AJUGA REPTANS L.

AN ABSTRACT OF THE THESIS OF

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Title THE EFFECTS OF TEMPERATURE, PHOTOPERIOD AND GROWTH REGULATORS ON DEVELOPMENT OF AJUGA REPTANS L.

Abstract approved (Major professor)

Four experiments involving photoperiod, temperature, gibberellic acid (GA_3) and B995 treatments were conducted to determine if growth of Ajuga reptans L. could be controlled. Growth was greatest at 70°F under a 16-hour photoperiod. A 1-hour light-break intercalated in the middle of a short-day dark period stimulated elongation of petioles but inhibited growth generally. Gibberellic acid at 200 and 300 ppm, irrespective of temperature and photoperiodic conditions, stimulated many-fold the growth of aboveground parts and caused axillary buds on primary stolons to develop into secondary stolons. Secondaries were produced only with GA_3 treatment. B995 retarded growth proportional to the concentration applied with 2000 and 2500 ppm having the greatest retarding effect. GA_3 released the plants from the growth retardation caused by B995. Those treated with 2000 and 2500 ppm B995 were stimulated by the GA_3 to grow especially vigorously, suggesting a synergistic growth stimulation by the two chemicals.

THE EFFECTS OF TEMPERATURE, PHOTOPERIOD AND GROWTH REGULATORS ON DEVELOPMENT OF *AJUGA REPTANS* L.

by

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INTRODUCTION

Ajuga reptans L. is a popular groundcover plant clothed in springtime with short spikes of blue to purplish blue flowers (Frontispiece). It propagates readily by division. Nurserymen in Oregon usually divide the plants in late summer and fall. The divisions, consisting of small rosette plantlets that had formed at the end of creeping stolons, are often planted singly in small pots or bands where they establish themselves. Each rosette in turn produces several stolons that grow during the winter in the greenhouse and by spring are entangled with those from adjoining plants. Then, at the time of sale, it is difficult to disentangle the plants without injuring them.

The purpose of the studies reported here was to develop ultimately methods nurserymen could use for controlling the growth of the plants. Therefore, the effects of temperature, photoperiod and two growth regulating chemicals were studied.

REVIEW OF LITERATURE

The response of plants to periodic alternations of light and darkness was observed as early as 1880, but Garner and Allard (1920) are credited with the discovery of photoperiodism.

Photoperiod controls plant processes other than flowering. Size and dry weight of leaves in several spring-flowering annuals were increased by long days (Lewis and Went 1945, Banga 1952), while short days sometimes increased the proportion of total dry matter accumulated in the leaves (Hughes and Evans 1963). Thomas (1961) noted leaf enlargement under both continuous short-day (SD) and long-day (LD) conditions. Higher leaves were more responsive than lower ones, indicating greater sensitivity of the former. Younger leaves expanded for a longer period of time than older leaves, LD treatment being more effective than SD. Schwabe (1956) noted on cocklebur (Xanthium pennsylvanicum) plants with 3-4 leaves, that leaf area decreased with increasing photoperiods but, on plants with 8-10 leaves, shorter photoperiods produced the largest leaves.

Parker and Borthwick (1939) showed that stems of 'Biloxi' soybean (Glycine max L.) elongated at both high and low internode positions under 8 to 18-hour photoperiods, but those at higher node positions elongated faster. Wareing (1954) economized by interrupting the dark period with 30 minutes of light at 100 ft-c, rather than extending the light period. Interruptions, either early or late in the dark period, prevented 'Biloxi' soybean from flowering. But Highkin and Hanson

(1954) inhibited growth of tomato by 2-hour light-breaks during the long dark period.

The effects of a light-break can be explained in part by the action of phytochrome, a pigment involved in flowering and other physiological processes (Parker et al. 1949, Borthwick et al. 1954, Downs 1955, Hendricks, Borthwick and Downs 1956, Butler et al. 1959, Mohr 1962, Foruya and Torrey 1964). For example, long days favor growth and short days induce dormancy in many woody species. This, like other processes regulated by photoperiod, depends partially on the phytochrome pigment system. Phytochrome has two reversible forms: one absorbs red light, the P_{660} form; the other absorbs far-red light, the P_{730} form. In light, red light is absorbed and the P_{660} form is converted to the P_{730} form. In darkness, or if the plant is exposed to far-red light, the P_{730} form reverts back to the P_{660} form. Downs and Borthwick (1956) found that Loblolly pine (Pinus taeda L.), under combinations of incandescent and fluorescent light, increased its growth rate upon entering the dark period. Far-red light from the incandescent lamps had favored the reversion of phytochrome from the P_{730} to the P_{660} form, thus the plant entered darkness with much of the phytochrome in the P_{660} form. The ratio of these two pigment forms can be controlled by the amount of supplemental light given. Herbaceous plants respond similarly to this pigment system.

Garner and Allard (1931) found that alternating light and darkness of equal duration inhibited the growth of many plants. Allard and Garner (1941) found that light-dark periods of unequal duration were better for plant growth, and that abnormal cycle lengths and continuous

illumination were harmful. Arthur, Guthrie and Newell (1930) and Arthur and Harvill (1937) observed that tomato plants grown under continuous illumination were abnormal, grew poorly and sometimes died.

Plants are sensitive to temperature. The growth curve for most plants rises rapidly in the 0-15°C range, rises less rapidly and levels off in the 16-30°C range and falls sharply at higher temperatures. High temperatures also tended to shorten the growth period (Barlow and Hancock 1959).

Temperature, as well as light, must fluctuate for normal plant development. Night temperature affected not only the growth rate, but also growth quality, earliness of flowering and intensity of fruiting (Went 1957). High night temperatures favored leaf elongation in the early stage of development of tomato, but, as the plants matured, longer leaves were produced under cooler night temperatures (Went 1944). Lewis and Went (1945) found that night temperatures had a pronounced effect on the number and size of leaves. The rate of leaf production was proportional to the temperature during vegetative development when night temperatures remained constant.

Temperature modifies responses to photoperiod and, therefore, must be considered in all such studies. Although light may be limiting only in the light phase of photosynthesis, temperature may be limiting in both the light and dark phases (Gaffron 1960). At low light levels the photosynthesis rate was directly proportional to light intensity but at higher intensities a saturation level was reached where this rate leveled off, which was governed by temperature. As temperature

increased, the light saturation level increased, but if light intensity were limiting there would be no response to increases in temperature.

Ketellapper (1960) and Tukey and Ketellapper (1963) found that the optimum length of the photoperiodic cycle decreased with increasing temperature. Small changes in cycle length had no effect on the rate of photosynthesis, respiration or stem elongation. But the rate of stem elongation increased rapidly when the light was turned off. Ketellapper further noted that plants grown under 24-hour cycles developed various injury symptoms in both high and low temperatures.

Hillman (1956) noted that certain photoperiodic cycles and continuous light at constant temperatures of 14 to 30°C injured tomato leaves. The symptoms were evident, however, only on leaves exposed to these temperatures during the early stages of development. Plants with 4 to 7 leaves were injured more quickly than were mature plants, and apical cuttings, whose mature leaves were removed, were injured more quickly than those with mature leaves intact.

Chemical control of plant growth has interested biological scientists for many years. In recent years, potent growth stimulating and growth retarding chemicals have been discovered. The most widely studied of the former have been the gibberellins.

Gibberellin research started with studies on the "bakanae" disease of rice caused by a fungus (Gibberella fujikuroi). Hori in 1898 had noted the extremely elongated stems of rice plants infected with this fungus. Kurosawa (1926), who first extracted the fungal secretion, was the instigator of early gibberellin research. Before 1952 the research was largely centered in Japan, but much of it has now shifted to

England and the United States. Simpson's (1963) bibliography, totaling 1200 gibberellin papers published between 1957 and 1963, attests to the extensive research on the subject.

Stimulation of stem elongation is one of the more noticeable responses to applied gibberellins. Marth, Audia and Mitchell (1956) obtained significant stem elongation on Pinto bean with .001 ppm gibberellic acid (GA), with maximum response at 1 ppm. When Bukovac and Wittwer (1956) applied 20 µg GA per plant, the stems of bush, semi-bush and pole bean elongated 51, 38 and 71 inches, respectively, while respective stem elongation for untreated plants were 15, 16 and 59 inches.

Elongation of pea stems caused by applied GA was almost entirely due to increased cell elongation, rather than increased cell numbers (Brian and Hemming 1955). The assumption of a pole-type habit by mutant dwarf bean after treatment with GA (Bukovac and Wittwer 1956, Phinney 1956) was one of the more dramatic responses to gibberellins.

Apical dominance is affected by GA treatment. It is weakened in some plants and enhanced in others. Runner formation in Fragaria vesca semperflorens 'Baron Solemacher', a normally runnerless cultivar, was induced by GA (Guttridge and Thompson 1963). Bonde and Moore (1958) with pea and Gray (1957) with bean found that application of GA induced lateral shoots from axillary buds that normally did not produce shoots. Bradley and Crane (1960) enhanced apical dominance in fruit trees with GA by inhibiting lateral buds and increasing internode elongation in shoots and spurs. In contrast, GA appears to weaken apical dominance in Kalanchoe, strawberry, bean and pea.

Gibberellin often changes leaf size and shape. Possibly the increased yield of some forage and vegetable crops following GA treatment is due to greater photosynthetic surfaces. Marth et al. (1956) increased the leaf area of Pinto bean 25% by a 1 ppm GA treatment. Petioles were longer, but the blades were thinner and lighter green. With GA treatment Bukovac and Wittwer (1957) increased leaf area of several bean species and cultivars by 16-29% in one experiment. The accelerated expansion of primary leaves in dwarf bean following initial GA stimulation, noted by Humphries (1958), was offset by a subsequent growth depression that resulted in no net gain in leaf area.

Gray (1957) changed the shape of leaves with GA sprays. Concentrations of 10-100 ppm changed the dentate leaf margins of tomato to entire or smooth. The margins of leaves expanded at the time of treatment were not affected, but the margins of those that expanded during the next three weeks were smooth. Following 20 ppm GA treatment, tobacco leaves became more elongate and the apex more acute and curved to one side, the smooth leaves of pepper became wrinkled, and African violet leaves became narrower, thinner and the apex more acute.

Gibberellic acid has generally had a positive effect on petioles. Increases in both length and width of petioles were shown by celery (Bukovac and Wittwer 1956) after treatment at the 3-4, 6-7 and 10-12 leaf stages with 20 and 40 µg GA per plant. The size of Cornell 19 petioles increased 100% over that of the control plants at the 40 µg GA treatment and 10-12 leaf stage. Guttridge (1963) showed that

strawberry petioles elongated more rapidly when treated with GA at early stages of development because of both increased number of cells and enlargement of cells.

The literature reports extreme effects of GA on fresh and dry weights of plants. The stems of some plants have elongated many-fold but their dry weight was not affected significantly. Increased fresh or dry weights of roots have seldom been reported.

One week after the application of 1 and 10 ppm GA to soybean plants, Marth et al. (1956) found increases in dry weight of 28% and 39%, respectively, over controls. But, after two weeks, he found very little difference in dry weight between treated and control plants. Tomatoes have responded little to concentrations of 2.5 to 25 ppm GA, but their dry weight definitely increased with GA treatment of 50 ppm and above (Rappaport 1957). Although the weights of the aboveground parts of bean, pea and sweet corn increased substantially, the dry weights of the roots of these cultivars were decreased (Wittwer and Bukovac 1957).

The chemicals that retard growth have been categorized as growth retardants because they inhibit cell division and cell elongation. Their effects are variable. A species or cultivar response to a retardant is no basis for similar responses by other species or cultivars or by the same kind of plant under different environmental conditions (Cathey and Stuart 1961).

Mitchell, Wirwille and Weil (1949) obtained the first reasonably good chemical reduction of growth with a nicotinium compound on snap bean. Plant height was also controlled by Wirwille and Mitchell (1950),

Downs and Cathey (1960), Halevy and Cathey (1960), Lindstrom and Tolbert (1960), and Riddell et al. (1962).

Certain growth alterations are noticeable when chemical growth retardants work well on plants. Most striking is the decrease in internode length and concomitantly in plant height. Leaves generally turn dark green, the stems thicken and the plant becomes compact and sturdy (Cathey and Stuart 1961).

Guttridge (1966) found that the effect of growth retardants was opposite to that of the gibberellins. Retardants inhibit or restrict biosynthesis rather than metabolism of native gibberellins. The effect of short photoperiods on strawberry was enhanced by application of 2-chloroethyltrimethylammonium chloride (CCC) but flower formation was not affected. However, the effects of CCC were nullified if GA was applied with CCC. GA induced elongation of strawberry stems which concurrent application of CCC did not inhibit, indicating that CCC does not interfere with metabolism of GA. The growth retardants, CCC and N-dimethyl amino succinic acid (B995), are far less destructive to apical meristems than are the retardants, paraquat and maleic hydrazide. The former only suppresses elongation of runners and petioles of strawberry but the latter actually kills tissue. When large doses of CCC or B995 prevented elongation, the buds sometimes developed later as branched crowns and the plants thereby increased in size. Application of 2-isopropyl-4-dimethylamino-5-methylphenyl-1-piperdine carboxyl methyl chloride (Amo 1618), 2,4-dichlorobenzyltributylphosphonium chloride (Phosfon), and CCC inhibited subapical extension and cell division in chrysanthemum (Sachs et al. 1960, Sachs

and Kofranek 1963). This inhibition was reversed or prevented by application of GA.

MATERIALS AND METHODS

Ajuga reptans L. was the experimental plant. A flower spike of Ajuga reptans L. arises from the apex of a rosette mother plant in the spring (Figure 1). Later in the spring and summer, several prostrate primary stolons develop from the axils of older leaves on the rosette mother plant. Each stolon, after producing about nine 3-cm long internodes, terminates with a rosette plantlet. This rosette plantlet initiates a single terminal inflorescence about the middle of September. It flowers the following spring on what is then a rosette mother plant because during the winter the interconnecting primary stolon dies. This cycle is repeated annually.

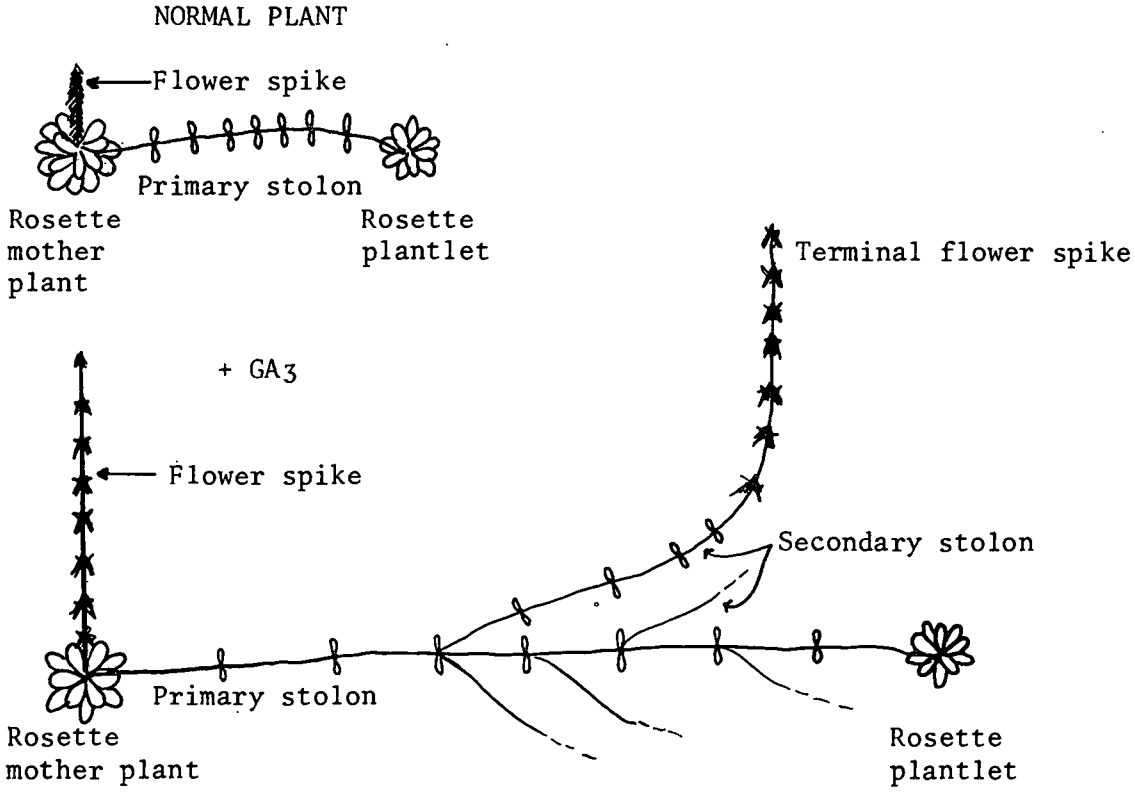

Figure 1. Diagram of the growth habit of Ajuga reptans L. for normal and GA3-treated plants.

Secondary stolons are not produced under natural conditions. When plants are treated with gibberellic acid, secondary stolons arise from axillary buds along the primary stolon. These secondary stolons do not form rosette plantlets but terminate directly as a flower spike. The flower spikes elongate enormously due to the gibberellic acid that also stimulates the existing primary stolons to elongate further.

Roots form on normal plants at the rosettes and sometimes at the nodes along the primary stolon. With gibberellic acid treatment, the primary and secondary stolons become weak structurally and lie on the surface of the soil and roots are formed at nearly every node. These stolons persist much longer than those not rooted along the length of the stolons as is seen under normal growing conditions.

Experiment I. Effect of Temperature and Photoperiod on Growth

This experiment studied growth responses to temperature and photoperiodic treatments.

Ninety plants, randomly selected from 200 plants, were divided into 3 lots of 30 plants each. Each lot was then grown in temperature controlled rooms at either 50, 60, or 70°F ±1° during photoperiodic treatment. Each 30-plant lot was subdivided into 10-plant sub-lots, making a total of 9 sub-lots. At each of the 3 temperatures, a 10-plant sub-lot was subjected to the following photoperiodic treatments: short day (SD), 8 hrs light + 16 hrs darkness; light-break (LB), 8 hrs light + 16 hrs darkness with 1 hour of light interpolated 8 hours after the beginning of darkness; and long day (LD), 16 hrs light + 8 hrs darkness. The time of photoperiodic treatments coincided with the time

of natural daylight. The SD and LB treatments were given in chambers, 48" long x 24" wide x 16" high, in each of the temperature-controlled rooms. The plants were illuminated with 800 ft-c. at leaf level, supplied by warm white KEN-RAD 96 T 12 lamps. During the light-break, light intensity of 35 ft-c. at the upper leaf surface was supplied by a Sylvania 25-watt tungsten lamp placed 12 inches above the plants. The lamps were controlled automatically and air within the chambers was exchanged by small, light-tight blowers.

The following measurements were made weekly during the 6 weeks of treatment: (1) length of each stolon, (2) average length of the third and fourth internodes, counting from the base of the stolon, on 5 randomly selected stolons, a total of 10 internodes, (3) average length of the petioles and length and width of the blades of 10 leaves selected at random.

Experiment II. Effect of Gibberellic Acid (GA_3) and Photoperiod on Growth

Growth responses to gibberellic acid and photoperiod were studied in this experiment.

Thirty-six rosette plants were collected randomly from a large campus planting and rooted under mist for 2 weeks. After planting in 4-inch clay pots to facilitate handling, the plants were divided into 3 lots of 12 plants each. Each 12-plant lot was in turn subdivided randomly into four 3-plant sub-lots. Groups of 12 plants, composed of four 3-plant sub-lots, were then sprayed with 0, 50, 200, or 400 ppm gibberellic acid (GA_3) by means of a Universal Aerosol spray kit. Tween 20 was used as a surfactant. Each plant was sprayed once a week

for 5 weeks. To prevent the GA_3 solution from drifting, a polyethylene bag was placed around each group of plants when they were sprayed. Twelve plants, composed of 3-plant sub-lots from each of the four GA_3 treatments, were then given SD, LB, and LD photoperiodic treatments in the greenhouse at 70°F day and 60°F night minimum temperatures. Three growth chambers, 9' long x 4' wide x 3' high, constructed of chrysanthemum shading cloth, were used for the photoperiodic treatments. Light conditions were the same as in Experiment I, except that the 800 ft-c. light-break was supplied by fluorescent, warm white KEN-RAD lamps. Large light-tight blowers replaced the air in the chambers and kept the temperature relatively constant. Time clocks controlled the photoperiodic durations. After 6 weeks of treatment, the roots were washed free of soil and fresh and dry weights of all plant parts were determined. Growth in length of primary and secondary stolons, length and numbers of their respective internodes, length and width of rosette and stolon leaves, and root length were also recorded.

Experiment III. Effect of Gibberellic Acid (GA_3) at Natural Prevailing Daylengths on Growth

It is simpler and cheaper to grow plants without resorting to control of the daylength. The effect of gibberellic acid was studied, therefore, under natural prevailing daylength in the greenhouse.

Sixty rosette plantlets were collected and rooted as in Experiment II. After the plantlets were rooted, 6 wooden flats were each planted with 10 randomly selected plants. Individual flats of plants were sprayed with 0, 50, 100, 200, 300, or 400 ppm of GA_3 as in Experiment II. Six weeks later the same data as in Experiment II were recorded.

Experiment IV. Effect of N-Dimethyl Amino Succinic Acid (B995) and Gibberellic Acid (GA_3) at Natural Prevailing Daylengths on Growth

The ability of GA_3 (a growth stimulant) and B995 (a growth retardant) to counteract each other's effect on vegetative growth was studied in this experiment.

Sixty rooted plants were brought to 30 grams each by snipping back both the roots and tops. They were then handled as in Experiment III and grown under natural prevailing daylengths at 70°F day and 60°F night minimum temperatures in the greenhouse. Concentrations of 0, 500, 1000, 1500, 2000, and 2500 ppm B995 were applied to individual lots of 10 plants. Thirty days later the length of the stolons was recorded. One application of 300 ppm GA_3 was then sprayed on half of the plants from each of the B995 treatments. The number of growing tips and the length of stolons were recorded again after an additional 30 days.

RESULTS

Experiment I

In this experiment the effect of temperature and photoperiod on growth was studied. A compilation of all data for this experiment is presented in Appendix Table A.

Primary Stolons

Temperature affected differently the number and elongation of stolons (Table 1). Seventy degrees was least favorable for production of numbers of stolons but was most favorable for their elongation. The orders of significant differences for stolon numbers were: because of temperature, 70° = 50°F, 70° < 60°F, 50° = 60°F; because of photoperiod, LD = SD < LB. Stolon elongation was stimulated by progressively warmer temperatures, but the effect of photoperiod was irregular. The orders of significant differences for stolon elongation were: because of temperature, 50° < 60° < 70°F; because of photoperiod, LB = SD, LB < LD, SD = LD.

Temperature and photoperiod interacted to affect stolon number (Figure 2). The orders of significant differences were: because of photoperiod, at 50° and 60°F, LD < SD = LB; and at 70°F, SD = LD < LB; because of temperature, under SD, 70° < 50° < 60°F; under LB, 50° = 70°F, 50° < 60°F, 70° = 60°F; and under LD, no significant differences. In general, LB treatment consistently promoted greater stolon numbers, irrespective of temperature.

Table 1. Main effects of temperature and photoperiod on number and length of primary stolons and size of primary stolon leaves.

	Temperature (°F)			Photoperiod			
	50	60	70	SD	LB	LD	LSD-5%
Stolons per plant (No.)	5.03	5.36	4.66	4.83	5.46	4.43	0.58
Avg. stolon length (cm)	13.72	19.17	24.08	18.68	16.66	21.63	4.12
Avg. leaf blade length (cm)	2.46	3.72	4.93	3.69	3.77	3.65	1.63
Avg. leaf blade width (cm)	1.90	2.46	3.07	2.56	2.40	2.46	0.93
Avg. petiole length (cm)	2.05	3.36	2.69	2.40	3.27	2.43	0.89

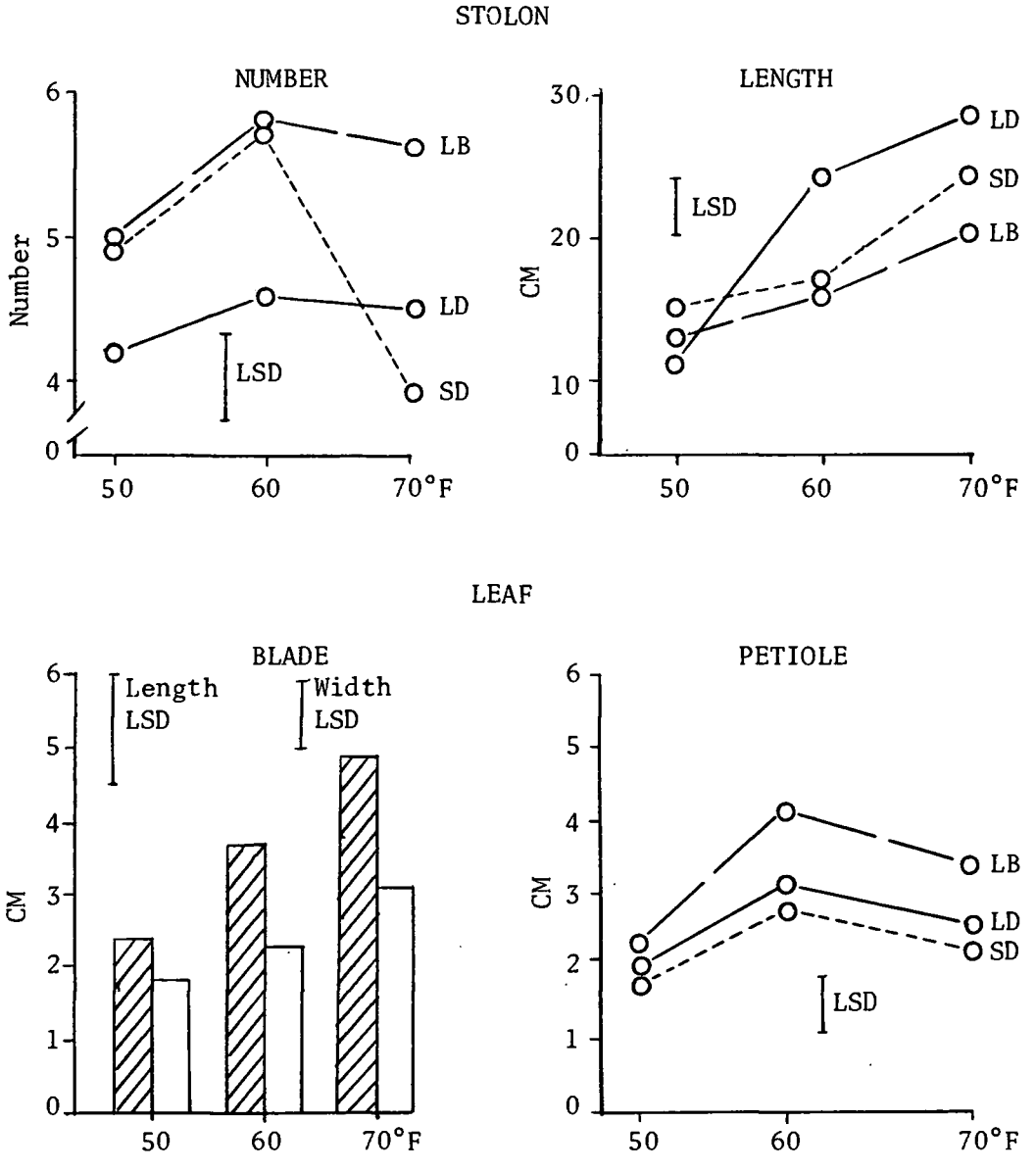

Figure 2. Effect of temperature and photoperiod on stolons and stolon leaves of Ajuga reptans L.

The closed and open bars on the bar graph represent the main effect of temperature on blade length and width, respectively.

LSD values (5% level) are shown as vertical lines in each figure.

Figure 2 also shows that under each photoperiodic treatment the stolons were increasingly longer at progressively warmer temperatures. The orders of significant differences in stolon length were: because of photoperiod, at 50°F, no significant differences; at 60°F, LB = SD < LD; and at 70°F, LB = SD, LB < LD, SD = LD; because of temperature, under SD, 50° = 60° < 70°F; under LB, 50° = 60°F, 50° < 70°F, 60° = 70°F; under LD, 50° < 60° < 70°F. The shortest and longest stolons occurred under LD treatment at 50° and 70°F, respectively.

Primary Stolon Leaves

The leaf blades became increasingly longer and wider at progressively warmer temperatures (Figure 2). Photoperiodic treatment had no consistent effect on the size of leaves (Table 1).

The elongation of the petioles was more variable than was growth of the leaf blades (Table 1). The order of significant differences were: because of temperature, 50° = 70°F, 50° < 60°F, 70° = 60°F; because of photoperiod, no significant differences. Elongation tended to be favored by 60°F and also by LB.

Temperature and photoperiod interacted to affect elongation of the petioles (Figure 2). The longest and shortest petioles occurred at 60°F under LB and at 50°F under SD, respectively. The orders of significant differences in petiole length were: because of photoperiod, at 50°F, no significant differences; at 60°F, SD = LD < LB; and at 70°F, LD = SD, LD < LB, SD = LB; because of temperature, under SD, 50° = 70°F, 50° < 60°F, 70° = 60°F; under LB, 50° < 70° = 60°F; and under LD, 50° = 70° < 60°F.

A comparison of the curves in Figure 2 reveals no consistent relationships between numbers and lengths of stolons under any of the photoperiodic treatments over the range of temperatures in this experiment, except, perhaps, under LB treatment. Here, increases in number and length of stolons were paralleled by increases in leaf blade dimensions at progressively warmer temperatures.

Experiment II

The effect of temperature and photoperiod on growth was studied in Experiment I. In this experiment the effect of GA_3 and photoperiod on growth was studied.

Stolon Number

Primary stolons reached a peak in number at 200 ppm GA_3 and decreased significantly at 400 ppm (Table 2). The number of stolons at each progressively greater concentration of GA_3 were significantly different from those at immediately adjoining concentrations, but those at 50 and 400 ppm were equal. Although secondary stolon number tended to increase in a step-wise manner from the control to 400 ppm GA_3, only the controls were significantly different from the others. The table also shows that primary stolon numbers differed significantly from their companions at LB photoperiodic treatment, but did not differ significantly under SD and LD. There were no significant differences in secondary stolon numbers due to photoperiodic treatment.

The families of curves in Figure 3 show that GA_3 and photoperiod differed in their effect on numbers of primary and secondary stolons

Table 2. Main effects of photoperiod and gibberellic acid (GA_3) treatment on the growth of stolons and leaves.

	GA_3 concentration (ppm)				Photoperiod			
	0	50	200	400	SD	LB	LD	LSD-5%
Stolons per plant (No.)								
Primary stolon	2.90	5.23	6.66	5.13	5.50	3.90	5.60	0.97
Secondary stolon	0.00	5.80	7.70	8.10	4.20	6.60	5.40	2.60
Stolon length per plant (cm)								
Primary stolon	33.00	309.00	307.00	337.00	252.00	212.00	281.00	102.35
Secondary stolon	0.00	14.00	31.00	36.00	12.00	18.00	31.00	9.70
Internodes per stolon (No.)								
Primary stolon	11.80	18.60	18.30	32.60	20.50	23.70	17.00	5.82
Secondary stolon	0.00	1.72	2.12	2.11	1.24	1.37	1.86	0.38
Rosette leaves (cm)								
Blade length	5.90	5.54	6.35	6.31	6.07	6.18	5.88	n.s.
Blade width	2.47	2.39	2.58	2.49	2.44	2.58	2.43	n.s.
Petiole length	5.16	5.54	5.97	5.88	5.62	5.73	5.58	0.51
Primary stolon leaves (cm)								
Blade length	1.00	4.49	4.59	4.68	3.42	3.33	4.32	0.91
Blade width	0.54	2.12	2.20	2.10	1.62	1.56	2.04	0.43
Petiole length	0.64	1.53	1.16	1.73	1.26	0.77	1.77	0.50

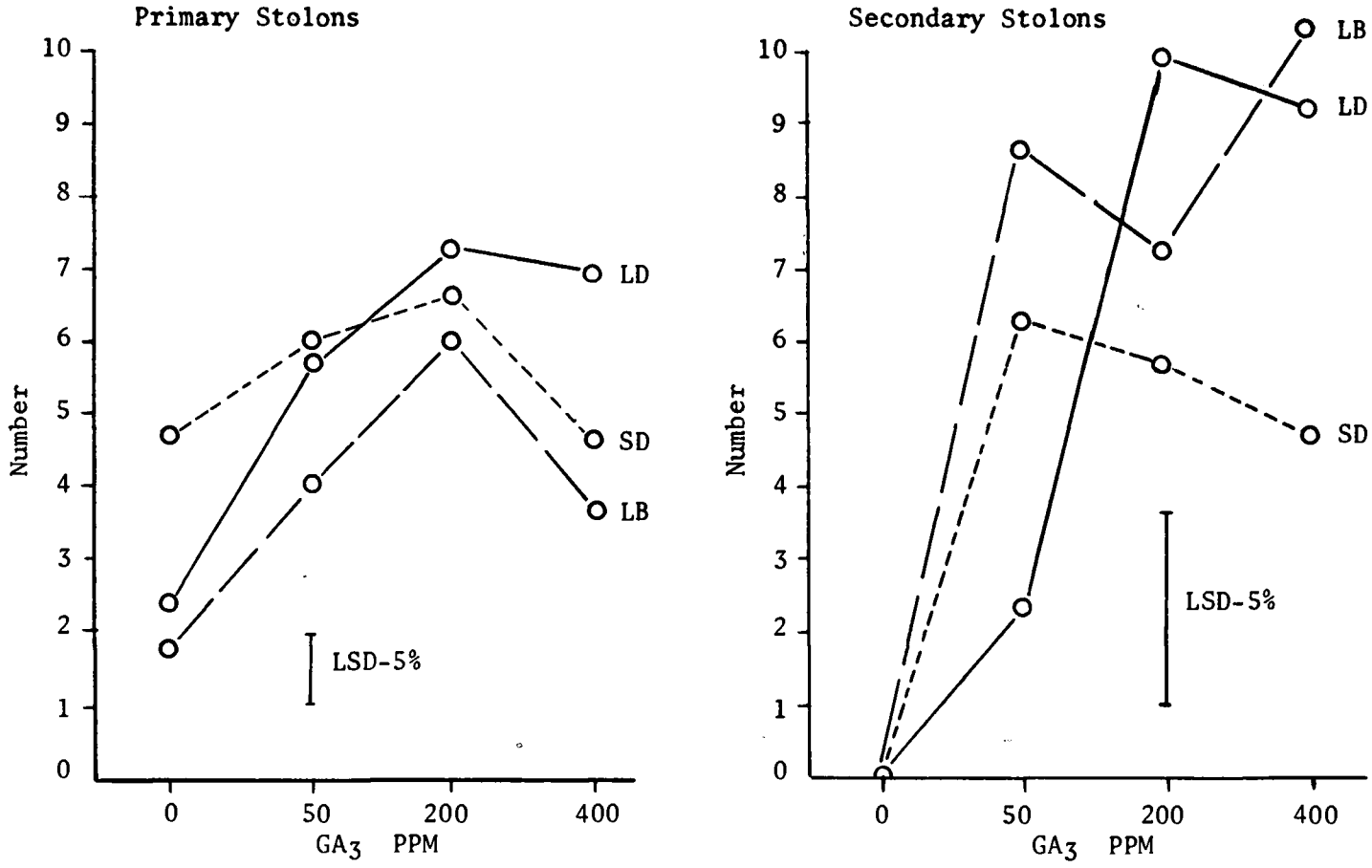

Figure 3. Effect of GA_3 and photoperiod on the number of primary and secondary stolons per plant.

(Appendix Table B). In general, primary stolons reached a peak at 200 ppm GA_3, irrespective of photoperiodic treatment. Their numbers decreased under SD and LB and remained unchanged under LD at 400 ppm. The curves suggest that the general order of effectiveness of photoperiodic treatment on numbers of primary stolons was LB < SD < LD. This did not apply to control plants because the number of primary stolons under SD was almost twice those under LB and LD. Particularly striking was the absence of secondary stolons unless GA_3 was applied. Secondary stolon numbers reached a plateau at 50 ppm GA_3 under SD and LD and at 200 ppm under LB. The order of significant differences in secondary stolon numbers for the several GA_3 treatments were: at 50 ppm, SD = LB > LD; at 200 ppm, SD = LB < LD; and at 400 ppm, SD < LB = LD.

Stolon Length

GA_3 significantly increased the elongation of primary stolons, but concentration of the chemical was without significance (Table 2). Photoperiod did not affect elongation. Differences in concentration of GA_3 resulted in significant differences in elongation of secondary stolons, the order being 0 ppm < 50 ppm < 200 ppm = 400 ppm.

Figure 4 and Appendix Table B show a great stimulus to elongation of primary stolons at 50 ppm GA_3 under all photoperiods and no further significant effect at higher concentrations, except for the reduction at 200 ppm under SD. No secondary stolons developed unless the plants were treated with GA_3. Differences in elongation of secondary stolons were non-significant under SD. Under LB, however, the elongation at

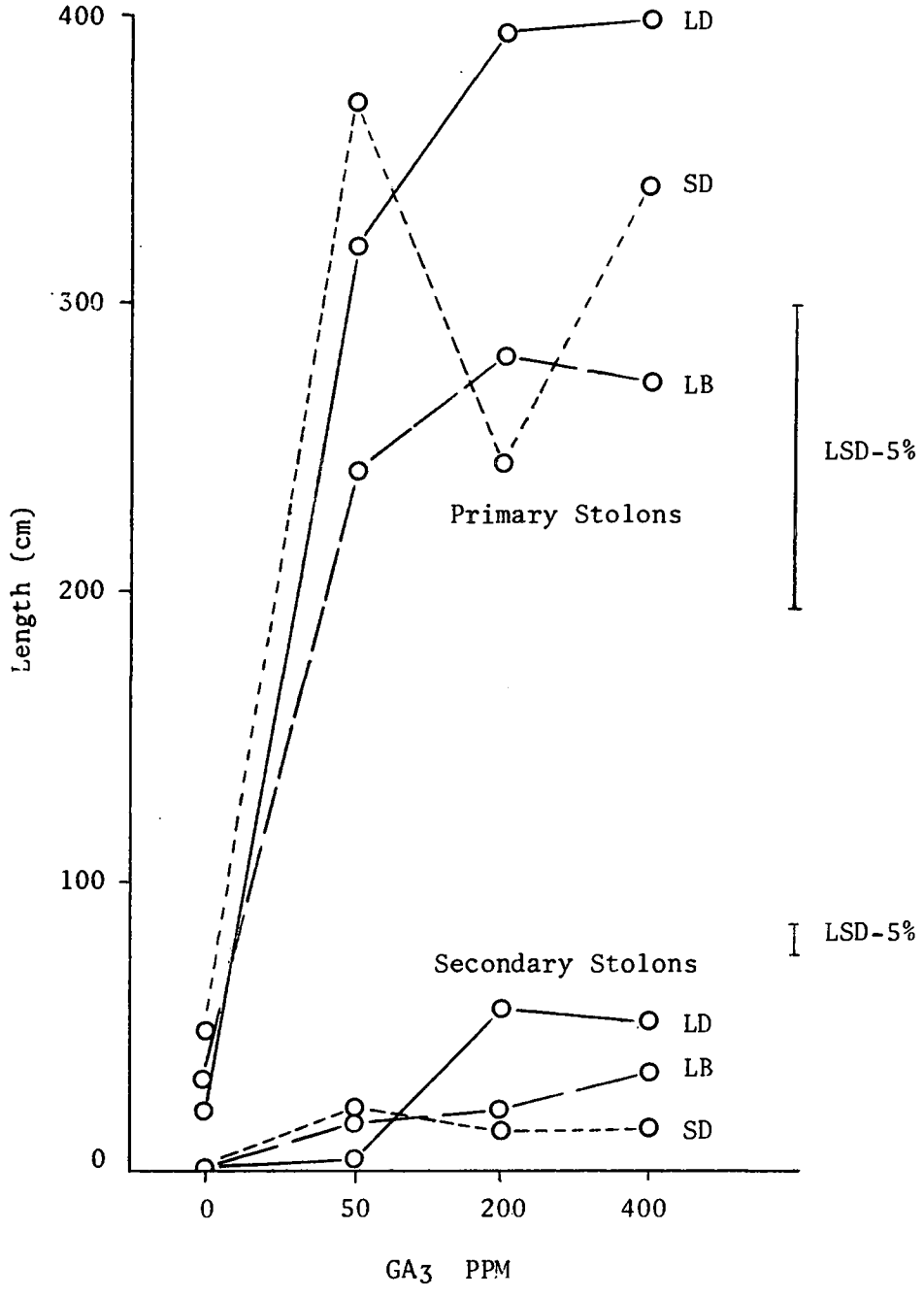

Figure 4. Effect of photoperiod and gibberellic acid (GA_3) on the total length per plant of primary and secondary stolons.

400 ppm was significantly greater than at the lower concentrations. While under LD, the order of significance for elongation of the secondary stolons was 50 ppm < 200 ppm = 400 ppm.

Internodes Per Stolon

Both photoperiod and GA_3 affected significantly the average numbers of internodes on primary and secondary stolons (Table 2). LB treatment tended to be most favorable for internode production on primary stolons; and LD, on secondary stolons. The orders of significant differences for internode numbers were: primary stolons, LD = SD, LD < LB, and SD = LB; secondary stolons, SD = LB < LD. The influence of GA_3 was more regular than was that of photoperiod on both types of stolons. The orders of significant differences were: Primary stolons, 0 ppm < 50 ppm = 200 ppm < 400 ppm; secondary stolons, 0 ppm < 50 ppm < 200 ppm = 400 ppm.

Figure 5 and Appendix Table C show the interaction of photoperiod and GA_3 on internode numbers per primary and secondary stolon. A primary stolon bore many more internodes than did a secondary one, but secondary stolons responded more uniformly to treatment. Except for the response under LD, 50 ppm GA_3 stimulated a sharp initial rise in primary internode numbers which then tended to plateau, although there were significant changes in both directions at specific combinations of GA_3 and photoperiod. The orders of significant differences in internode numbers on primary stolons at the several GA_3 concentrations because of photoperiod were: 0 ppm, no significant differences; 50 ppm, SD < LB = LD; 200 ppm, LD = SD < LB; and 400 ppm, LD < LB < SD.

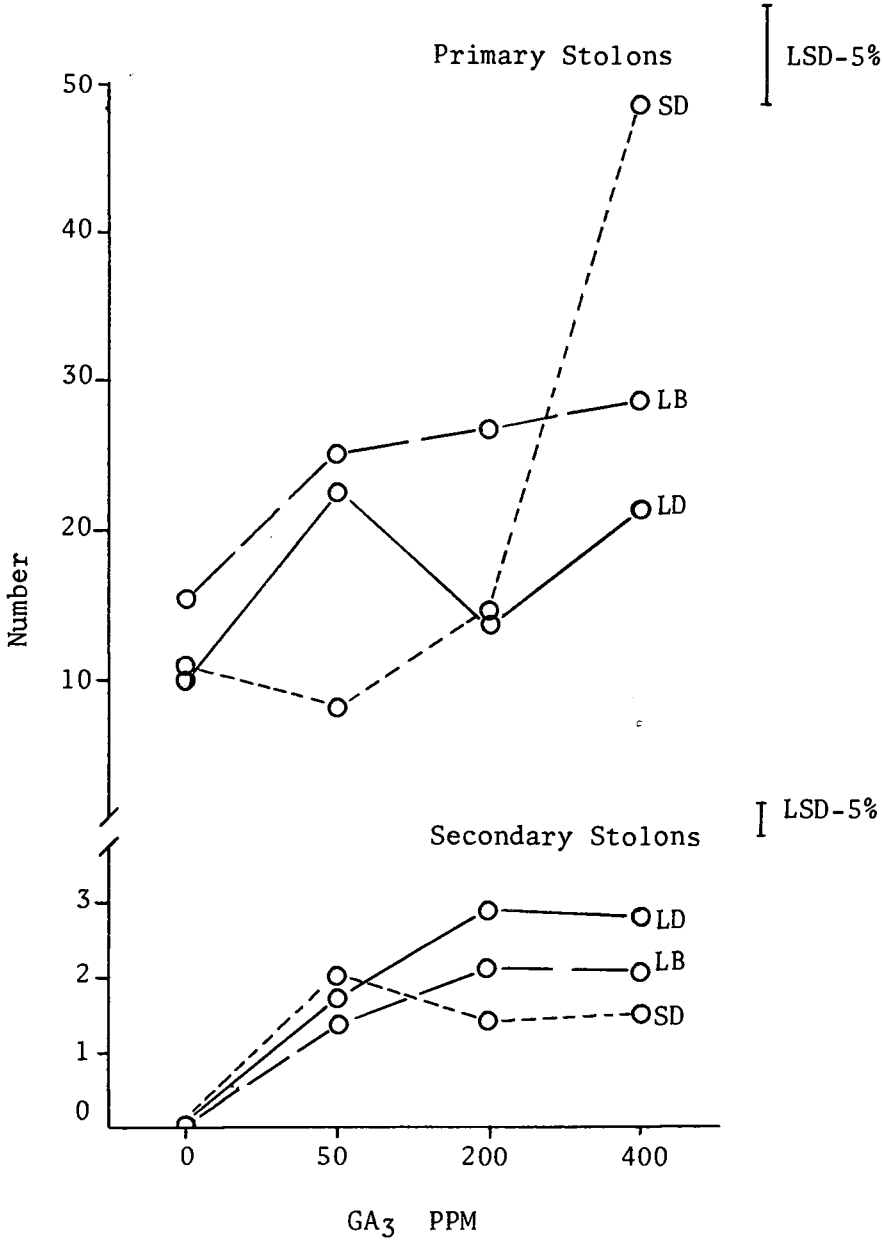

Figure 5. Effect of photoperiod and gibberellic acid (GA_3) on the number of internodes per primary and secondary stolon.

The internode number under SD at 400 ppm GA_3 was almost twice that of any other treatment. The orders of significant differences under the photoperiod treatments because of GA_3 were: under SD, 50 ppm = 0 ppm, 50 ppm < 200 ppm, 0 ppm = 200 ppm, 0 ppm < 400 ppm, 200 ppm = 400 ppm; under LB, 0 ppm < 50 ppm = 200 ppm = 400 ppm; under LD, 0 ppm = 200 ppm < 50 ppm = 400 ppm. The response per secondary stolon is thus seen not to fit a regular pattern.

The family of curves for internodes per secondary stolon (Figure 5) were of much less magnitude than those for internodes per primary stolon, but they were more regular. In general, LD treatment was more favorable than were LB and SD. The orders of significant differences in these internodes at the several GA_3 concentrations because of photoperiod were: 0 ppm, no secondary stolons; 50 ppm, LB = LD < SD; and at 200 and 400 ppm, SD < LB < LD. The orders under the photoperiodic treatments because of GA_3 were: under SD, 0 ppm < 200 ppm = 400 ppm < 50 ppm; and under LB and LD, 0 ppm < 50 ppm < 200 ppm = 400 ppm.

Rosette Leaves

GA_3 and photoperiod had no significant effects on the length and width of the leaf blades (Table 2). Photoperiod also had no significant main effect on petiole length, but GA_3 above 50 ppm significantly increased their length, those at 50 ppm were not different from those at the higher concentrations. Figure 6 and Appendix Table D show a significant reduction in petiole length at 50 ppm under SD. Under LB, the petioles tended to lengthen at progressively higher concentrations of GA_3, but their lengths at 0 to 200 ppm GA_3 were not significantly

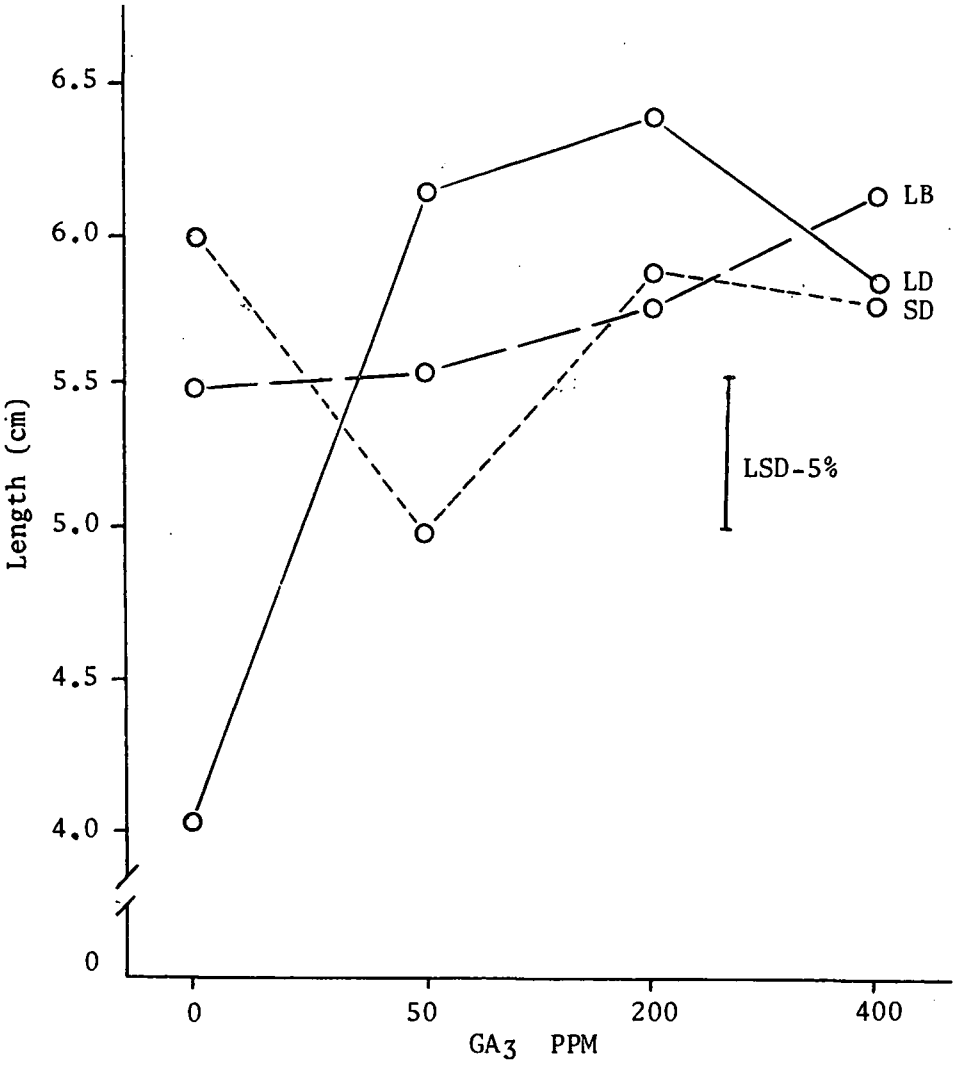

Figure 6. Effect of gibberellic acid (GA_3) and photoperiod on petiole length of rosette leaves.

different, nor were they at 200 and 400 ppm. Under LD, all concentrations of GA_3 induced significant elongation of the petioles compared with the control, peaking at 200 ppm. Their lengths at 50 and 200 ppm GA_3 and 50 and 400 ppm were not significantly different.

Primary Stolon Leaves

Leaves on primary stolons were more sensitive to GA_3 and photoperiod than were rosette leaves (Table 2). The longest and shortest leaves were produced under LD and LB treatments, respectively, but those under LB were not significantly different from those under SD which in turn were different from the LD leaves. All concentrations of GA_3 caused the leaves to be significantly longer than the control leaves, but the differences in length because of GA_3 treatment were non-significant. LD photoperiodic treatment resulted in a significant broadening of the leaves. The effect of GA_3 on width paralleled its effect on length.

Figure 7 and Appendix Table E show that the interaction of photoperiod and GA_3 on length and width of the leaf blade were similar, but differed in magnitude. The response to LD treatment without GA_3 equalled that of SD and LB with GA_3. Concentrations above 50 ppm GA_3 had no further effect on the dimensions of the leaf blades.

The pattern for elongation of petioles superficially resembled that for the stimulation in length and width of the leaf blades (Figure 8 and Appendix Table E). LD alone stimulated maximum elongation which equalled that at 50 and 400 ppm GA_3, while the petioles at 200 ppm were significantly shorter than the others. These petioles at 200 ppm were

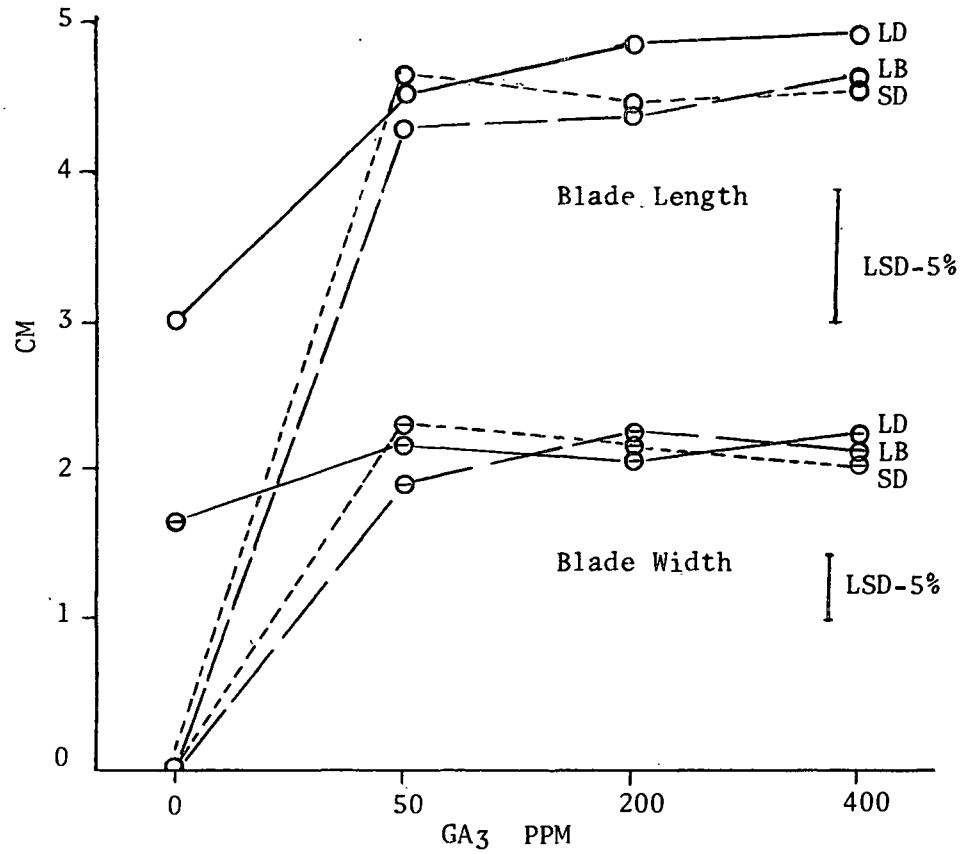

Figure 7. Effect of photoperiod and gibberellic acid (GA_3) on blade length and width of primary stolon leaves.

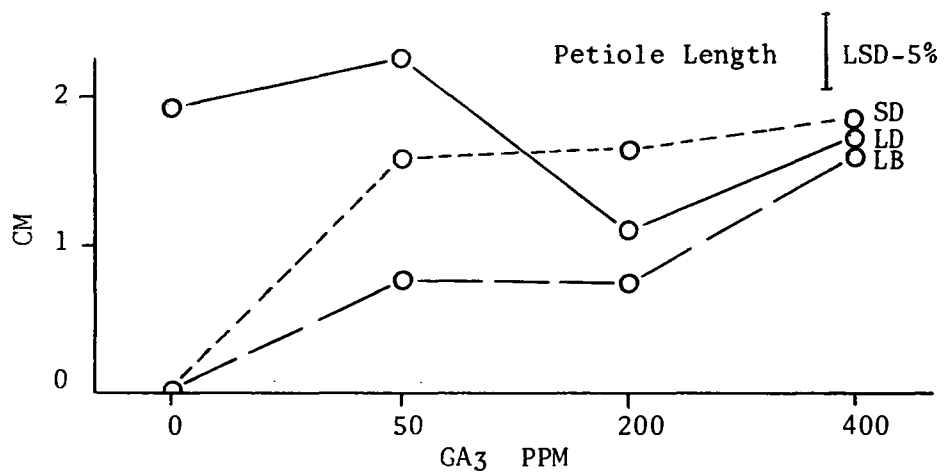

Figure 8. Effect of photoperiod and gibberellic acid (GA_3) on petiole length of primary stolon leaves.

the only ones under LD which were not significantly longer than or equal to those under SD and LB. LB treatment was least favorable for elongation of petioles, and it was only at 400 ppm GA_3 that petioles under this photoperiod equalled in length those of the other treatments.

Weight of Entire Plant and Organs

Except for increased dry weight of primary stolons under LD at 200 and 400 ppm GA_3, experimental treatment did not significantly affect the dry weight of the plant nor its organs (Table 3 and Appendix Table F). The fresh weight of the plant, primary and secondary stolons, and primary stolon leaves, however, were significantly affected (Table 3). Treatment did not affect the fresh weight of the rosette leaves nor of the roots. Photoperiod did not affect fresh weight of the entire plant, but all GA_3 concentrations were equally effective. Photoperiod did not affect fresh weight of primary stolons, but with each increment in concentration of GA_3 up to 200 ppm the increases in fresh weight were significant, as was the decrease at 400 ppm. Fresh weight of the primary stolons at 50 and 400 ppm were not significantly different. The order of significant differences for fresh weight of secondary stolons because of photoperiod was: SD = LB, SD < LD, and LB = LD; because of GA_3, 0 ppm = 50 ppm < 200 ppm = 400 ppm. Photoperiod did not affect fresh weight of primary stolon leaves, but the increasing concentrations of GA_3 applied was paralleled by a non-significant upward trend in fresh weight of the leaves.

Figure 9 and Appendix Table G show that photoperiod and GA_3 interacted to affect fresh weight of the entire plant and some of its organs.

Table 3. Main effects of photoperiod and gibberellic acid (GA_3) treatment on the dry and fresh weights of the entire plant and organs. (gm)

	GA_3 concentration (ppm)				Photoperiod			
	0	50	200	400	SD	LB	LD	LSD-5%
Dry weight								
Entire plant	1.81	2.34	2.57	2.72	2.26	2.01	2.82	n.s.
Primary stolons	0.07	0.44	0.52	0.50	0.35	0.29	0.52	0.36
Secondary stolons	0.00	0.02	0.04	0.09	0.04	0.03	0.06	n.s.
Rosette leaves	0.99	0.85	1.00	0.94	0.95	0.89	1.00	n.s.
Primary stolon leaves	0.25	0.63	0.57	0.50	0.47	0.35	0.64	n.s.
Roots	0.56	0.40	0.43	0.44	0.44	0.39	0.50	n.s.
Fresh weight								
Entire plant	12.28	16.12	18.79	18.62	16.28	15.19	17.89	3.29
Primary stolons	0.63	3.23	4.33	4.02	2.92	2.62	3.87	1.07
Secondary stolons	0.00	0.21	0.41	0.48	0.19	0.24	0.41	0.21
Rosette leaves	6.93	5.84	7.05	6.44	6.64	6.73	6.31	n.s.
Primary stolon leaves	1.79	4.22	4.35	5.12	3.51	3.35	4.74	1.28
Roots	2.97	2.23	2.62	2.43	3.83	3.02	3.40	n.s.

In general, SD at low concentrations of GA_3 and LD at higher concentrations tended to favor gains in fresh weight of the entire plant. The orders of significant differences in fresh weight of the entire plant at the several concentrations of GA_3 because of photoperiod were: at 0 ppm, LD = LB < SD; at 50 ppm, LB < SD = LD; at 200 ppm, SD < LB = LD; and at 400 ppm, SD = LB < LD. The orders of significant differences under the several photoperiods because of GA_3 were: under SD, 0 ppm = 200 ppm = 400 ppm < 50 ppm; under LB, 0 ppm = 50 ppm < 200 ppm = 400 ppm; and under LD, 0 ppm < 50 ppm < 200 ppm = 400 ppm.

The families of curves in Figure 10 showing the effects of GA_3 and photoperiod on fresh weights of primary and secondary stolons were similar in trend, but not in magnitude (Appendix Table G). Primary stolons were considerably heavier than secondary stolons, and, of course, none of the latter were produced in the absence of GA_3, irrespective of photoperiod, except at 50 ppm under LD. The most pronounced responses were the sharp increases in weight of primary stolons at 50 ppm GA_3 under all photoperiods, of secondary stolons at 50 ppm under SD and LB and at 200 ppm under LD. The orders of significant differences in fresh weight of primary stolons at the several concentrations of GA_3 because of photoperiod were: at 0 ppm, SD = LB = LD; at 50 and 400 ppm, SD = LB < LD; and at 200 ppm, SD < LB < LD. The orders of significant differences under the several photoperiods because of GA_3 were: under SD, 0 ppm < 50, 200, and 400 ppm and 200 ppm = 400 ppm < 50 ppm; under LB, 0 ppm < 50, 200, and 400 ppm and 50 ppm = 400 ppm < 200 ppm; and under LD, 0 ppm < 50 ppm < 200 ppm = 400 ppm. The orders of significant differences in fresh weight of

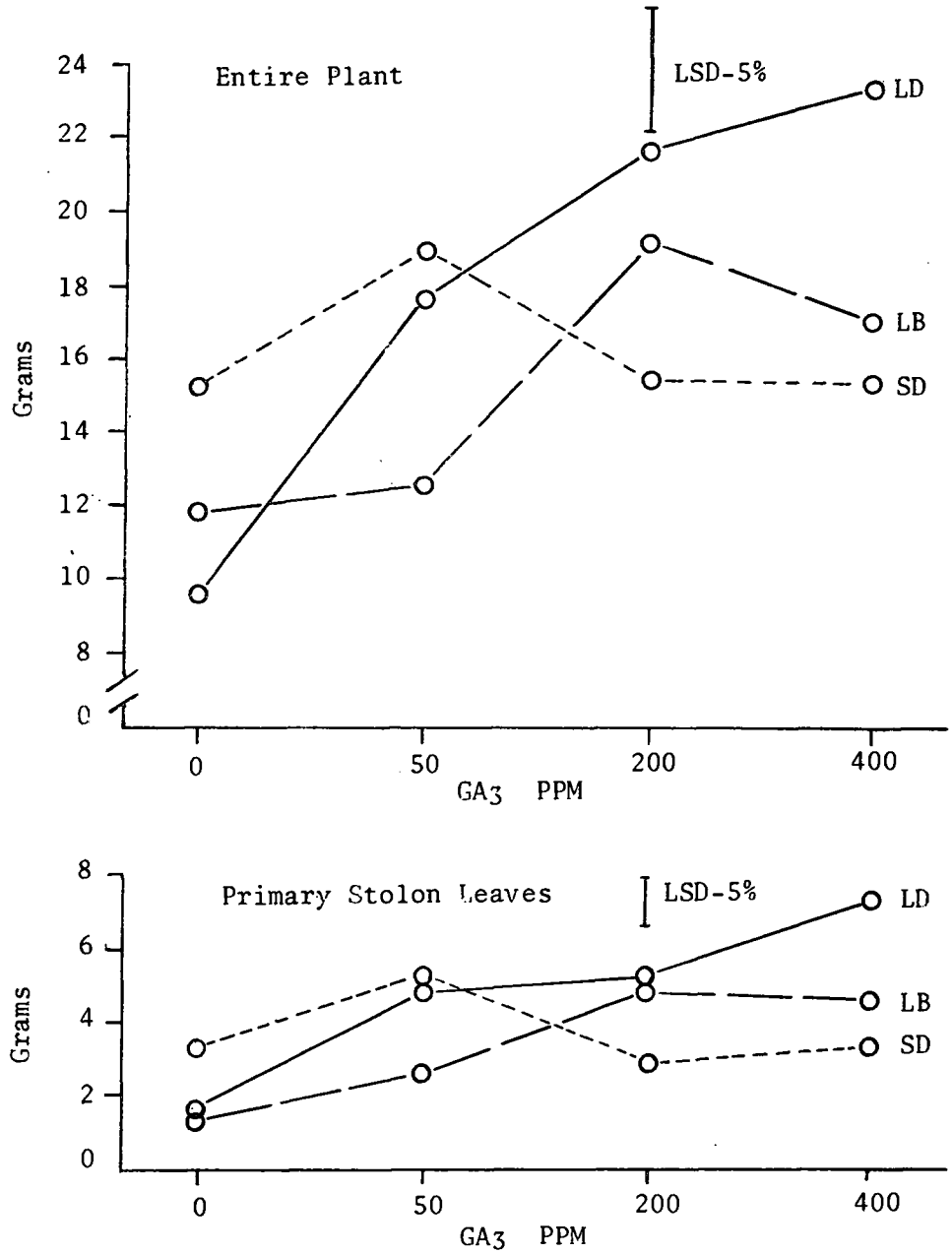

Figure 9. Effect of photoperiod and gibberellic acid (GA_3) on the fresh weight of the entire plant and primary stolon leaves.

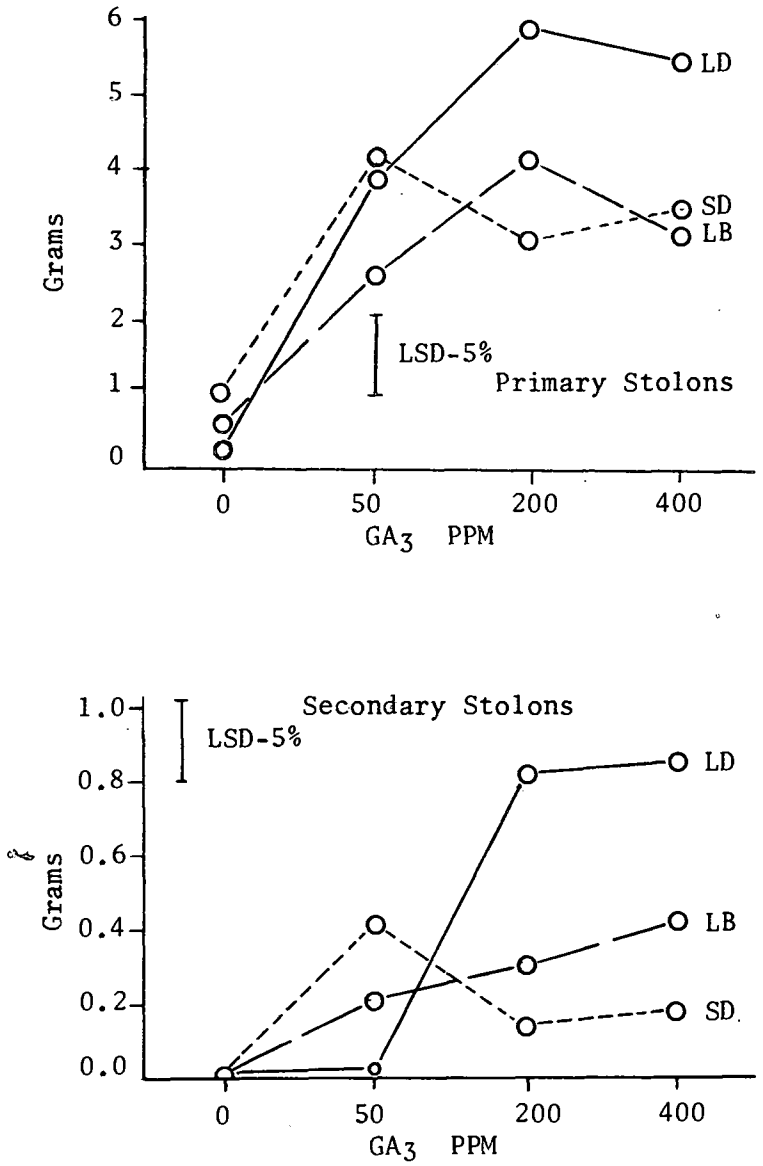

Figure 10. Effect of photoperiod and gibberellic acid (GA_3) on the fresh weight of primary and secondary stolons.

secondary stolons at the several concentrations of GA_3 because of photoperiod were: 0 ppm, no stolons; at 50 ppm, LB = LD < SD; at 200 ppm, SD = LB < LD; and at 400 ppm, SD < LB < LD. The orders of significant differences in fresh weight of secondary stolons under the several photoperiods because of GA_3 were: under SD, 0 ppm = 200 ppm = 400 ppm < 50 ppm; and under LB and LD, 0 ppm = 50 ppm < 200 ppm = 400 ppm.

The effects of GA_3 and photoperiod on fresh weight of primary stolon leaves are graphed in Figure 9. In general, LD and the higher concentrations of GA_3 favored gain in fresh weight (Appendix Table G). The orders of significant differences at the several GA_3 concentrations because of photoperiod were: at 0 and 50 ppm, LB = LD, LB < SD, and LD = SD; at 200 ppm, SD = LB, LB = LD, and SD < LD; and at 400 ppm, SD = LB < LD. The orders of significant differences under the several photoperiods because of GA_3 were: under SD, 0 ppm = 200 ppm = 400 ppm < 50 ppm; under LB, 0 ppm < 50 ppm < 200 ppm = 400 ppm; and under LD, 0 ppm < 50 ppm = 200 ppm < 400 ppm.

Experiment III

In this experiment the effects of five concentrations of GA_3 on plants grown under prevailing daylength were studied. Appendix Table H presents a compilation of all data for this experiment.

Stolons

Although primary stolon numbers per plant tended to increase at progressively higher concentrations of GA_3 applied, the increases in

number beyond 50 ppm GA_3 were non-significant (Figure 11). The same statistical relationship between numbers of secondary stolons and GA_3 concentration was found as for primary stolons, but the magnitude of response was greater in the case of secondary stolons. GA_3 was necessary, furthermore, before secondary stolons were produced.

The relation between number and length of primary and secondary stolons was diametrically opposite, i.e., lesser numbers but longer primary stolons versus greater numbers but shorter secondary stolons. With both kinds of stolons, 50 ppm GA_3 stimulated the greatest increment in stolon elongation. Primary stolons elongated in a step-wise manner with each progressively greater concentration of GA_3 applied up to 300 ppm. After the initial elongation at 50 ppm GA_3, elongation of secondary stolons was not affected by concentrations up to 300 ppm. A significant reduction in elongation of both kinds of stolons occurred at 400 ppm GA_3.

Internodes

The families of curves for internode number per plant and internode length per stolon form patterns similar in shape and magnitude (Figure 12). Total primary internodes per plant and average internode length per primary and secondary stolon increased in a step-wise manner with each progressively higher concentration of GA_3 up to 300 and 200 ppm, respectively. After the initial significant increase at 50 ppm GA_3, neither total internode number per plant nor average internode length per stolon responded differently until the concentration of GA_3 reached 300 ppm. At first glance, it appears that the value for

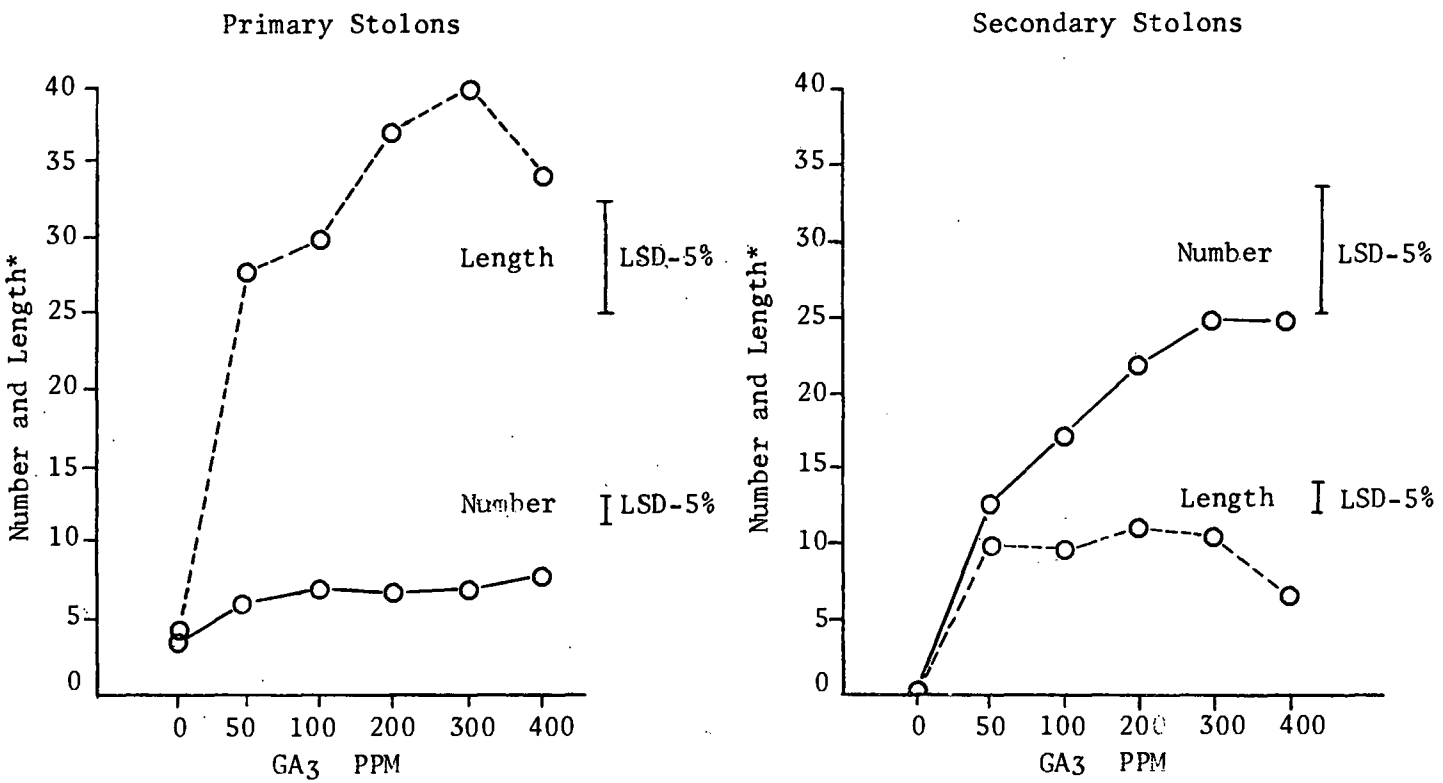

Figure 11. Effect of gibberellic acid (GA_3) on the numbers of primary and secondary stolons per plant and the average length per primary and secondary stolon (under prevailing daylengths of August and September).

* Length in centimeters.

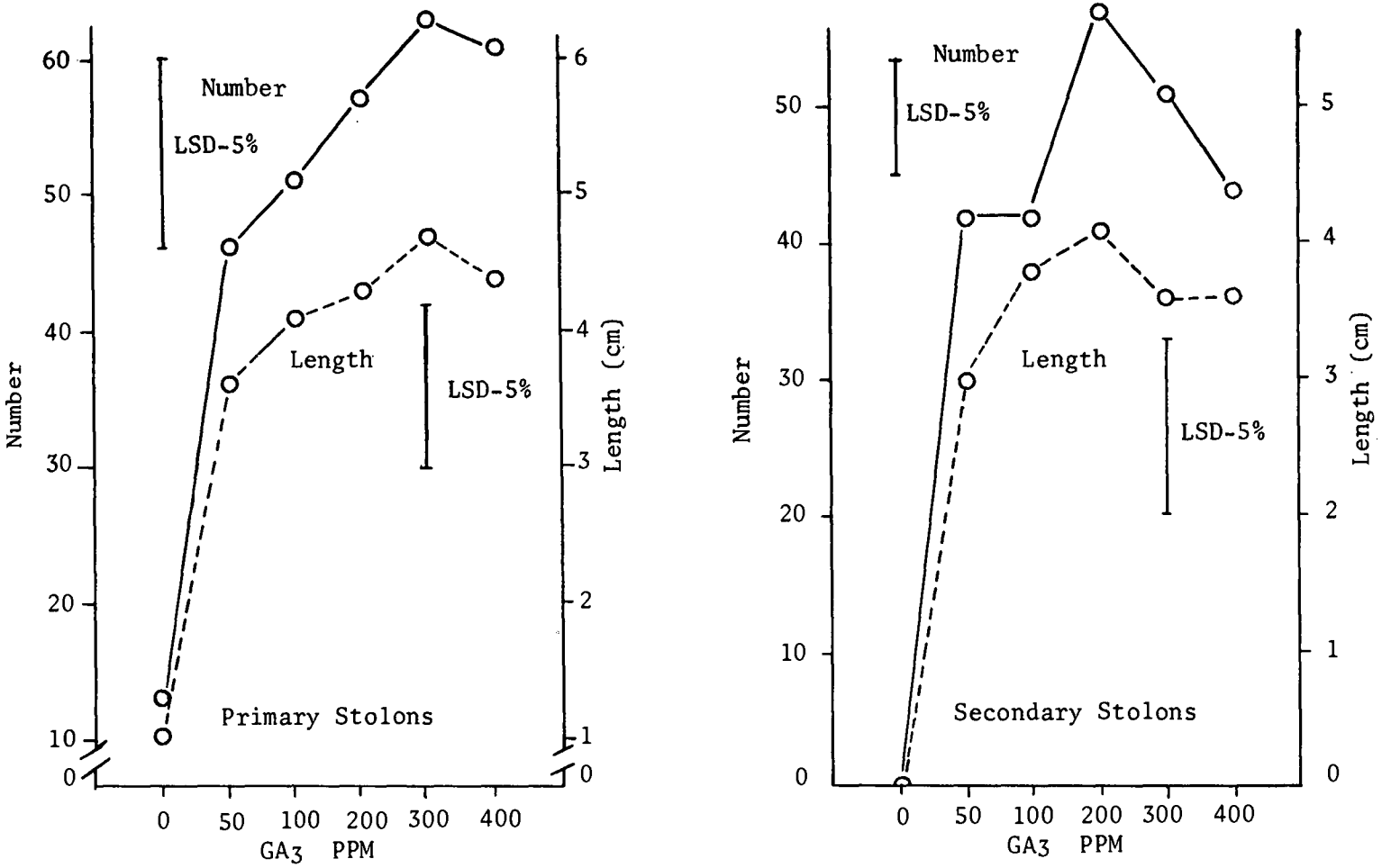

Figure 12. Effect of gibberellic acid (GA_3) on number of primary and secondary internodes per plant and average internode length per primary and secondary stolon (under prevailing daylengths of August and September).

average length of stolon does not agree with the values for internode numbers and internode length. This is due to the fact that stolon length represents average length per stolon while the internode number represents total internodes per plant and internode length represents average length per stolon. Therefore, the product of internode number by internode length represents the total length of stolon per plant rather than average length per stolon. For complete statistical data see Table H in the appendix.

Leaves

Leaves were separated into those on rosette and those on primary stolons. Rosette leaves were present at the time of the GA_3 treatment, but stolon leaves were produced after the GA_3 treatment.

The shape of the curves for rosette and stolon leaf number differed strikingly (Figure 13). That for rosette leaf number tended to be flat and that for primary stolon leaf number climbed sharply to 300 ppm GA_3. Although the statistical analysis showed a significant difference in rosette leaf number between control and 50, 300 and 400 ppm GA_3 treatments, only 50 ppm GA_3 reduced the rosette leaf numbers because all concentrations of GA_3 caused about 6 (3 leaf bearing nodes) of the original rosette leaves to be carried upward on the elongating primary stolon, and these leaves were then counted as stolon leaves. In general, numbers of primary stolon leaves tended to increase with progressively greater concentrations of GA_3 so that the order of significant differences was: 0 ppm < 50 ppm = 100 ppm < 200 ppm = 300 ppm = 400 ppm.

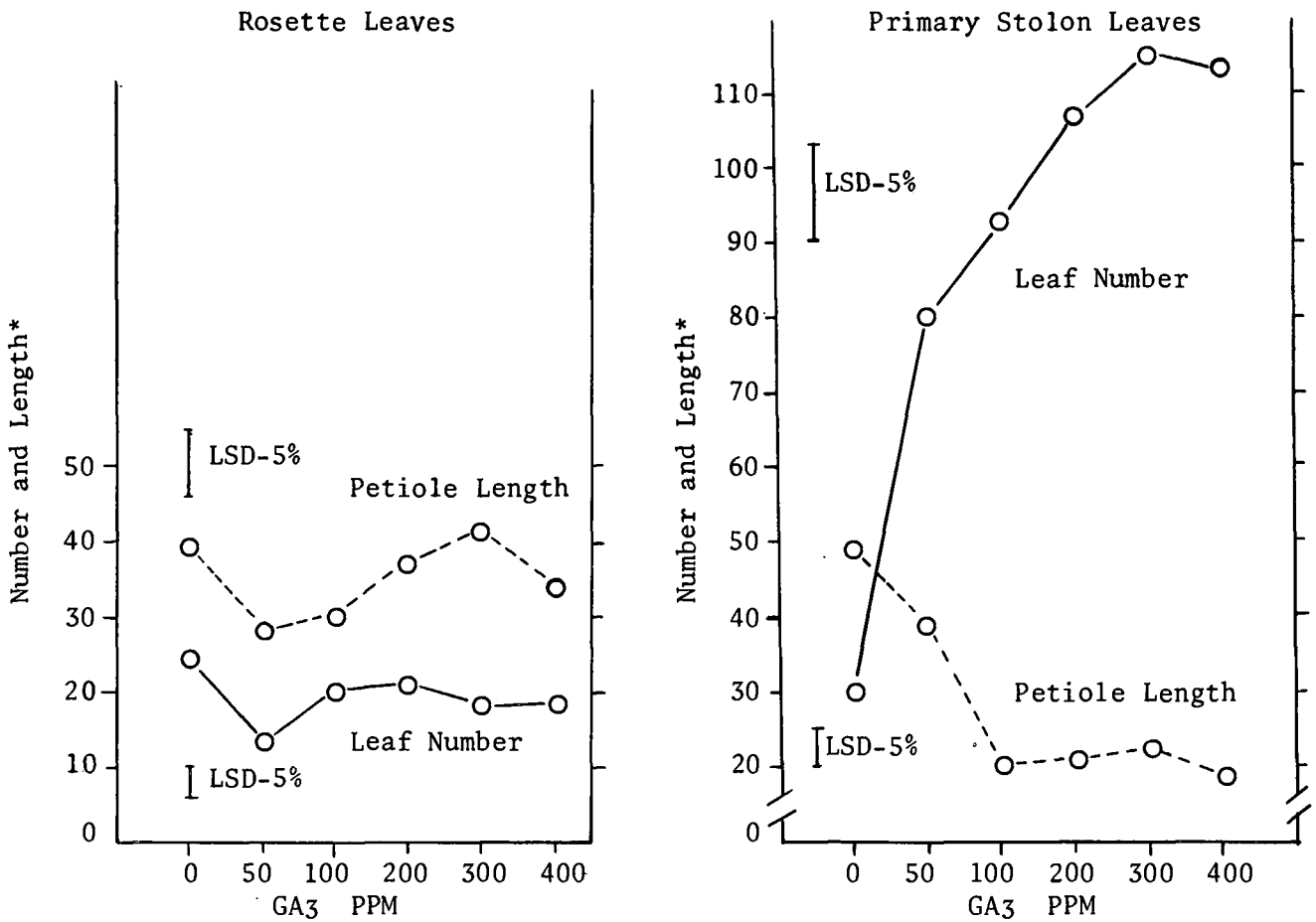

Figure 13. Effect of gibberellic acid (GA_3) on petiole length and leaf number of rosette and primary stolon leaves (under prevailing daylengths of August and September).

* Length in centimeters.

GA_3 significantly reduced the length of rosette leaf petioles only at 50, 100, and 400 ppm, but all concentrations of GA_3 reduced significantly the length of primary stolon leaf petioles (Figure 13). The reduction was pronounced and progressively greater at concentrations of 50 and 100 ppm GA_3, with concentrations above 100 ppm exerting no further depressive action.

The curves for leaf blade lengths for rosette and primary stolon leaves tended to be flat except for the significant decrease at 50 ppm and a slight peak at 100 ppm in both (Figure 14). The curves for rosette leaf blade width showed, except for 200 ppm GA_3, a significant reduction at all concentrations from the control, with the dip at 50 ppm being of lesser magnitude than it was in the curve for blade length. The curve for leaf blade width for primary stolons was essentially flat: a significant reduction occurred only at 50 ppm GA_3.

Weight of Entire Plant and Organs

In general, the effects of GA_3 on dry weight of the entire plant and on the aboveground parts were non-significant. All concentrations of GA_3 significantly increased the dry weight of primary stolons, but the increases were not significantly different from each other (Figure 15). Similarly, GA_3 increased significantly the dry weight of secondary stolons, and those at 50 and 400 ppm weighed significantly less than those at 200 ppm. The roots were less responsive to GA_3 than the aboveground part of the plant because none of the dry weights at any GA_3 concentration were different from the control. Dry weights at 50 and 300 ppm were significantly less than at 200 ppm.

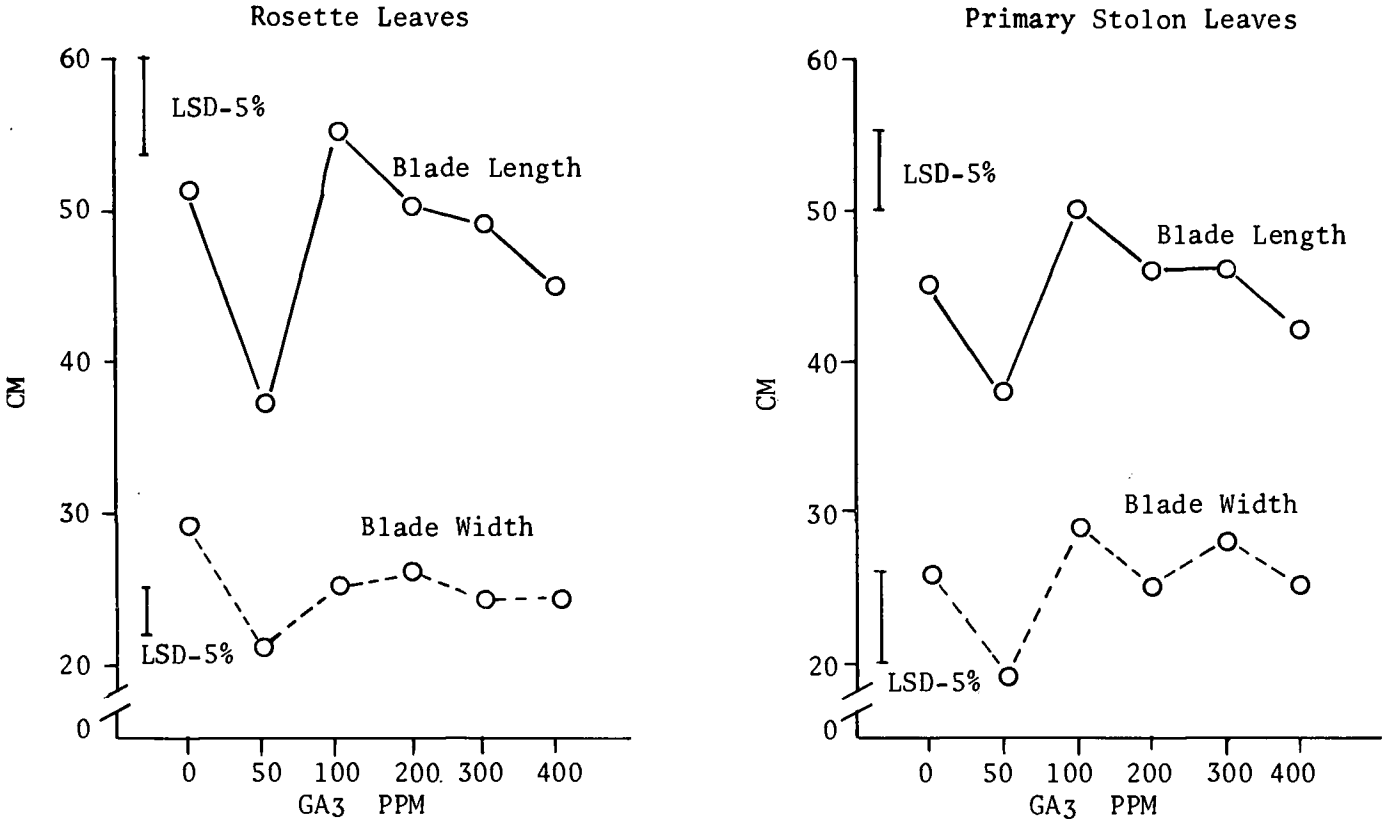

Figure 14. Effect of gibberellic acid (GA_3) on blade length and width of rosette leaves* and primary stolon leaves* (under prevailing daylengths of August and September).

* Total of 10 leaves.

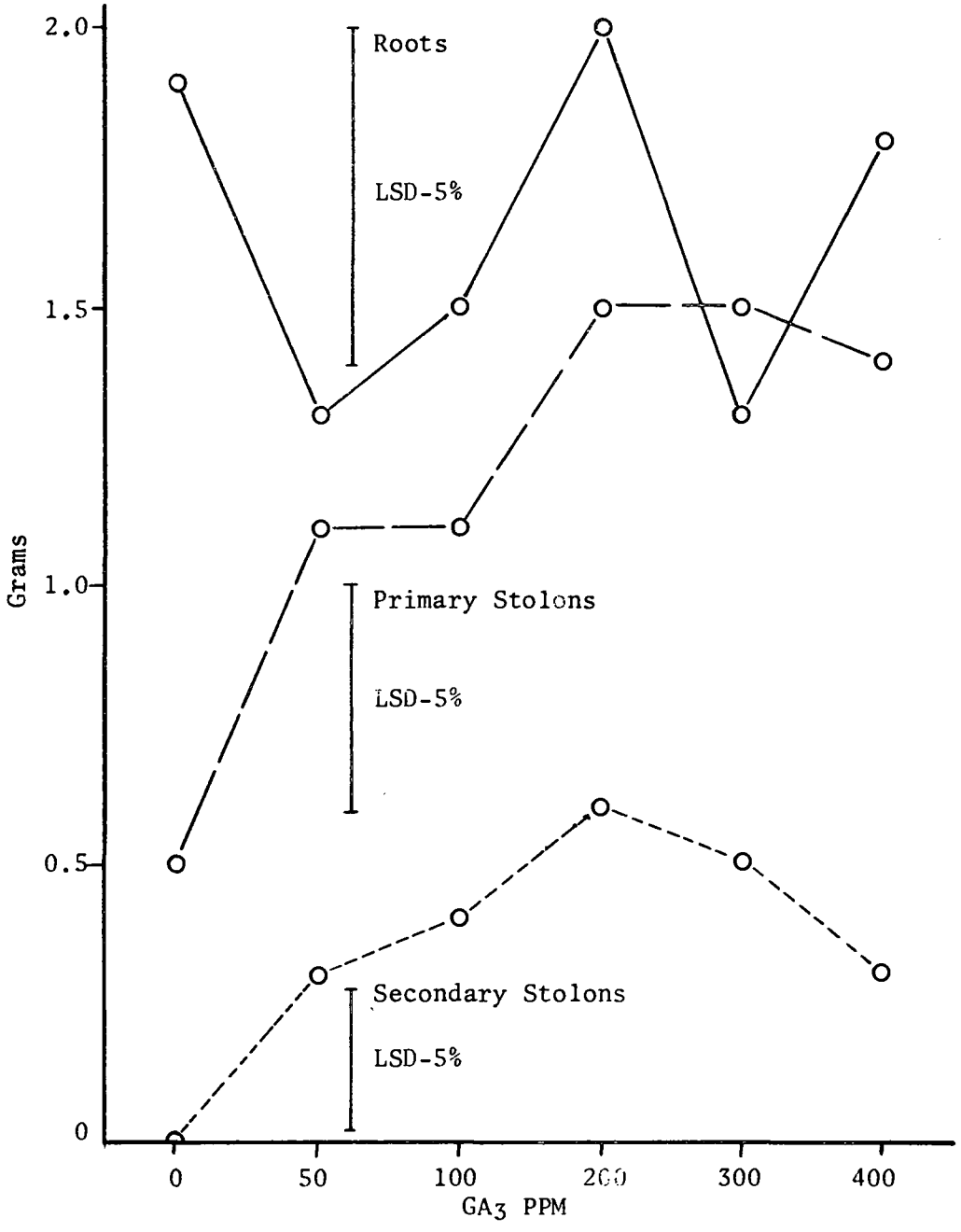

Figure 15. Effect of gibberellic acid (GA_3) on dry weight of primary stolons, secondary stolons and roots (under prevailing daylengths of August and September).

Except for a significant increase in fresh weight at 200 ppm, GA_3 did not significantly affect the fresh weight of the entire plant, but the fresh weight at 50 ppm was significantly less than at 400 ppm (Figure 16). The curves for fresh weight of primary and secondary stolons were similar in trend but not in magnitude. The primary stolons were considerably heavier than the secondary stolons. The only statistically significant change in fresh weight of primary stolons was the increase between the control and 100 ppm, with the order of significance being as follows: 0 ppm = 50 ppm, 0 ppm < 100 ppm, 200 ppm, 300 ppm and 400 ppm. The fresh weight of secondary stolons increased significantly with each increment in GA_3 concentration up to 200 ppm. Above 200 ppm GA_3 the curve turned downward with fresh weight at 400 ppm being significantly less than at 200 ppm but equal to that at 50 ppm. GA_3 did not significantly affect the fresh weights of leaves. All concentrations of GA_3 tended to decrease the fresh weight of roots compared to the control, but only those at 50 ppm were significantly less than the control. There were no differences in the fresh weight of roots at any of the GA_3 concentrations.

Experiment IV

In this experiment the effects of GA_3 and B995 on stolon growth were studied.

Stolons

Primary stolon numbers, aside from a small reduction at all concentrations of B995, were little affected by B995 or GA_3 (Table 4). Secondary stolons were produced only after treatment with GA_3; then,

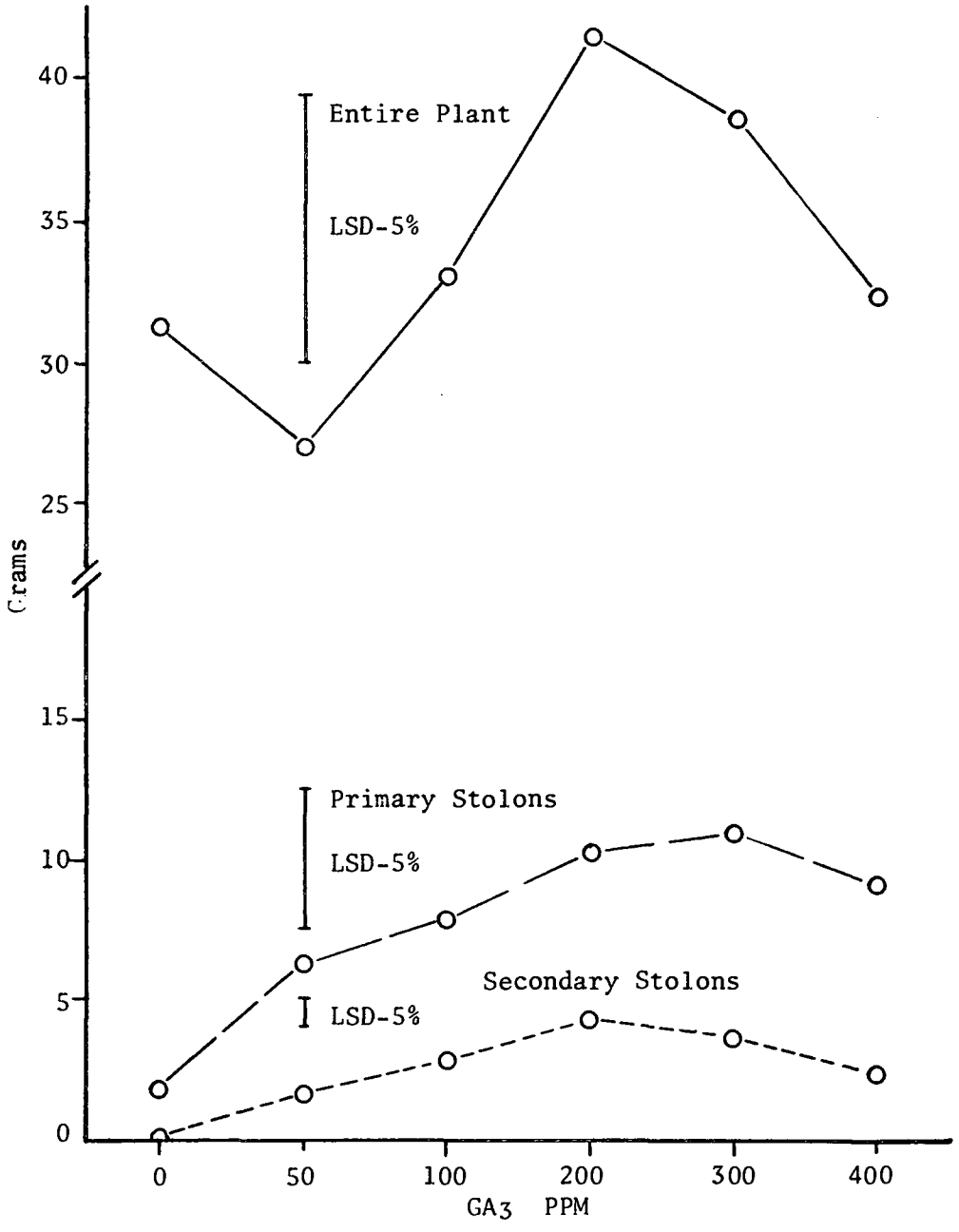

Figure 16. Effect of gibberellic acid (GA_3) on fresh weight of the entire plant, primary stolons, and secondary stolons (under prevailing daylengths of August and September).

the greater the concentration of B995 applied, the greater their subsequent production. GA_3 effected no change in primary stolon numbers regardless of whether the plants had or had not been treated previously with B995. But the production of secondary stolons was much enhanced, especially on those plants that had been treated with the higher concentrations of B995. Stolon numbers about doubled with each 500 ppm increment in the concentration above 1500 ppm.

Table 4. The stolon retarding effect of B995 and its reversal by GA_3. B995 was applied to 10 plants per treatment. Data were recorded 30 days later. Each 10-plant lot was then divided into two 5-plant sub-lots, one was treated with 300 ppm GA_3 ($+GA_3$), the other was not ($-GA_3$). Thirty days later data were recorded again, that is, 60 days from the time B995 was applied.

B995 conc.	After 1st 30 days		After 2nd 30 days			
			-GA_3		+GA_3	
	Primary	Secondary	Primary	Secondary	Primary	Secondary
	NUMBER OF STOLONS PER PLANT					
0	3.2	0	5.8	0	5.8	5.4
500	2.5	0	4.6	0	4.6	13.0
1000	1.4	0	2.6	0	2.4	16.6
1500	2.7	0	2.6	0	2.8	11.8
2000	1.9	0	2.0	0	1.8	20.8
2500	2.1	0	2.2	0	2.0	41.6
	TOTAL LENGTH OF STOLONS PER PLANT (cm)					
0	26.4[a]		55.0[a]		247.0[b]	
500	8.5		15.6		284.6	
1000	4.0		4.6		244.6	
1500	1.9		2.8		243.6	
2000	0.6		0.6		353.2	
2500	0.2		0.8		736.2	

a. All primary stolons. Secondary stolons were not produced unless GA_3 was applied to the plants.

b. Combined lengths of primary and secondary stolons.

Elongation of stolons was greatly retarded by B995 (Table 4). The retardation was directly proportional to the concentration. Above 1500 ppm, retardation was almost total. During the 30 days elapsing from the time GA_3 was applied, stolons on control plants and plants treated with 500 ppm B995 almost doubled their lengths, but those on the other B995-treated plants essentially did not elongate further. But stolon elongation on the GA_3-treated plants was stimulated greatly, irrespective of previous treatment. Total stolon lengths per plant were essentially equal on control plants and those treated with B995 at concentrations less than 2000 ppm. Above 1500 ppm B995, total stolon elongation was greatly stimulated, increasing about 45 per cent between 1500 and 2000 B995 and about 200 per cent between 2000 and 2500 ppm. Figure 17 shows the striking ability of GA_3 to stimulate stolon elongation on plants whose stolons had been almost completely retarded by applications of 2000 and 2500 ppm B995.

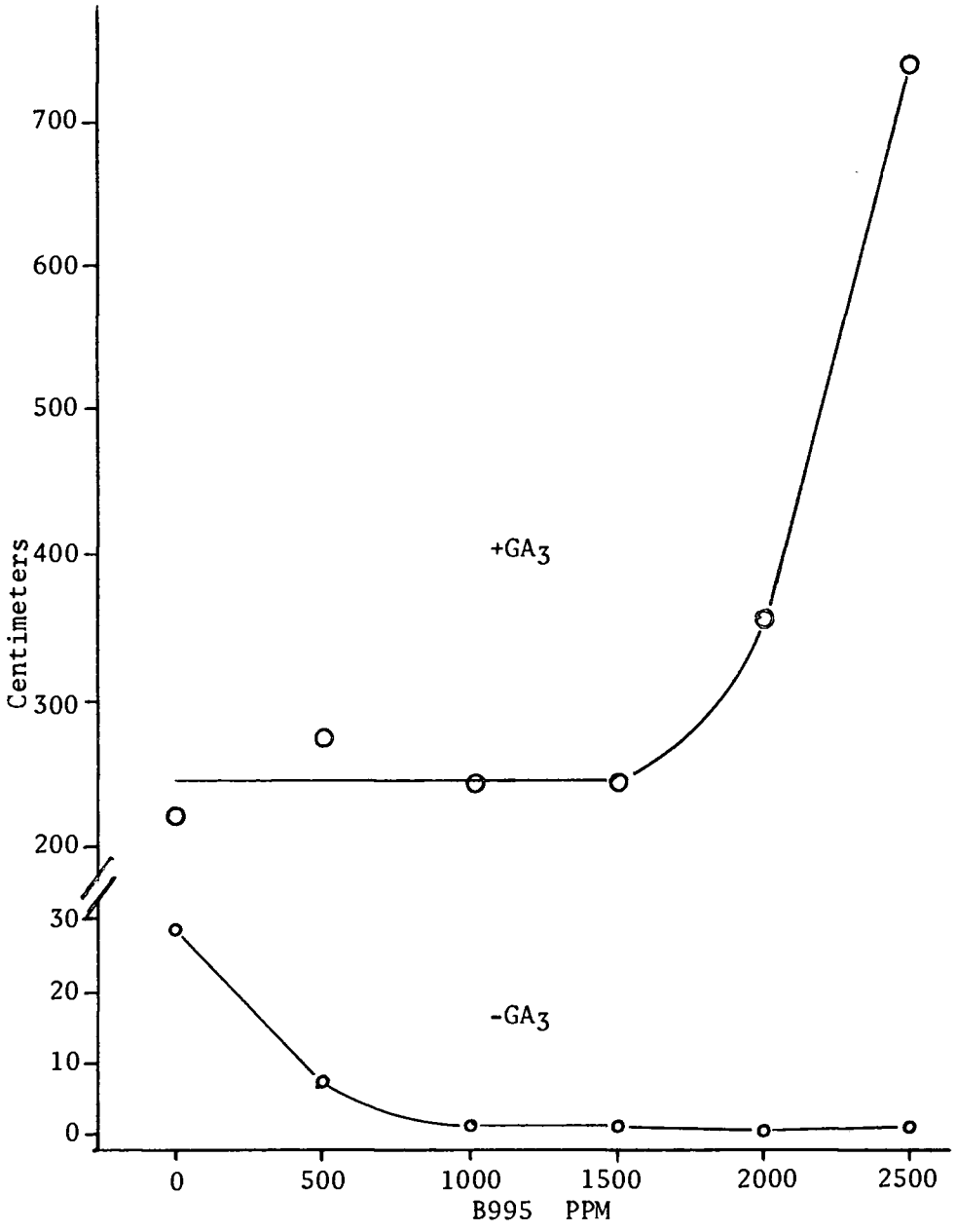

Figure 17. Net change in total length of stolons per plant after application of 300 ppm GA_3 to plants that had been treated with B995 thirty days earlier compared with change in length of stolons in the same 30-day period on plants that were not treated with GA_3.

DISCUSSION AND SUMMARY

The most important observations from these experiments on Ajuga reptans L. were:

1. Temperature controlled growth more than did photoperiod.
2. A light-break in the middle of a short-day dark period inhibited growth.
3. Gibberellic acid (GA_3) stimulated growth.
4. B995 inhibited growth.
5. Gibberellic acid (GA_3) overcame the B995 inhibition of growth and the greater the concentration of B995 applied, the more GA_3 stimulated growth.

The data of Experiment I show clearly that temperature controlled growth more than did photoperiod. Stolons became longer and leaf blades became longer and wider with progressively higher temperatures, but lengthening of the photoperiod from 8 to 16 hours did not elicit similar growth responses. These results supported the findings of Lewis and Went (1945), Banga (1952), and Barlow and Hancock (1959).

From Table 1 and information from other researchers, it seems that when adequate light was available for normal photosynthetic reactions growth was more dependent on temperature than on the length of the photoperiod.

Growth was inhibited, except for elongation of petioles, by a light-break in the middle of the short-day dark period compared to that under short-day and long-day treatments. This is puzzling because a light-break usually resembles long-day in its effects. However,

Highkin and Hanson (1954) have reported a similar growth inhibition by a light-break with tomato. Parker et al. (1946) reported that elongation of strawberry petioles was stimulated by a light-break treatment. Neither of the above authors attempted to explain the growth effects resulting from this treatment. But their papers were published before the discovery of phytochrome and before the implications of circadian rhythms in regulating plant growth and development were appreciated. I used incandescent lamps for the light-break illumination. These lamps emit light rich in the far-red part of the spectrum. It might be that this light-break irradiation created a ratio in the red and far-red absorbing forms of phytochrome unfavorable for growth of Ajuga. Bünning (1956) has contended that growth and development of plants are mediated by an endogenous rhythm having a 24-hour rhythmicity. During part of the rhythm, the photophile phase, light is favorable in its effects and during part, the skotophile phase, light is unfavorable. It might be that an endogenous rhythm is important in the growth of Ajuga. Perhaps the time of intercalation of the light-break into the short-day dark period coincided with the skotophile phase, hence growth was inhibited. These ideas can only be verified by further research. Liverman (1955) reported that the auxin level goes down during the dark period in both long-day and short-day plants. A light-break also caused a rise in the auxin content in soybean (Kujosawa 1960). Perhaps the stimulating effect of the light-break on elongation of petioles is related to such an increase in auxin level in Ajuga, although it is difficult to visualize the concomitant inhibition of growth of other parts of the plant.

Gibberellic acid stimulated growth irrespective of photoperiodic conditions. Production and elongation of stolons were the most striking responses elicited by GA_3. Total elongation of stolons was increased by GA_3 about 23 times in Experiment II and 29 times in Experiment III. These data agreed with those obtained with bean (Bukovac and Wittwer 1956, Greulach and Haesloop 1958), pea (Brian and Hemming 1955), and Fuchsia (Sachs and Bretz 1962).

The effects of applied gibberellic acid on apical dominance differ from species to species. It enhances apical dominance in some species and weakens it in others. Ajuga produced secondary stolons only after GA_3 was applied, indicating that apical dominance was weakened. The verb weakened is used because elongation of the primary stolons was also stimulated. Guttridge and Thompson (1963) and Gray (1957) also weakened apical dominance and stimulated the production of secondary stolons with strawberry and bean, respectively. These secondary stolons comprised 20% and 45% of total stolon length in Experiments II and III, respectively. Gibberellic acid did not stimulate the initiation of new nodes with their axillary buds, it only stimulated axillary buds already present to grow into stolons. This observation is in agreement with Lockhart (1956).

Although GA_3 stimulated concomitantly an increase in fresh weight with the increase in growth, dry weight was affected little. Results comparable to these were reported for soybean (Rappaport 1957) and bean and sweet corn (Bukovac and Wittwer 1957).

A major objective of my research was achieved when B995 suppressed the growth of stolons. The results show plainly that a treatment of

500 ppm B995 can prevent stolons from invading adjoining plants even though the Ajuga were grown in 2-inch plant bands.

The most exciting result was the complete reversal by GA_3 of the growth inhibition caused by B995. B995 does not kill or destroy plant cells, it simply slows down growth. Guttridge and McC Anderson (1966) reported similar results with strawberry. Their plants regained normal growth rate after treatment with GA_3. The growth stimulation elicited by GA_3 following application of low concentrations of B995 was comparable to that elicited by GA_3 alone. But following 2000 and 2500 ppm B995, which severely retarded growth, the great stimulation of growth by GA_3 suggests that the two materials acted synergistically. Sachs et al. (1960) and Sachs and Kofranek (1963) have reported similar responses with Chrysanthemum. It seems that GA_3 reactivated the mechanism that had been inhibited by B995, yielding a greater growth stimulation than could GA_3 itself. Similar observations are reported with Pharbitis and Bryophyllum (Wittwer and Tolbert 1960), strawberry (Guttridge and Gordon 1966), and cucumber (Halevy and Cathey 1963).

Important horticultural aspects of these experimental results are:

1. Nurserymen can retard the growth of Ajuga for at least 60 days with only one application of B995.
2. More plants can be grown in a smaller greenhouse area and their entanglement will be avoided.
3. One treatment with 300 ppm GA_3 will reactivate the plants immediately. The plants will then grow faster and become larger than normal.

4. Because GA_3 causes secondary stolons to be produced and the formerly retarded plants to grow faster, a lesser number of plants would need be planted to establish a groundcover on the same area.

Some nurserymen and gardeners might find the production of secondary stolons objectionable. Their control awaits further research and would be of horticultural and physiological interest.

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APPENDIX

Table A. Experiment I. The effect of temperature and photoperiod on stolons and stolon leaves (10 plants per treatment).

	Photoperiod	Temperature (°F) 50	60	70	Photoperiod average
Stolons per plant (No.)	SD	4.90	5.70	3.90	4.83
	LB	5.00	5.80	5.60	5.46
	LD	4.20	4.60	4.50	4.43
	Temperature average	5.03	5.36	4.66	LSD-5% = 0.58
Avg. stolon length (cm)	SD	15.03	16.95	24.06	18.68
	LB	13.30	16.64	20.04	16.66
	LD	12.82	23.93	28.16	21.63
	Temperature average	13.72	19.17	24.08	LSD-5% = 4.12
Avg. leaf blade length (cm)	SD	2.40	4.08	4.59	3.69
	LB	2.28	3.49	5.56	3.77
	LD	2.70	3.60	4.65	3.65
	Temperature average	2.46	3.72	4.93	LSD-5% = 1.63
Avg. leaf blade width (cm)	SD	1.99	2.70	3.00	2.56
	LB	1.83	2.37	3.01	2.40
	LD	1.89	2.31	3.19	2.46
	Temperature average	1.90	2.46	3.07	LSD-5% = 0.93
Avg. petiole length (cm)	SD	1.86	2.83	2.52	2.40
	LB	2.30	4.14	3.37	3.27
	LD	2.00	2.10	2.19	2.43
	Temperature average	2.05	3.36	3.69	LSD-5% = 0.89

Table B. Experiment II. The effect of photoperiod and gibberellic acid (GA_3) treatment on number and length of primary and secondary stolons.

	Photoperiod	GA_3 concentration (ppm) 0	50	200	400	Photoperiod average
Stolons per plant (No.)						
Primary stolon	SD	4.70	6.00	6.70	4.70	5.50
	LB	1.70	4.00	6.00	3.70	3.90
	LD	2.30	5.70	7.30	7.00	5.60
	GA_3 average	2.90	5.23	6.66	5.13	LSD-5% = 0.97
Secondary stolon	SD	0.00	6.30	5.70	4.70	4.20
	LB	0.00	8.70	7.30	10.30	6.60
	LD	0.00	2.30	10.00	9.30	5.40
	GA_3 average	0.00	5.80	7.70	8.10	LSD-5% = 2.60
Stolon length per plant (cm)						
Primary stolon	SD	49.00	368.00	248.00	342.00	252.00
	LB	32.00	241.00	281.00	273.00	212.00
	LD	18.00	319.00	392.00	396.00	281.00
	GA_3 average	33.00	309.00	307.00	337.00	LSD-5% = 102.35
Secondary stolon	SD	0.00	21.00	13.00	13.00	12.00
	LB	0.00	17.00	20.00	37.00	18.00
	LD	0.00	5.00	62.00	57.00	31.00
	GA_3 average	0.00	14.00	31.00	36.00	LSD-5% = 9.70

Table C. Experiment II. The effect of photoperiod and gibberellic acid (GA_3) treatment on number of internodes per primary and secondary stolon.

	Photoperiod	GA_3 concentration (ppm) 0	50	200	400	Photoperiod average
Internodes per stolon (No.)						
Primary stolon	SD	10.20	8.30	14.60	48.70	20.50
	LB	13.30	25.00	26.80	27.60	23.70
	LD	10.00	22.50	14.00	21.40	17.00
	GA_3 average	11.80	18.60	18.30	32.60	LSD-5% = 5.82
Secondary stolon	SD	0.00	2.06	1.40	1.49	1.24
	LB	0.00	1.38	2.05	2.04	1.37
	LD	0.00	1.73	2.90	2.80	1.86
	GA_3 average	0.00	1.72	2.12	2.11	LSD-5% = 0.38

Table D. Experiment II. The effect of photoperiod and gibberellic acid (GA_3) treatment on rosette leaves.

	Photoperiod	GA_3 concentration (ppm) 0	50	200	400	Photoperiod average
Rosette leaves (cm)						
Blade length	SD	6.84	5.24	6.02	5.99	6.07
	LB	5.98	5.95	6.25	6.52	6.18
	LD	4.88	5.43	6.79	6.43	5.88
	GA_3 average	5.90	5.54	6.35	6.31	LSD-5% = n.s.
Blade width	SD	2.89	2.31	2.36	2.30	2.44
	LB	2.47	2.55	2.63	2.65	2.58
	LD	2.04	2.41	2.75	2.51	2.43
	GA_3 average	2.47	2.39	2.58	2.49	LSD-5% = n.s.
Petiole length	SD	5.97	4.97	5.79	5.73	5.62
	LB	5.47	5.51	5.75	6.17	5.73
	LD	4.05	6.14	6.38	5.75	5.58
	GA_3 average	5.16		5.97	5.88	LSD-5% = 0.51

Table E. Experiment II. The effect of photoperiod and gibberellic acid (GA_3) on primary stolon leaves.

	Photoperiod	GA_3 concentration (ppm) 0	50	200	400	Photoperiod average
Primary stolon leaves (cm)						
Blade length	SD	0.00	4.64	4.48	4.56	3.42
	LB	0.00	4.29	4.45	4.58	3.33
	LD	3.00	4.54	4.85	4.90	4.32
	GA_3 average	1.00	4.49	4.59	4.68	LSD-5% = 0.91
Blade width	SD	0.00	2.27	2.16	2.04	1.62
	LB	0.00	1.90	2.28	2.06	1.56
	LD	1.62	2.19	2.15	2.21	2.04
	GA_3 average	0.54	2.12	2.20	2.10	LSD-5% = 0.43
Petiole length	SD	0.00	1.58	1.61	1.85	1.26
	LB	0.00	0.75	0.74	1.59	0.77
	LD	1.93	2.25	0.13	1.76	1.77
	GA_3 average	0.64	1.53	1.16	1.73	LSD-5% = 0.50

Table F. Experiment II. The effect of photoperiod and gibberellic acid (GA_3) treatment on dry weight of entire plant and organs.

	Photoperiod	GA_3 concentration (ppm) 0	50	200	400	Photoperiod average
Dry weight (gm)						
Entire plant	SD	2.05	2.66	2.04	2.27	2.26
	LB	1.63	1.60	2.54	2.25	2.01
	LD	1.76	2.77	3.13	3.64	2.82
	GA_3 average	1.81	2.34	2.57	2.72	LSD-5% = n.s.
Primary stolons	SD	0.11	0.48	0.33	0.43	0.35
	LB	0.05	0.29	0.48	0.32	0.29
	LD	0.05	0.55	0.74	0.75	0.52
	GA_3 average	0.07	0.44	0.52	0.50	LSD-5% = 0.36
Secondary stolons	SD	0.00	0.04	0.02	0.08	0.04
	LB	0.00	0.02	0.03	0.04	0.03
	LD	0.00	0.00	0.08	0.15	0.06
	GA_3 average	0.00	0.02	0.04	0.09	LSD-5% = n.s.

Table F. (Continued)

	Photoperiod	GA_3 concentration (ppm) 0	50	200	400	Photoperiod average
Rosette leaves	SD	1.11	0.90	0.92	0.87	0.95
	LB	1.02	0.73	0.93	0.88	0.89
	LD	0.85	0.93	1.16	1.07	1.00
	GA_3 average	0.99	0.85	1.00	0.94	LSD-5% = n.s.
Primary stolon leaves	SD	0.33	0.72	0.38	0.43	0.47
	LB	0.15	0.34	0.59	0.32	0.35
	LD	0.26	0.82	0.74	0.75	0.64
	GA_3 average	0.25	0.63	0.57	0.50	LSD-5% = n.s.
Roots	SD	0.50	0.52	0.38	0.38	0.44
	LB	0.41	0.21	0.51	0.43	0.39
	LD	0.60	0.47	0.41	0.53	0.50
	GA_3 average	0.56	0.40	0.43	0.44	LSD-5% = n.s.

Table G. Experiment II. The effect of photoperiod and gibberellic acid (GA_3) treatment on fresh weight of entire plant and organs.

	Photoperiod	GA_3 concentration (ppm) 0	50	200	400	Photoperiod average
Fresh weight (gm)						
Entire plant	SD	15.24	19.00	15.45	15.41	16.28
	LB	11.93	12.66	19.13	17.05	15.19
	LD	9.66	16.71	21.78	23.41	17.89
	GA_3 average	12.28	16.12	18.79	18.62	LSD-5% = 3.29
Primary stolons	SD	1.02	4.18	3.02	3.46	2.92
	LB	0.58	2.60	4.13	3.16	2.62
	LD	0.28	3.91	5.85	5.43	3.87
	GA_3 average	0.63	3.23	4.33	4.02	LSD-5% = 1.07
Secondary stolons	SD	0.00	0.41	0.14	0.19	0.19
	LB	0.00	0.21	0.30	0.42	0.24
	LD	0.00	0.01	0.81	0.84	0.41
	GA_3 average	0.00	0.21	0.41	0.48	LSD-5% = 0.21

Table G. (Continued)

	Photoperiod	GA3 concentration (ppm) 0	50	200	400	Photoperiod average
Rosette leaves	SD	8.03	5.93	6.84	5.75	6.64
	LB	7.58	5.85	6.91	6.57	6.73
	LD	5.11	5.75	7.39	7.00	6.31
	GA_3 average	6.93	5.84	7.05	6.44	LSD-5% = n.s.
Primary stolon leaves	SD	2.63	5.13	2.93	3.37	3.51
	LB	1.25	2.66	4.87	4.63	3.35
	LD	1.48	4.86	5.25	7.36	4.74
	GA_3 average	1.79	4.22	4.35	5.12	LSD-5% = 1.28
Roots	SD	3.57	3.16	2.52	2.24	2.87
	LB	2.52	1.35	2.93	2.27	2.27
	LD	2.82	2.19	2.41	2.77	2.55
	GA_3 average	2.97	2.23	2.62	2.43	LSD-5% = n.s.

Table H. Experiment III. The effect of gibberellic acid (GA_3) on Ajuga grown under prevailing daylengths of August and September.

	GA_3 concentration (ppm)						
	0	50	100	200	300	400	LSD-5%
Primary stolons							
Stolons per plant (No.)	3.70	5.70	6.90	6.50	6.90	7.40	1.70
Length per stolon (cm)	3.90	27.80	30.00	37.00	40.10	34.00	7.60
Length per plant (cm)	15.00	168.00	209.00	249.00	295.00	261.00	57.00
Internodes per plant (No.)	13.00	46.00	51.00	57.00	63.00	61.00	14.00
Internode length per stolon (cm)	1.10	3.60	4.10	4.30	4.70	4.40	1.20
Secondary stolons							
Stolons per plant (No.)	0.00	12.60	17.00	21.40	24.60	24.40	8.52
Length per stolon (cm)	0.00	9.84	9.41	10.97	10.12	6.35	1.80
Length per plant (cm)	0.00	124.00	160.00	235.00	249.00	155.00	31.10
Internodes per plant (No.)	0.00	42.00	42.00	57.00	51.00	44.00	8.70
Internode length per stolon (cm)	0.00	3.00	3.80	4.10	3.60	3.60	1.30
Rosette leaves							
Leaves per plant (No.)	24.00	13.00	20.00	21.00	18.00	18.00	4.00
Petiole length* (cm)	39.00	28.00	30.00	37.00	41.00	34.00	9.00
Blade length* (cm)	51.00	37.00	55.00	50.00	59.00	45.00	7.00
Blade width* (cm)	29.00	21.00	25.00	26.00	24.00	24.00	3.00
Primary stolon leaves							
Leaves per plant (No.)	30.00	80.00	93.00	107.00	115.00	112.00	13.00
Petiole length* (cm)	49.00	39.00	20.00	21.00	23.00	19.00	5.00
Blade length* (cm)	45.00	38.00	50.00	46.00	46.00	42.00	6.00
Blade width* (cm)	26.00	19.00	29.00	25.00	28.00	25.00	4.00

Table H. (Continued)

	GA3 concentration (ppm)						
	0	50	100	200	300	400	LSD-5%
Dry weight (gm)							
Entire plant	4.30	4.70	5.20	7.10	6.10	5.50	n.s.
Primary stolons	0.50	1.10	1.10	1.50	1.50	1.40	0.40
Secondary stolons	0.00	0.30	0.40	0.60	0.50	0.30	0.24
Rosette leaves	1.40	0.80	1.20	1.40	1.10	1.00	n.s.
Primary stolon leaves	0.90	1.20	1.00	1.50	1.60	1.20	n.s.
Roots	1.90	1.30	1.50	2.00	1.30	1.80	0.60
Fresh weight (gm)							
Entire plant	31.20	25.70	33.10	41.40	38.50	32.30	9.30
Primary stolons	1.90	6.20	7.80	10.10	10.90	9.10	5.00
Secondary stolons	0.00	1.70	2.80	4.00	3.60	2.40	0.90
Rosette leaves	9.80	4.20	7.00	7.80	5.80	5.50	n.s.
Primary stolon leaves	6.30	6.70	7.30	9.60	10.10	6.80	n.s.
Roots	13.30	6.80	8.30	9.80	8.00	8.50	5.60

* Total of 10 leaves