CHANGES IN ENDOGENOUS GROWTH REGULATOR LEVELS AND BRANCHING RESPONSES OF SOYBEAN TO LIGHT QUALITY ALTERED BY VELVETLEAF (ABUTILON THEOPHRASTI MEDIK.)

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CHANGES IN ENDOGENOUS GROWTH REGULATOR LEVELS AND BRANCHING RESPONSES OF SOYBEAN TO LIGHT QUALITY ALTERED BY VELVETLEAF (*ABUTILON THEOPHRASTI* MEDIK.)*

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BEGONIA G. B. and ALDRICH R. J. *Changes in endogenous growth regulator levels and branching responses of soybean to light quality altered by velvetleaf* (Abutilon theophrasti *Medik.*). BIOTRONICS **19**, 7–18, 1990. Lateral branching of soybean is considered a major contribution of additional fruiting sites for high yields. The present study was conducted to expand our understanding of how lateral bud development in soybean is reduced by early-season velvetleaf interference. Our results suggested that the significantly higher levels of endogenous indole-3-acetic acid (IAA) at the terminal buds and internodes of soybeans, when exposed to shadelight of low red: far-red ratio (R: FR), induced an increased synthesis of abscisic acid (ABA) in the axillary buds. The elevated amount of ABA in turn was responsible for the suppression of axillary bud outgrowth (branching). Zeatin riboside, a major cytokinin in soybean, did not appear to play a significant role in the release of soybean lateral buds from low R: FR-induced apical dominance.

Key words: light quality; *Abutilon theophrasti* Medik.; indoleacetic acid; abscisic acid; cytokinin; branching; apical dominance.

INTRODUCTION

Due to preferential absorption of red and blue light by chlorophyll and carotenoid pigments and almost total transmission of far-red light by leaves (*10*, *12*, *28*), canopies serve as selective absorption filters. Plants growing beneath or within them are subjected to a high proportion of light in the far-red wavelength.

Considerable evidence suggest that a modified spectral quality (low R: FR ratio; the ratio of photon fluence rates in 10 nm bandwidths centered on 660 and 730 nm) plays a major role in the mechanisms controlling morphological development.

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The most conspicuous developmental response to low R: FR is a marked increase in stem elongation rate (*11*, *18*, *19*) and a concomitant reduction in branching. Similar studies linking far-red light enhancement of apical dominance and consequent suppression of axillary bud outgrowth have been demonstrated in tobacco (*Nicotiana tabacum* L.) (*12*), pea (*Pisum sativum* L.) seedlings (*14*), tomato (*Lycopersicon esculentum* Mill.) seedlings (*24*), common lambsquarters (*Chenopodium album* L.) (*2*), and young (21-day old) soybean (*Glycine max* (L.) Merr.) (*13*). Light interference studies with velvetleaf (*Abutilon theophrasti* Medik.) of various canopy heights and duration revealed significantly reduced branching in velvetleaf-shaded soybeans (*20*). Using broad band-pass acetate filters to simulate the effects of red or far-red light on soybean, recent investigations (*1*) demonstrated that far-red light substantially diminished the production of fruiting branches. Due to significant positive correlation between branching and soybean yield (*3*, *20*), it is imperative that the light quality existing under canopies of velvetleaf-shaded soybeans be characterized in detail using spectroradiometry.

Early studies indicated that red light treatments led to a low indole-3-acetic acid (IAA) content in *Phaseolus vulgaris* L., however, if the red light was contaminated by far-red light, the IAA content was increased (*7*). The same investigators (*8*) attributed this to a stimulation of IAA conversion to indol-3yl-aldehyde more readily in red than in far-red light. Later studies involving the responses of several crops to light quality, both under controlled and field conditions, strongly suggested that changes in spectral quality (low R: FR ratio) trigger events that modify the balance of growth regulators and thus influence the degree of branching (*12*, *13*). Quantitative analyses of the suspected change in endogenous growth regulators were never attempted in these earlier studies.

In an effort to explain the phenomenon of apical dominance or correlative inhibition in cocklebur (*Xanthium strumarium* L.), Tucker and Mansfield (*22*, *23*) investigated the influence of light spectral distribution on levels of endogenous growth regulators and the correlation with branching behavior. They found that gibberellins did not play a major role in apical dominance but may have been important for bud extension following a release from dominance. Cytokinin levels were much higher in inhibited buds than in released buds. The cytokinins present were not able to participate in bud growth because of auxin-induced accumulation of abscisic acid (ABA) in the buds. These observations were further substantiated in studies of apical dominance in broad bean (*Vicia faba* L.) which showed an inverse correlation between ABA levels in axillary buds and bud outgrowth (*5*, *6*).

Whether this altered balance of endogenous growth regulators in some species exposed to far-red light occurs in velvetleaf-shaded soybeans had not been proven. In an attempt to explain why branching in soybeans is reduced by early-season velvetleaf interference, this study was conducted with the following objectives:

(1) to determine the light quality (R: FR) under soybean canopies shaded by velvetleaf of varying canopy heights,

(2) quantify the endogenous growth regulators (e.g. IAA, ABA, cytokinins) in velvetleaf-shaded soybeans,

(3) correlate light quality and endogenous growth regulator levels with

branching responses in soybeans.

MATERIALS AND METHODS

Field experiment

The experiment was conducted from May to October 1987 at the Agronomy Research Center, University of Missouri-Columbia on a Mexico silt loam soil, a member of the fine, montmorillonitic, mesic Udollic Ochraqualfs. Plots were arranged in a randomized complete block design with four replications. Each plot consisted of 12 rows, each 7.9 m long, spaced 25 cm apart. Soybeans (cv. Williams 82) were seeded on 19 May 1987. Likewise, previously scarified velvetleaf seeds were broadcast using a Brillon seeder at the rate of 23 kg/ha (approximately 40 velvetleaf plants/m^2). Soybean plants were considered fully emerged on 1 June 1987 when each plant had a pair of fully expanded unifoliolate leaves. Thinning was done 7 days after emergence (DAE) to achieve a population density of 310 000 soybean plants/ha.

Immediately before planting, phosphorous and potassium fertilizers were broadcast each at the rate of 112 kg/ha. Seeds were inoculated with a commercial soybean inoculant prior to seeding. Pest management measures were provided whenever necessary. To prevent any confounding effect of water stress, plants were irrigated an equivalent 25 mm of water as needed using an overhead sprinkler.

Three treatments were imposed from 2 to 6 weeks (14 to 42 days) after soybean emergence (DAE) as follows: (1) weed-free (all weeds were clipped as they emerged) (2) vl-75% ht (velvetleaf canopy height maintained at 75% relative to soybean height), and (3) weedy (velvetleaf left uncontrolled). To maintain velvetleaf canopy height at 75% of soybean height (treatment 2), velvetleaf were clipped to the desired height twice a week using hand-held electric grass shears powered from a high clearance sprayer. Moreover, in treatments 2 and 3, weeds other than velvetleaf were also clipped at the ground level as they emerged. Upon termination of the shading treatments, all plots were kept weed-free until harvest.

Measurement of spectral quality

Spectral distributions of light were monitored at least twice a week from 2 to 7 weeks after soybean emergence using a LI-COR Spectroradiometer LI-1800 (LI-COR Inc., Lincoln, Nebraska, USA) equipped with a remote cosine receptor on a fiber optic probe. Spectral distributions of radiation at 2 nm intervals between 300 and 850 nm were measured at 30 cm (midcanopy) and 50 cm (upper canopy) above ground level. Spectral irradiances at 660 and 730 nm were used to calculate red: far-red photon fluence rate ratios.

Leaf area index (LAI)

During the first sampling, soybean and velvetleaf plants were clipped from a 0.5 m^2 sampling area (2 rows, 1 m long). All expanded leaves were separated and their areas immediately determined using a LI-COR 3000 (LI-COR, Inc., Lincoln, Nebraska, USA) leaf area meter. LAI was calculated by dividing total leaf

area by the ground area. Subsequent LAI determinations were obtained from a subsample of two plants from each sampling area. The total leaf area of these two plants were measured, dried at 70°C for 3 days and weighed. The ratio derived by dividing leaf area by leaf weight was used to estimate the total leaf area per sampling area.

Axillary bud or branch length (cm)

Ten consecutive soybean plants randomly selected from a row segment of each plot were tagged and used for weekly determinations of bud lengths. Axillary bud or branch lengths were determined from the point of insertion in the stem to the bud or branch tip using a metric ruler.

Quantitative analyses of endogenous growth regulators

From 20 randomly selected plants in each treatment, plant tissues (axillary buds, apical buds including young unfolded leaves, internodes) were separated, immediately weighed, frozen in liquid nitrogen and stored in a deep freezer. Sampling was done 35 DAE. An additional sampling was made at 2 days (44 DAE) after the termination of the shade treatment. The endogenous growth regulators were extracted and assayed using modifications of previously described techniques, details of which are described below.

Extraction procedures

Endogenous plant growth regulators [IAA, ABA, trans-zeatin riboside (t-ZR)] were extracted using a modification of the method of Weiler *et al.* (*26*). Plant materials were ground to a fine powder in liquid nitrogen with a mortar and pestle. The powder was further homogenized in (per gram fresh weight of starting material) 20 ml freshly prepared cold 80% MeOH (pH 7.5) containing 10 mg/l of 2,6-di-tert-butyl-*p*-cresol (BHT; Sigma Chemical Co., St. Louis, MO, USA) and 100 mg/ml polyvinyl pyrrolidone (PVP). Appropriate internal standards (3-indolyl[1-^{14}C] acetic acid, 1.8×10^{9} Bq/mmol; DL-[G-^{3}H]abscisic acid, 1.1×10^{12} Bq/mmol; Amersham, Arlington Heights, IL, USA) were also added. The homogenate was incubated in the dark at −20°C for 24 h after which it was centrifuged at $3000\times g$ for 5 min. A 5-ml aliquot of the supernatant was purified by passing it through a reverse-phase C_{18} column (Sep-Pak; Waters Associates, Milford, MA, USA). ABA passes through the column with mean recoveries of 92 ± 1.3%. For ELISA of ABA and t-ZR, one ml of C_{18} column-purified eluate was diluted 10-fold with 25 mM Tris-buffered saline (TBS; 25 mM Trizma base, 0.1 M NaCl, 1.0 mM $MgCl_2\cdot 6H_2O$), pH 7.5. For IAA, 100 μl of C_{18} column-purified eluate was pipeted into a 4-ml vial then dried under nitrogen at 35°C. The dried sample was reacted with 1 ml of freshly prepared ethereal diazomethane for 5 min, then dried again under nitrogen. The resulting methylated sample was dissolved in 1 ml absolute MeOH then diluted 10- or 100-fold with 25 mM TBS preparatory to ELISA. Mean percentage recovery of ^{14}C-IAA at this stage was 93 ± 1.1%.

Enzyme-linked immunosorbent assay (ELISA)

The ELISA was performed essentially as previously described (*26*, *27*). Unless otherwise specified, all working reagents were added with 0.1% sodium azide (NaN_3) as an antimicrobial agent and kept in a refrigerator at 4°C. In a carefully timed sequence, each of the monoclonal antibody-coated wells [(phytodek-IAA, #P-01D-096); (phytodek-ABA, #P-02D-096); (phytodek-t-ZR, #P-03D-096); Idetek, Inc., San Bruno, CA, USA] was added with 100 μl of either standard or sample. The B_0 value (=maximum enzyme binding to coated surface) was determined in the absence of a standard by using 100 μl TBS, pH 7.5. Likewise, for the determination of nonspecific binding (NSB) 100 μl of an excess standard (500 pmol IAA; 100 pmol ABA; 100 pmol t-ZR) was added. The appropriately diluted plant growth regulator-alkaline phosphatase conjugate or enzyme tracer [(IAA tracer, #P-A02-001); (ABA tracer, #P-A03-001); (t-ZR tracer, #P-A04-001); Idetek, Inc., San Bruno, CA, USA] was subsequently added (100 μl/well) to all wells. After mixing the reactants by gently tapping the plate, the wells were covered with plate sealer and incubated in a refrigerator at 4°C for 3 h. At the end of the 3-h incubation period, the solution from each well was decanted. Wells were washed three times by adding 200 μl of the wash solution (saline-0.5% Tween solution, pH 7). For the assay of surface-bound alkaline phosphatase activity, 200 μl of a freshly prepared 1 mg/ml solution of *p*-nitrophenyl phosphate in DEA buffer, pH 9.8 (0.9 M diethanolamine, 0.3 mM $MgCl_2 \cdot 6H_2O$) was added to each well. After covering the wells with a plate sealer, the enzyme reaction was allowed to proceed for 90 min by incubating the wells in an oven maintained at 37°C. The enzyme reaction was terminated by the addition of 50 μl 1 M NaOH per well. Five minutes after addition of NaOH the reaction solutions from wells were transferred to 4-ml vials containing 250 μl sterile distilled H_2O and absorbance readings were taken at 405 nm using a Perkin-Elmer Lambda 3 UV/VIS Spectrophotometer.

Growth chamber experiment

On 21 January 1988, 5 soybean seeds (cv. Williams 82) were planted in each 15 cm-diameter plastic pot containing soil, sand and commercial potting mixture (Pro-Mix) thoroughly mixed in equal proportions of 1:1:1 by volume. The seedlings were thinned to 2 plants/pot one week after planting. On 30 January 1988, all plants having a pair of fully expanded unifoliolate leaves were transferred to designated controlled-environment growth chambers with appropriate light treatments.

One growth chamber (designated as −FR treatment) was lighted with 16 GTE Sylvania cool-white fluorescent tubes (160 W) only. The other growth chamber (designated as +FR treatment) had 10 Sylvania cool-white fluorescent tubes (160 W) plus 22 G.E. 50 W incandescent bulbs. In both growth chambers, all plants were subjected to the same temperature (day, 25°C; night, 25°C) and photoperiod (12 h). The racks supporting the potted plants were adjusted each week so that the amount of photosynthetically active radiation (PAR, 400–700 nm) received at pot level were 180 μmol m^{-1} s^{-1} in both growth chambers as measured with a LI-COR Spectroradiometer LI-1800. Only the light quality (R: FR) differed be-

tween the two growth chambers.

Plants were maintained inside the growth chambers for 28 days, and provided with adequate nutrition and water. At the end of the light treatment period, lengths of axillary buds at each node were measured with a metric ruler. Likewise, internodes of similar morphological age and position were separated, quickly frozen in liquid nitrogen then stored in a deep freezer until analyzed. Extraction and quantitative analyses of endogenous IAA were carried out as described above. IAA levels were determined at each internode position. The internode between the unifoliolate and first trifoliolate nodes was designated as internode 1. Successive upper internodes were designated as internodes 2, 3, 4 and 5, respectively. Six internodes obtained from 3 pots made up a replicate. There were 6 replicates per light treatment.

RESULTS

R: FR, LAI and lateral bud development

Seasonal differences existed in the attenuation of incident radiation in canopies of weed-free and velvetleaf-shaded soybeans. A typical spectral energy distribution curve (Fig. 1) revealed that maximal absorption was in the blue and red wavelength bands with less in the green. Minimal absorption occurred in the far-red. The extent of the depletion of these wavelength bands depended on the LAI. When seasonal trends in R: FR of shadelight were compared to seasonal variations in LAI (Figs. 2A, B vs. Fig. 2C), it was very evident that R: FR was inversely correlated with LAI. For instance, R: FR values at the upper and middle canopies of velvetleaf-shaded soybeans were lower than those of the weed-free soybeans because of the greater canopy density in the weedy plots. Velvetleaf removal however, led to a pronounced increase in R: FR at 44 and 49 days after emergence (DAE). In contrast, R: FR ratio underneath canopies of weed-free soybeans was higher than in velvetleaf-shaded soybeans because of the lower LAI. Since LAI was still

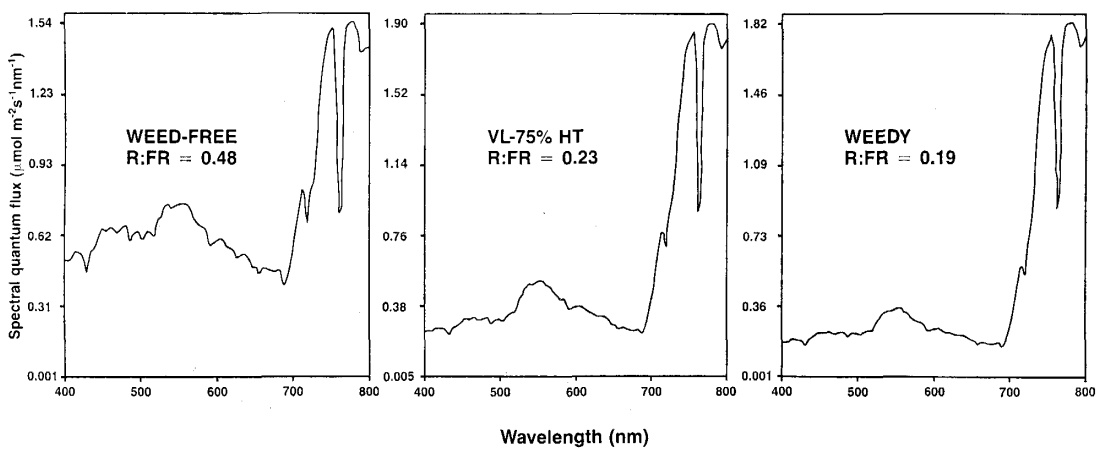

Fig. 1. Typical spectral energy distribution at the middle canopy of velvetleaf-shaded and weed-free soybeans. Data were obtained on 24 June 1987 (23 DAE), 1000 h central daylight time, clear sky condition.

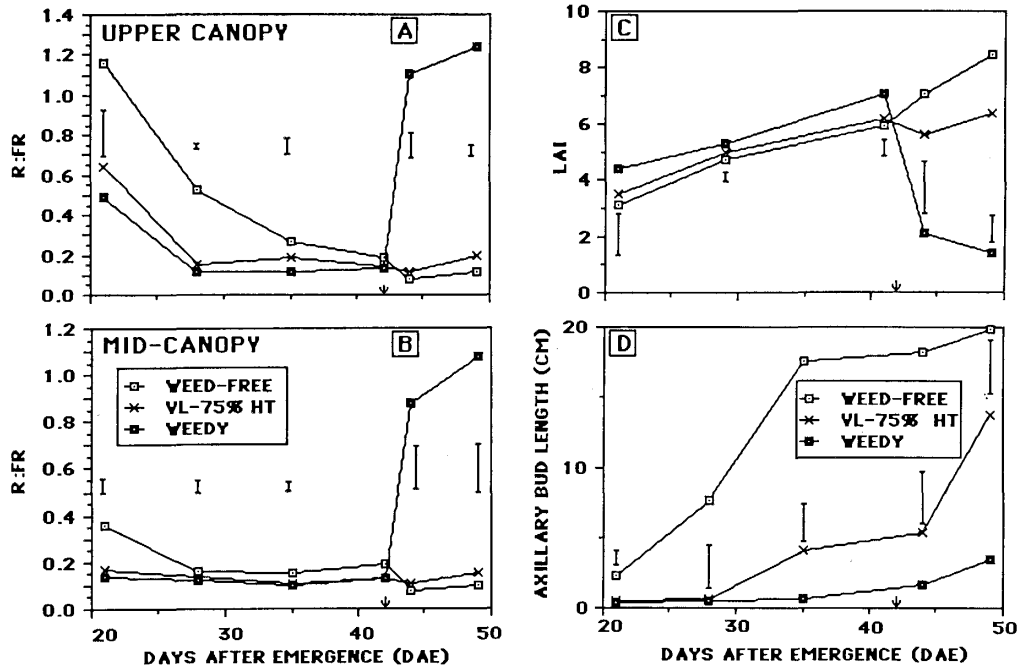

Fig. 2. Seasonal changes in R: FR of shadelight occurring at the (A) upper and (B) middle canopies, and comparative development of (C) LAI and (D) axillary buds (branches) of velvetleaf-shaded and weed-free soybeans. Vertical bars represent LSD (0.05) values; downward arrow indicates end of weed shading period.

increasing 42 to 49 DAE in weed-free soybeans, the R: FR ratio in the shade continued to decrease.

Growth of lateral buds was almost nonexistent in soybeans that were shaded by velvetleaf (Fig. 2D). In the weedy treatment for example, axillary buds grew only from 0.4 cm at 21 DAE to 0.6 cm at 35 DAE. However, a 3-fold growth (1.7 cm) occurred even as early as 2 days (44 DAE) after velvetleaf removal and this event coincided with the dramatic rise in R: FR of the existing shadelight (Figs. 2A, B). Underneath canopies of weed-free soybeans, axillary buds developed and continued to grow during the shading period.

IAA contents of terminal buds

During the shading period (35 DAE), the IAA level (36.6 nmol gfw^{-1}) at the terminal buds of velvetleaf-shaded soybeans was significantly higher than that of weed-free soybeans which contained an average concentration of only 14.9 nmol IAA gfw^{-1} (Fig. 3A). Terminal buds of soybeans in the "vl-75% ht" treatment had a mean IAA level of 26.9 nmol gfw^{-1}, which was intermediate between levels in the weedy and weed-free treatments. When the R: FR of shadelight was increased due to velvetleaf removal (Figs. 2A, B), the IAA contents at the terminal buds of soybeans previously shaded by velvetleaf decreased 4-fold to 9.2 nmol gfw^{-1}, even as early as 2 days (44 DAE) after velvetleaf removal. During the same period, the IAA levels in the shoot apices of soybeans from both weed-free and "vl-75% ht" treatments were 13.1 and 13.2 nmol gfw^{-1}, respectively.

IAA levels in internodes

The patterns of IAA concentrations in internodes of velvetleaf-shaded soybeans were similar to those present at the terminal buds, although the magnitudes were smaller (Fig. 3B). At 35 DAE, the IAA content in internodes in the weedy treatment was 5.7 nmol gfw^{-1}. This was significantly higher than the 3.6 and 4.2 nmol gfw^{-1} values of the weed-free and "vl-75% ht" treatments, respectively. At 44 DAE the increase in R : FR of shadelight due to velvetleaf removal led to decreased IAA level (3.5 nmol gfw^{-1}) in internodes of the previously velvetleaf-shaded soybeans. Similarly during this same period, IAA contents from both weed-free and "vl-75% ht" internodes were 4.3 and 3.4 nmol gfw^{-1}, respectively.

ABA and t-ZR contents of axillary buds

Concomitant with the higher IAA levels in shoot apices and internodes during

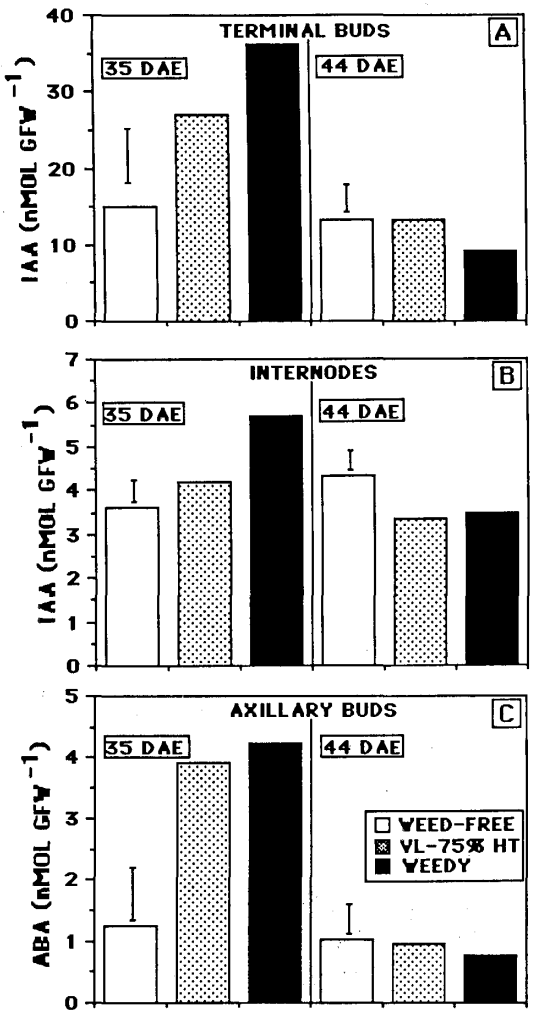

Fig. 3. IAA levels in (A) terminal buds and (B) internodes, and (C) ABA concentrations in axillary buds of weed-free and velvetleaf-shaded soybeans during shading (35 DAE) and 2 days (44 DAE) after velvetleaf removal. Vertical bars at each observation date represent LSD (0.05) values.

weed shading (35 DAE), we observed higher ABA contents in axillary buds of velvetleaf-shaded soybeans as opposed to those of weed-free soybeans (Fig. 3C). For example, the ABA level of inhibited axillary buds in weedy soybeans was 4.2 nmol gfw^{-1} at 35 DAE, which then decreased almost 6-fold to 0.77 nmol gfw^{-1} 2 days after velvetleaf removal (44 DAE). Similarly, the ABA content in the axillary buds of soybeans exposed to "vl-75% ht" treatment was 3.9 nmol gfw^{-1} at 35 DAE. This ABA level decreased to 0.96 nmol gfw^{-1} two days (44 DAE) after the termination of the shading treatment. In contrast, the ABA content at the axillary buds of weed-free soybeans was 1.2 nmol gfw^{-1} at 35 DAE then decreased only slightly to 1.0 nmol gfw^{-1} at 44 DAE.

During weed shading period (35 DAE) and even at 2 days (44 DAE) after velvetleaf removal, we did not observe significant differences in t-ZR contents of lateral buds between velvetleaf-shaded and weed-free soybeans (data not shown). We noticed however, that t-ZR contents increased with age as previously reported by Heindl *et al.* (*9*).

Growth chamber experiment

Generally, there were significantly greater outgrowths of lateral buds at various node positions in soybeans exposed to −FR light treatment than those exposed to +FR light treatment (Fig. 4A). Regardless of light treatment, growth of axillary

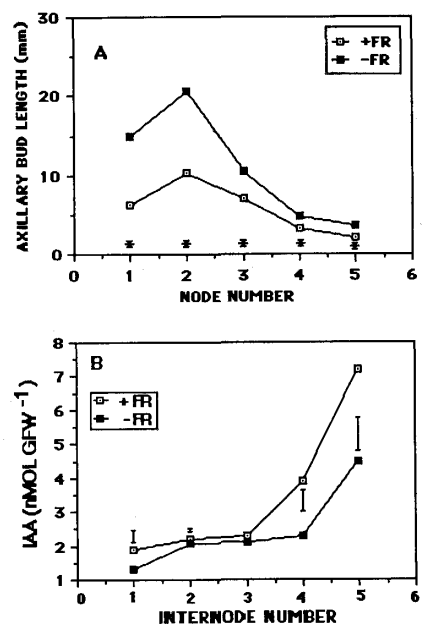

Fig. 4. Axillary bud lengths at various node positions (A) and levels of IAA at different internodes (B) of soybeans subjected to two light regimes. [For A, node number 1 refers to the unifoliolate node and succeeding upper trifoliolate nodes are denoted by nodes 2 to 5; an asterisk above each node denotes significant difference in bud lengths between light treatments using LSD (0.05). For B, internode 1 refers to the internode between the unifoliolate and first trifoliolate node, successive upper internodes are denoted by internodes 2 to 5; vertical bars at each internode position represent LSD (0.05) values].

buds was greatest in nodes most distant and least in nodes closest to the shoot apex. An exception to this trend was the growth of axillary buds at the unifoliolate node.

On a fresh weight basis, the concentration of IAA was maximal in the upper (youngest) internode nearest the terminal bud and least in the lowermost internode (Fig. 4B). This pattern was similar in both light treatments although the magnitude of IAA was greater in the +FR treatment compared to the −FR treatment.

DISCUSSION

The present study was designed to expand our understanding of how lateral bud growth in soybeans is reduced by velvetleaf competition. When the R: FR ratio in shadelight was high due to lower canopy density (Figs. 2A, B, C) axillary bud growth in weed-free soybeans was evident at 21 DAE (Fig. 2D). In contrast, the significantly greater LAI in velvetleaf-shaded soybeans resulted in a considerable decrease in the R: FR ratio in shadelight. Such far-red enriched shadelight inhibited the outgrowth of lateral buds during most of the shading period. However, lateral bud growth became discernible as early as 2 days (44 DAE) after velvetleaf removal when R: FR of shadelight was increased dramatically. These observations are compatible with previous findings, demonstrating that far-red-enriched radiation (low R: FR) enhanced apical dominance resulting in the suppression of axillary bud growth in various crops (*12–14, 24*).

Kasperbauer and colleagues (*12, 13*) suggested that control of lateral branching in red- or far-red-irradiated tobacco and soybeans was dependent on the balance of growth substances in the plant. Various studies (*16, 17, 21*) also showed that a growth factor (presumably a hormone) produced in the apex (including young unexpanded leaves) and internode was responsible for the R: FR sensitivity in *Phaseolus vulgaris* and *Sinapis alba.*

In the present study, the levels of IAA in the terminal buds (Fig. 3A) and internodal tissues (Fig. 3B) of velvetleaf-shaded soybeans were significantly greater than those of weed-free soybeans. A corollary growth chamber experiment also showed a relation between the IAA levels in soybean internodes and the degree of inhibition of axillary buds (Fig. 4). Moreover, inhibited axillary buds of velvetleaf-shaded soybeans had higher ABA levels than the actively growing buds of weed-free soybeans (Fig. 3C). When the R: FR of shadelight was increased considerably due to velvetleaf removal (Figs. 2A, B), the outgrowth of lateral buds (Fig. 2D) coincided with decreases in concentrations of IAA in both terminal buds and internodes of soybeans. Concomitant with these IAA decreases was a 6-fold diminution of ABA.

A low R: FR-induced inhibition of lateral bud growth in velvetleaf-shaded soybeans was therefore interpreted to be mediated by the sequential action of both IAA and ABA. This means that the higher levels of IAA at the terminal buds and internodes of soybeans exposed to low R: FR (i.e. velvetleaf-shaded) may have induced the formation of ABA in the axillary buds themselves, a phenomenon previously observed in broad-bean, *Vicia faba* L. (*5, 6*) and *Phaseolus vulgaris* L. (*15*). The higher amount of ABA in turn was responsible for correlative inhibition

of lateral buds. Such indirect action of high levels of apically-synthesized IAA on increased ABA synthesis and subsequent inhibition of lateral bud outgrowth had been found to be operative in far-red-exposed tomato (*25*), cocklebur (*22*, *23*), *Phaseolus vulgaris* (*16*) and *Pisum sativum* (*4*).

Heindl *et al.* (*9*) found an increase in t-ZR contents of soybean root pressure exudates beginning early flowering to full bloom stage. We also observed an increase in t-ZR levels of soybean lateral buds from 35 DAE to 44 DAE. However, there was no significant difference in t-ZR concentrations of lateral buds between velvetleaf-shaded and weed-free soybeans. It is possible that t-ZR did not play a significant role in the release of axillary buds from low R : FR-induced apical dominance.

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