J Plant Growth Regul (1997) 16:123–127

Journal of Plant Growth Regulation

Gibberellic Acid Treatment Reduces the Tolerance of Field-Grown Common Bean to Leaf Removal

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Received December 6, 1996; accepted March 5, 1997

Abstract. I studied the influence of gibberellic acid (GA_3) treatment in a field population of common bean on plant tolerance to leaf removal. Individual bean seedlings were treated with a foliar application of 10 μM GA_3 on day 7 and day 14 after emergence, which led to a significant increase in height in GA_3-treated plants. Twenty-eight days after emergence, either zero, one, two, or three leaflets from each trifoliate leaf were removed from each of 20 GA_3-treated and 20 control plants. All pods were harvested from each plant after plants became senescent 6 weeks later. Multivariate analyses revealed that leaf removal produced significant reductions in several yield components in both GA_3-treated and control plants, although the effects were not pronounced until at least two leaflets from each trifoliate leaf (67% of the total leaf area) were removed. However, GA_3-treated plants suffered greater reductions in total pod wall mass and total seed number than control plants after 33 and 67% leaf area removal. These results indicate that GA_3 treatment may have altered the assimilatory capacity or resource allocation pattern of treated plants in such a way as to decrease their ability to tolerate leaf removal, a negative consequence of the hormonal alteration of traits important to plant compensation for biotic stressors.

Key Words. Compensatory growth—Defoliation—Gibberellic acid—Phaseolus vulgaris

Many studies of plant hormone application as a means to increase yield and/or quality of agronomic and ornamental species have been conducted with varying degrees of success (e.g. Rajapakse and Kelly 1991, Weaver and Johnson 1985). Most of these studies have simply involved the application of a particular hormone followed by the subsequent measurement of some trait of interest (e.g. growth, flowering, yield). However, most of these studies have failed to consider the outcome of the interaction of hormone-modified plants with such biotic stresses as herbivore damage as a component in the success of the particular hormone treatment.

It is well known that even moderate amounts of herbivore damage can significantly reduce growth and reproduction in both wild and cultivated species (Marquis 1984, Vranjic and Gullan 1990). However, plants can often compensate for substantial tissue losses to herbivores through increased assimilatory input from resource-harvesting organs (roots and leaves) as well as remobilization of stored reserves from these organs (Ericsson et al. 1980, Lefevre et al. 1991, Rosenthal and Kotanen 1994, Waters et al. 1980). Regrowth following leaf damage by herbivores or pollutants such as ozone or sulfur dioxide is often directed to the shoot at the expense of roots to replace lost leaf area and to maintain root/shoot ratios similar to those of undamaged plants (Bloom et al. 1985, Mihaliak and Lincoln 1989, Pell et al. 1994). Depending on such factors as the type and timing of the damage, plant developmental stage, and plant genotype, such compensatory responses can often enable damaged plants to maintain a degree of growth and reproduction which approaches (and sometimes equals) that of undamaged plants (Rosenthal and Kotanen 1994).

Because of the numerous effects that exogenously applied hormones can have on plant growth, it is possible that a particular plant hormone treatment can alter a plant's assimilatory capacity and/or resource allocation pattern (e.g. root/shoot ratio) in such a way that it could interfere with the ability of that plant to recover from a carbon stress like defoliation, whereas effects on hormone-treated, but otherwise healthy, plants not under

Abbreviations: GA_3, gibberellic acid; MANOVA, multivariate analysis of variance.

biologic stress might go largely unnoticed. For example, gibberellic acid (GA_3) treatment in plants characteristically stimulates dry matter production in the shoot at the expense of dry weight increases in the root system, primarily through the creation of stronger photoassimilate sinks in the shoot (Brian et al. 1954, Lovell 1971, Morris and Arthur 1985). If remobilization from root reserves is a component in the compensatory response of plants to leaf area removal, then GA_3-treated plants may have fewer root reserves available to compensate for defoliation than untreated plants and may suffer greater growth and reproductive consequences following a defoliation event.

I investigated the possibility that treatment of field-grown bush bean plants with a foliar application of GA_3 would affect their ability to compensate for leaf area removal as measured in pod and seed production. Although GA_3 is not currently used commercially to control growth of bean in the field, the extensive literature on the effects of GA_3 on bean growth and physiology (e.g. Hayes and Patrick 1985, Morris and Arthur 1985) combined with the literature on the effects of defoliation on bean growth and reproduction (e.g. von Caemmerer and Farquhar 1987) make bean a useful model for this study. I administered a range of defoliation treatments to examine whether the influence of GA_3 treatment on pod and seed yield varied with different amounts of leaf area removal.

Materials and Methods

Plant Material and Growth Conditions

Seeds of a bush Blue Lake variety of common bean (*Phaseolus vulgaris* cv. OSU 4091-G) were sown in a 10-m × 50-m field plot on June 7, 1995, at the Russell E. Larson Agricultural Experiment Station at Rock Springs, PA. Soils at the station are characterized as Hagerstown Silt Loam. The plot was prepared initially by chisel plowing followed secondarily by disking and finished with an S-tine cultivator. Prior to planting, the plot was treated with commercially recommended coverages of two herbicides, Eptam 7E and Dual 8E, to control the growth of weeds and fertilized with 10-10-10 N-P-K slow release fertilizer. Seeds were planted one every 0.15 m in rows 0.75 m apart. Although natural levels of herbivory were very low, plants used in this experiment were treated once with a spray application of Isotox (Agway) midway through the experiment to ensure continued low levels of herbivory throughout the season.

Gibberellic Acid Treatment

Eighty bean plants were selected randomly from the plot to receive treatment with a foliar application of GA_3. Crystalline GA_3 was dissolved in a small amount of ethanol and made to a concentration of 10 μM using distilled water containing 0.1% Tween 20. Individual plants were sprayed until runoff with this solution on day 7 and day 14 after emergence from the ground. Eighty randomly selected control plants were sprayed on the same days with the same solution minus GA_3. GA_3-treated plants were staked with 1-cm-diameter bamboo rods. Heights of a subsample of GA_3-treated and water-treated plants were taken 2 weeks following the final GA_3 treatment to confirm the effectiveness of GA_3 at increasing stem elongation in this cultivar.

Defoliation Treatment

Defoliation treatments were administered 4 weeks after emergence just as plants were beginning to flower. Either zero, one, two, or three leaflets from each trifoliate leaf were removed with sterile scissors on each of 20 randomly chosen GA_3-treated and 20 randomly chosen water-treated plants constituting the removal of either 0, 33, 67, or 100% of the leaf area from each experimental plant.

Harvest and Analysis

All pods were harvested from each experimental plant when plants became senescent 6 weeks following the defoliation treatments. Pods were dried and separated into pod walls and seeds. Because the bean used in this study is a snap bean variety and was bred for pod wall characteristics such as thickness, treatment effects may be evident not only in seed production but also in pod wall mass. The separation of such yield characters allows a more careful examination of where treatment effects may lie. Therefore, pod walls were included in this analysis. Pod number, total pod wall mass, seed number, and total seed mass were recorded from each plant. Specific pod wall mass and specific seed mass were calculated from these data. Pod number and seed number were square root transformed, and all other variables were log transformed. To protect from multiple tests, these data were analyzed first with MANOVA on the SAS statistical package (SAS Institute) with GA_3 treatment, defoliation, and their interaction as main effects followed by univariate ANOVA and means separation for each variable separately. The strength of the effects in the overall MANOVA and in the separate ANOVA analyses were in general agreement with each other. The two levels of GA_3 treatment (+ or −) and the four levels of defoliation (0, 33, 67, and 100%) were administered in a completely randomized fashion allowing the use of a 2 × 4 full factorial design. Asterisks on figures illustrate where significant differences occur between GA_3, treatments at $\alpha = 0.05$.

Results

GA_3 treatment increased height significantly in treated plants relative to controls. GA_3-treated plants were about twice as tall as water-treated plants (GA_3, 60 ± 5.1 cm; control, 32.1 ± 3.8 cm; $p < 0.05$). Analysis of a greenhouse study indicated that increases in height induced by GA_3 treatment in this bush bean cultivar are accompanied by increased allocation to stem biomass and decreased allocation to root biomass (Cipollini, unpublished data), an effect seen commonly in GA_3-treated plants (Morris and Arthur 1985). Although entire plants

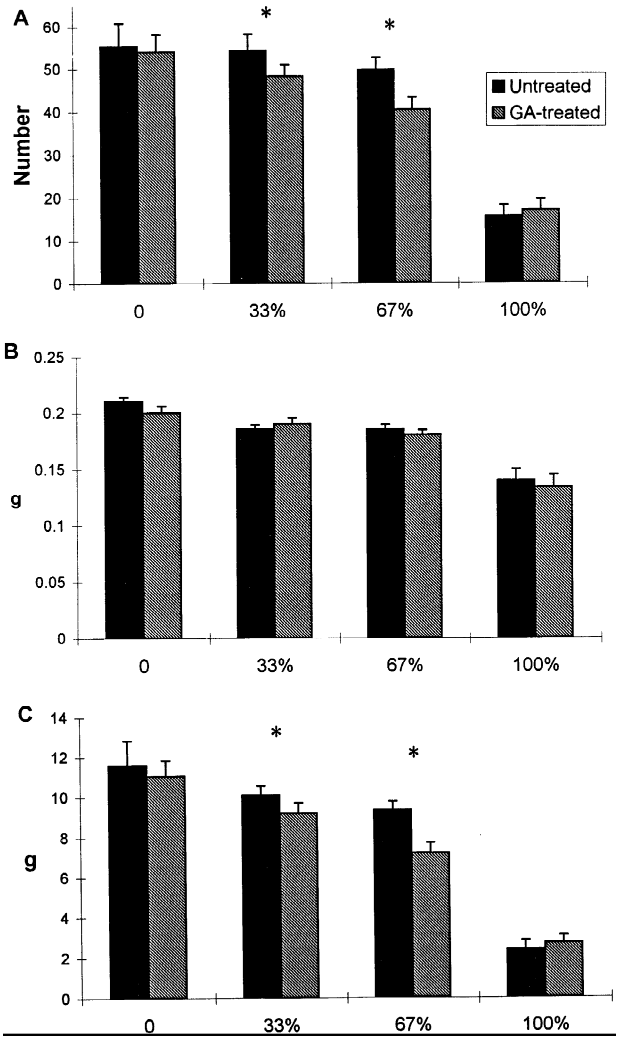

Fig. 1. *A,* total seed number of GA_3-treated and untreated plants at four levels of defoliation. *B,* specific seed mass of GA_3-treated and untreated plants at four levels of defoliation. *C,* total seed mass of GA_3-treated and untreated plants at four levels of defoliation. Each *bar* represents the mean (±S.E.) of 20 plants. *Asterisks* denote significant differences between GA_3-treated and untreated plants at $\alpha = 0.05$.

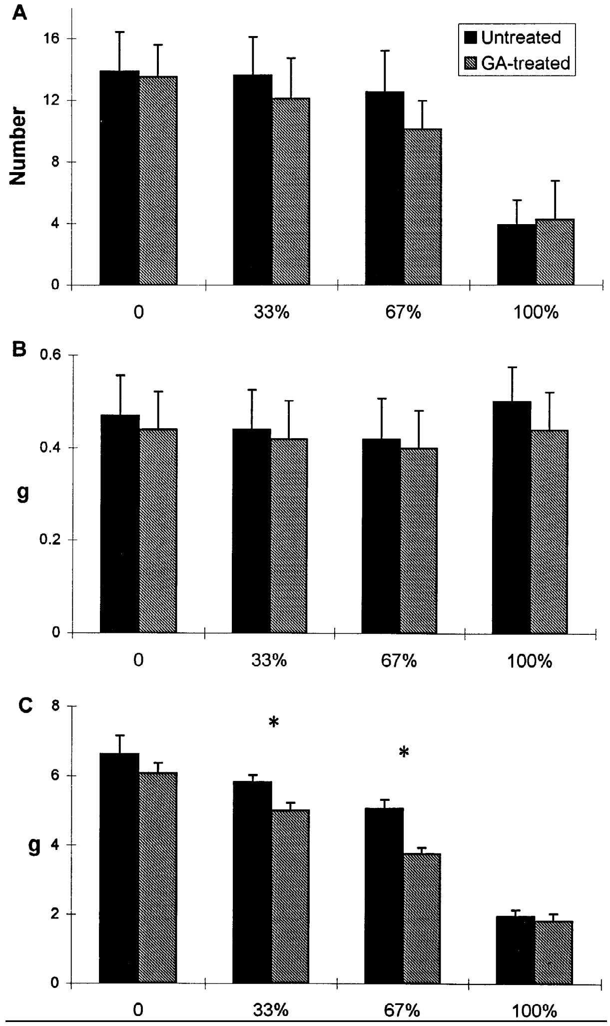

Fig. 2. *A,* total pod number of GA_3-treated and untreated plants at four levels of defoliation. *B,* specific pod wall mass of GA_3-treated and untreated plants at four levels of defoliation. *C,* Total pod wall mass of GA_3-treated and untreated plants at four levels of defoliation. Each *bar* represents the mean (± S.E.) of 20 plants. *Asterisks* denote significant differences between GA_3-treated and untreated plants at $\alpha = 0.05$.

were not examined in this study, it is assumed that GA_3 treatment led to the same root/shoot allocation pattern in the field.

Although the effect of GA_3 treatment alone on all variables measured only approached significance (MANOVA, Pillai's Trace, $F = 2.24$, $p = 0.067$), the effect of defoliation alone on all variables measured was strongly significant (MANOVA, Pillai's Trace, $F = 11.52$, $p < 0.0001$). The overall negative effect of defoliation on yield increased linearly from 0 to 67% leaf area removal, then became very pronounced at 100% leaf area removal. Although 67% leaf area removal decreased yield by about one third, 100% leaf area removal decreased yield by about two thirds. Both seed number (Fig. 1*A*) and specific seed mass (Fig. 1*B*) were reduced greatly by defoliation leading to decreased total seed mass (Fig. 1*C*). Specific pod wall mass remained constant across all treatments (Fig. 2*B*), but pod number (Fig. 2*A*) was reduced greatly by defoliation, leading to decreased total pod wall mass (Fig. 2*C*).

No overall statistical interaction between GA_3 treatment and defoliation on yield was detected (MANOVA, Pillai's Trace, $F = 0.339$, $p = 0.981$). However, there was a strong tendency, in some cases significant, for defoliation to be more detrimental to GA_3-treated plants than to water-treated plants in some yield components. Although defoliation led to no greater decreases in specific seed mass or specific pod wall mass in GA_3-treated plants than in water-treated plants at any defoliation level (Figs. 1*B* and 2*B*), 33 and 67% leaf area removal did lead to greater decreases in seed number and total pod wall mass in GA_3-treated plants than in water-treated plants (Figs. 1*A* and 2*C*). Total seed mass (a function of specific seed mass and seed number) (Fig. 1*C*) was also more reduced in GA_3-treated plants than in water-treated plants at these two levels of defoliation. Because specific pod wall mass was constant across treatments, the tendency for pod number to be more greatly reduced on GA_3-treated plants by defoliation led to significant decreases in total pod wall mass at 33 and 67% leaf area removal.

Discussion

Defoliation to field-grown bush bean plants led to significant decreases in overall pod and seed yield in this study. Defoliated plants produced fewer pods with smaller seeds as the level of defoliation increased. These results are in agreement with the general observation that defoliated plants have fewer resources with which to reproduce, which can lead to reduced flower production, selective fruit abortion, and/or reduced fruit and seed production (Reichman and Smith 1991, Stephenson 1980). However, this is the first study to demonstrate reduced tolerance of GA_3-treated plants to defoliation relative to untreated plants as seen primarily in reduced total pod wall mass and seed production.

Most studies attribute the ability of GA_3 to stimulate shoot production in plants to the creation of stronger photoassimilate sinks in the stem than in the roots and not to alterations in root or leaf assimilatory capacity induced by GA_3 treatment (Lovell 1971, Morris and Arthur 1985, Mulligan and Patrick 1979). Because GA_3 treatment is known to increase biomass allocation to stem at the expense of roots in the bean cultivar used in this study, I attribute the reduced tolerance of GA_3-treated plants seen here primarily to the presence of fewer available root reserves to remobilize following defoliation and not to altered assimilatory capacity. In a similar fashion, it has been shown that increased allocation to shoot production and reduced root/shoot ratio induced by nitrate addition in *Heterotheca subaxillaris* reduced the ability of this plant to tolerate chronic herbivory (Mihaliak and Lincoln 1989).

Because *P. vulgaris* uses stored resources for adjacent leaves as well as from stem and root reserves to fill seeds during reproductive development (Waters et al. 1980), it is also possible that leaflets remaining on defoliated GA_3-treated plants contained fewer reserves that could be used to set fruit and fill seeds than those on defoliated water-treated plants. If this were the case, effects on yield induced by GA_3 treatment should be seen in undefoliated plants as well as defoliated plants but were not found. von Caemmerer and Farquhar (1984) have shown that enhanced photosynthesis can occur in undamaged leaves of partially defoliated *P. vulgaris* plants as a compensation mechanism for the loss of leaf area. It is also possible that GA_3 treatment somehow reduces this compensatory photosynthetic enhancement in defoliated GA_3-treated plants relative to defoliated controls. Because such indications of assimilatory capacity as CO_2 exchange rates or root uptake rates were not measured in this study, I cannot entirely rule out the possibility that these functions or some other relevant aspects of plant metabolism were altered by GA_3 treatment leading to reduced tolerance.

Although not widely used in the field, application of both natural and synthetic plant growth regulators has proven to be useful in controlling the growth and development of a variety of agricultural and ornamental species (e.g. Zeevaart 1985). However, the results presented here illustrate how the positive effects of a particular hormone treatment on yield or quality in plants may be overestimated when the interaction of hormone-modified plants with biotic stressors has not been not investigated. Although the conclusions using GA_3-modified plants in this study may not apply to the use of all plant growth regulators, these results illustrate that care must be taken to ensure that a particular plant growth regulator application does not compromise plant health when applied in a realistic context including interacting biotic and abiotic stresses. Moreover, this study illustrates some of the negative consequences of inducing alterations in traits which may be fundamentally important for plant compensation for leaf area removal.

Acknowledgments. I thank Jack Schultz, Ben Hollister, Paul Rebarchak, and Kendra Lentz for their contributions to this work. Bean seeds were the kind gift of the Roger's NK Seed Co., Boise, ID. Funding for this work was supplied by the Department of Entomology, Penn State University and National Science Foundation Grant DEB-318073 to Jack Schultz.

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