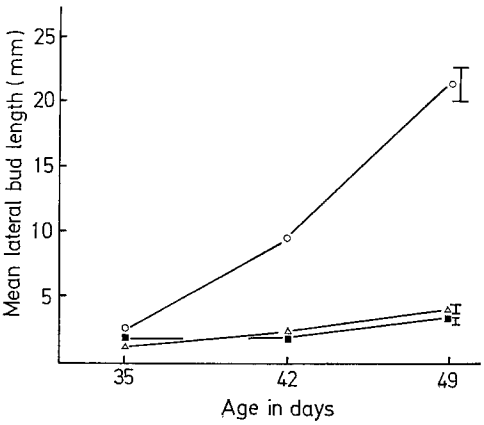

Fig. 4. Effect of removing the three youngest leaves on lateral bud growth in *Xanthium strumarium*. Mean bud lengths from twelve replicate plants. All plants were grown under the +FR treatment. Plants grown under a light source consisting of tungsten lamps only showed no bud outgrowth whether or not the young leaves were removed. The vertical bars represent the standard errors of the means. ○ 3 youngest leaves removed after 35 days; ■ apex only removed after 35 days; △ intact control plants

buds is a critical factor in the response to a change in illumination. It might be further suggested that this response is due to changes affecting individual axillary buds rather than being dependent on overall changes in the plant. However, previous workers have concluded that control over the growth of laterals in *Xanthium* emanates from the three youngest leaves, these being the primary source of inhibitors of axillary bud growth. McIlrath and Bogorad's (1960) finding that the removal of these leaves leads to bud outgrowth irrespective of the quality of the illumination received was, however, only partially confirmed in the present work. In the absence of the three leaves considerable axillary bud growth did develop under both the +FR and −FR treatments, but under a photoperiod of 16.5 hours with illumination from tungsten lamps only (3.6×10^4 mJ cm^{-2} s^{-1}), no growth of buds occurred whether or not the young leaves were removed (Fig. 4).

The above experiments demonstrate the ease with which it is possible to alter the amount of apical dominance in *Xanthium* with subtle changes in illumination. Associated hormone changes which might feasibly be investigated are the role of auxin or other compounds produced in the leaves, and the local changes in the buds themselves. In this initial study, attention has been paid to changes in cytokinins

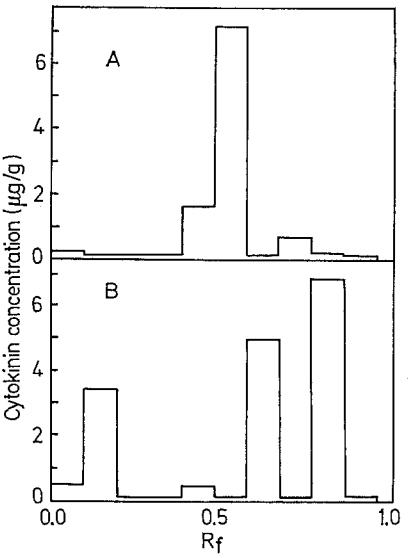

Fig. 5A and B. Chromatographic analysis of cytokinins from $8^1/_2$-week old plants of *Xanthium strumarium*. All plants were grown in the +FR treatment. A Outer part of inhibited lateral buds; B Central part of inhibited lateral buds

Table 1. *Cytokinin concentrations in plants of* Xanthium strumarium. *µg/g fresh weight of plant tissue*

	+FR		−FR	
	8 weeks old	9 weeks old	8 weeks old	9 weeks old
Apical buds and 3 young leaves	0.029	0.022	0.019	0.025
Axillary buds	0.357	7.320	0.064	0.018
Mature leaves	0.017	0.006	0.039	0.022

and abscisic acid, and the role of auxins and gibberellins will be examined in later work.

For the analysis of the levels of cytokinin-like compounds the plants were divided into three regions: (i) the shoot apex and three youngest leaves; (ii) the other leaves; (iii) the axillary buds. The highest cytokinin concentrations were found in the inhibited axillary buds of plants grown in the +FR treatment (Table 1). Eight weeks after germination there was a 6-fold difference in the level of cytokinins

Table 2a. *Abscisic acid concentrations* in 7-week old plants of* Xanthium strumarium. *µg/kg dry weight of plant tissue*

	+FR	−FR
Apical bud and 3 young leaves	247	<242
axillary buds	12220	193
Mature leaves	< 57	<66

Table 2b. *Abscisic acid concentrations* in 7-week old plants of* Xanthium strumarium *grown under a 16.5-hour photoperiod from tungsten lamps only. µg/kg dry weight of plant tissue*

Apical bud and 3 young leaves	306
Axillary buds	19174
Mature leaves	374

*ABA-like activity given as an equivalent ABA concentration

in the inhibited buds of the +FR treatment and the non-inhibited ones of the −FR treatment. The cytokinin level showed a 20-fold increase during the 9th week in the inhibited buds, whereas it declined to an even lower level as the buds in the −FR treatment continued to grow. Chromatographic analysis of extracts of inhibited buds on $8^1/_2$-week old plants showed the presence of at least three substances exhibiting cytokinin-like activity, differing in amounts between the outer part of the bud and the central part containing the meristematic region. The total cytokinin-like activity from the central part of the buds was higher than in the outer parts (Fig. 5).

Extraction and bioassay of ABA-like activity showed by far the greatest concentration to be in the inhibited buds (Table 2a). Measured on a dry weight basis, the amount was between 50 and 250 times those levels found in all the other parts examined in 7-week old plants.

Analysis of the inhibited axillary buds of plants of a comparable age grown under a 16.5 hour photoperiod with illumination provided only from tungsten lamps (intensity 3.6×10^4 mJ cm^{-2} s^{-1}) showed an even higher concentration of ABA, which was located almost entirely in the outer part of the bud (Table 2b).

Discussion

Apical dominance, like many other phenomena in plants, appears to be influenced by changes in the balance of red and far-red wavelengths. Although the importance of these spectral regions in this

connection has been noticed by several investigators in the past, this has often been in the context of some other investigation, for example into the mechanism of flowering. Studies in relation to apical dominance alone are few. Meijer (1957) showed that the development of laterals in *Salvia occidentalis* was more or less inhibited when the plants were grown in infra-red radiation. More recently Kasperbauer (1971) demonstrated that branching in *Nicotiana tabacum* occurred from the axils of lower leaves on red-irradiated plants, but no branches developed on plants that received far-red light at the end of each photoperiod. Several workers, e.g. Khan (1963), Seckbach (1965) have noted that branching is considerable when *Xanthium strumarium* is grown under fluorescent lights, but under tungsten filament lamps branching is weak or absent. They also found that branching was prevented by as little as 15 minutes of far-red light given after 20-hour photoperiods, which do not induce flowering in *Xanthium*.

Borthwick *et al.* (1952) reported that exposure to far-red light prior to the dark period shortened the length of the critical night for flowering in *Xanthium*. According to Salisbury (1969) this experiment "could never be repeated in the Beltsville laboratory nor anywhere else". Some of the present experiments resembled the treatment supposed to shorten the critical night length, and flowering was never observed. Flowering in *Xanthium* is accompanied by a loss of apical dominance, but the phenomena reported here were unaccompanied by the characteristic changes in the apex associated with flowering.

It is thus possible that control of apical dominance by light quality, quite independent of flowering, is of widespread occurrence. Kasperbauer (1971) noted the lack of branching at the lower nodes of a field of tobacco plants, which he attributed to the increased far-red content of the illumination lower in the canopy due to selective filtering of radiation in the red part of the spectrum by the overlying leaves. Field observation shows the same pattern in *Chenopodium album* and *Polygonum persicaria*, both of which show a lack of lateral growth when in a closed community, but branch profusely in open ground. A reponse of this kind to a balance of wavelengths thus has considerable ecological implications.

In previous work importance has been attached to the presence of growth inhibitors in the leaves of *Xanthium* (Bonde, 1953, Bonde and Khudairi, 1954, Geissman, 1962, Geissman and Deuel, 1957). As noted earlier, McIlrath and Bogorad (1960) considered that the inhibition of lateral bud growth came primarily from the three youngest leaves.

Xanthatin (Little *et al.*, 1950) and xanthinin (Geissman *et al.*, 1954) are two growth inhibitors found in leaves of *Xanthium*. Khan (1963) considered that their concentration was inversely correlated with the

degree of branching. He showed that xanthatin was restricted entirely to the young leaves and that xanthinin was of more general distribution throughout the plant. Seckbach (1965) found that the activity of xanthinin deacylase, an enzyme which catalyses the hydrolysis of xanthinin to xanthatin and acetate, did not appear to be closely correlated with branching. He also found that the inhibitory effect of applying xanthinin and xanthatin to leaves could be duplicated by auxin. Thus the significance of xanthinin and xanthatin in apical dominance in this species is uncertain; the present study and that of Seckbach suggest that several better known growth substances might play a major part. The effect of removal of young leaves, which are major sinks for metabolites and some hormones, and probable sources of auxin, cannot unquestionably be attributed to changes in the supply of xanthinin and xanthatin.

It is probable that control of lateral branching is achieved by changes in the balance of hormones within the plant. Antagonisms and synergisms have been shown to exist between groups of growth regulating substances, changes in their relative concentrations influencing growth expression (Letham, 1967). Recent work on apical dominance, for example that of Hillman (1970), has stressed the importance of hormone interactions.

In this study we have examined only the levels of two hormones, the cytokinins and ABA. Very high concentrations of cytokinins were found in inhibited buds, and it is possible that their localization was unfavourable for bud growth. It was, however, shown (Fig. 5) that more cytokinin activity was present in the central as opposed to the outer part of the buds. The data suggest that the cytokinin level in the inhibited buds increases with age, and it thus seems unlikely that availability of these hormones is the limiting factor. An alternative view is that bud growth is limited by the high levels of ABA. The lack of axillary bud outgrowth following removal of the three youngest leaves from plants grown entirely in tungsten illumination might be explained by the increased levels of ABA (Table 2b).

We were not able to measure the changes in gibberellin content together with those of cytokinins and ABA. Reid *et al.* (1968) showed that there was an increase in gibberellin synthesis in leaves of barley after subjection to red light. Lockhart (1964) postulated the movement of a precursor of gibberellin from the apex and young leaves to the elongating region of the stem, its conversion to "active" gibberellin being prevented by red and promoted by far-red radiation. Gibberellin is known to act as an antagonist of ABA in apical dominance (Jacobs *et al.*, 1967), and so for a full understanding of the situation a knowledge of changes in amounts of gibberellin would be necessary. The data do clearly indicate, however, that ABA synthesis or accumulation is

also influenced by the quality of illumination. Judging from the wavelengths that we have found to be effective, the control is brought about through the phytochrome system. This system is clearly of major importance in determining the distribution of hormones in plants. The similarity of the effects of kinetin and red light are well-documented. Fletcher and Zalik (1964) showed that the IAA content of *Phaseolus vulgaris* decreased with red light treatment, but red light contaminated with far-red increased the IAA content. A single physiological response to light quality, like the one reported here, could thus be the result of a very complex interaction between all the major growth hormones.

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