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EFFECTS OF LIGHT AND NUTRIENTS ON
TOMATO PLANT COMPENSATION FOR HERBIVORY BY
MANDUCA SEXTA (LEPIDOPTERA: SPHINGIDAE)

Anita K. Gertz and Catherine E. Bach¹

ABSTRACT

This preliminary study examined how two resources (light and nutrients) influence the ability of tomato plants to show growth compensation for defoliation by the tobacco hornworm (*Manduca sexta*). Growth rate and biomass of plants grown under high and low levels of light and nutrients, and exposed to 4 levels of defoliation by *Manduca sexta* were measured. Nutrients affected plant growth rate much more strongly than did light. Light and nutrients, however, each influenced how herbivory affected plant growth. Defoliation significantly decreased growth rate only under conditions of low light and high nutrients. Biomass, on the other hand, was low under all resource treatments except high levels of both light and nutrients, and defoliation significantly decreased biomass only under high levels of both resources. Thus, plants appeared to compensate for damage, in terms of biomass, only under conditions of either low light and/or low nutrients.

Although herbivory clearly decreases plant fitness in many insect-plant systems (Louda et al. 1990, Huntly 1991), many plants are able to compensate for herbivore damage (Paige and Whitham 1987, Maschinski and Whitham 1989, Hjalten et al. 1993, Meyer and Root 1993, Trumble et al. 1993). Compensation is typically defined as equal growth and/or reproduction of plants experiencing herbivory and control plants experiencing no herbivory. There is much current interest in examining the conditions under which plant compensation occurs (Maschinski and Whitham 1989). Trumble's (1993) review emphasizes the importance of studying the role of exogenous factors in influencing the compensatory ability of plants.

Coley et al. (1985) predicted that herbivory would be a stronger selective force on plant species growing under low resource conditions than under high resource conditions, because foliage lost to herbivory is more expensive to replace. If this hypothesis is applied to plants within the same species, then compensation would be predicted to occur more often under conditions of high resources. Few studies are available to test this prediction, and the results are equivocal; compensation occurs more frequently at higher resource levels in some systems (Cox and McEvoy 1983, Maschinski and Whitham 1989, Pieron et al. 1990, Hjalten et al. 1993), whereas there is a higher incidence of compensation at lower resource levels in other systems (Georgiadis et al. 1989, Oosterheld and McNaughton 1991, Meyer and Root 1993). Despite the importance of interactions between resources in influencing plant growth, few stud-

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ies have examined how two or more resources interact to influence compensation for herbivory.

The purpose of this preliminary study was to investigate the effect of light level and nutrient level on the ability of tomato plants (*Lycopersicon esculentum*) to compensate for damage by the tobacco hornworm, *Manduca sexta* (L.). Welter (1991) compared the effects of simulated and real herbivory by *Manduca sexta* on tomato plants, but did not vary resource levels. In this study, we addressed the following questions: (1) Do tomato plants compensate for herbivory, in terms of growth rate and above-ground biomass?, and (2) If so, does resource level (light and/or nutrients) influence the level of compensation? In particular, do resources interact to influence the level of compensation?

METHODS

The experimental design was a $4 \times 2 \times 2$ factorial design, with 4 levels of herbivory (0%, 25%, 50%, and 75% defoliation), 2 light levels (low and high), and 2 nutrient levels (low and high). Plants in the low light level treatment (LL) were exposed to fluorescent grow lights for 8h/d, whereas high light level plants (HL) were exposed to the same grow lights supplemented with 75-watt light bulbs for 12h/d. Light levels averaged approximately 100 lumens for the LL treatment and approximately 300 lumens for the HL treatment. We will refer to the combination of increased light intensity/spectrum and increased photoperiod as the high light level condition. Because the incandescent bulbs gave off some heat, temperatures were also slightly higher in the HL treatment (28–30°C) than in the LL treatment (26–27°C). Plants in the low nutrient level treatment (LN) received no fertilizer; plants in the high nutrient level treatment (HN) received liquid fertilizer (standard dilution of 15–30–15 fertilizer) at each watering. There were six replicates of each treatment combination, for a total of 96 plants.

Seeds of *Lycopersicon esculentum* (variety Big Boy) were planted on 20 February, 1992 in a growing medium (Sunshine mix) in 9.5 cm diameter plastic pots. Plants were grown in a greenhouse and fertilized once on 3 March. Defoliation treatments were established on 17 March by placing one larva of *Manduca sexta* on each plant receiving defoliation. Larvae were removed after the desired percentage of leaf area was removed (Welter 1991).

After the defoliations had occurred, all plants were grown for 4 weeks on light benches in a laboratory at Eastern Michigan University. Because low and high light plants were grown on different light/dark cycles, they were grown on separate light benches. For ease of watering, plants receiving each nutrient treatment were placed on the same half of each bench, and position of pots within each light/nutrient treatment was haphazard. At each watering (approximately every 2 d), plants in each nutrient treatment were switched to the other side of the bench, and pot position was again haphazardly determined.

Plant height was measured one week (24 March) and four weeks after defoliation (14 April). Plants were harvested on 14 April, cut at the soil level, and their above-ground dry masses were determined after drying for 72 h at 60°C. Data were analyzed with 3-way ANOVA testing for effects of defoliation level, light level, nutrient level, and all interactions. To compare the four defoliation treatments, 1-way ANOVAs were conducted on final masses and growth rates (change in height) for plants in each treatment combination of light and nutrients. Because biomass is a more accurate indicator of plant growth than is change in height, the lack of a significant difference in biomass

Table 1. Results from 3-way ANOVAs of growth rate (change in height over a 3-week period) and final biomass. F-values, degrees of freedom, and significance levels are presented from ANOVAs testing for effects of defoliation level, light, nutrients, and all possible interactions.

Effect	Growth Rate			Biomass		
	F	df	P	F	df	P
Defoliation	7.1	(3,74)	***	15.2	(3,75)	***
Light	29.8	(1,74)	***	200.6	(1,75)	***
Nutrients	176.8	(1,74)	***	204.1	(1,75)	***
Defoliation × Light	5.6	(3,74)	**	3.4	(3,75)	*
Defoliation × Nutrients	2.8	(3,74)	*	14.0	(3,75)	***
Light × Nutrients	37.6	(1,74)	***	162.8	(1,75)	***
Def. × Light × Nutrients	1.9	(3,74)		6.6	(3,75)	***

* = $P < .05$; ** = $P < .01$; *** = $P < .001$

between control and damaged plants was used as evidence for plant growth compensation.

RESULTS

Plant growth rate, measured as change in height over the 3-week period, was significantly affected by defoliation level, light, and nutrients (Table 1, Fig. 1). Although the significance level for each of these effects was less than .001, the magnitude of the nutrient effect was much greater, as evidenced by

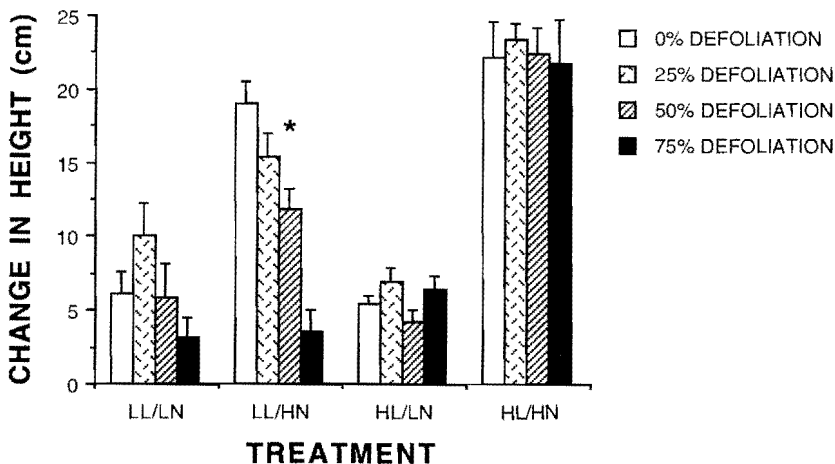


Figure 1. Growth rate (change in height (cm) over a 3-week period) of plants receiving four levels of defoliation and grown under four sets of conditions: low light/low nutrients (LL/LN), low light/high nutrients (LL/HN), high light/low nutrients (HL/LN), and high light/high nutrients (HL/HN). Means and standard errors are presented for six replicates of each treatment. The * indicates a significant effect of defoliation from 1-way ANOVAs within treatment groups.

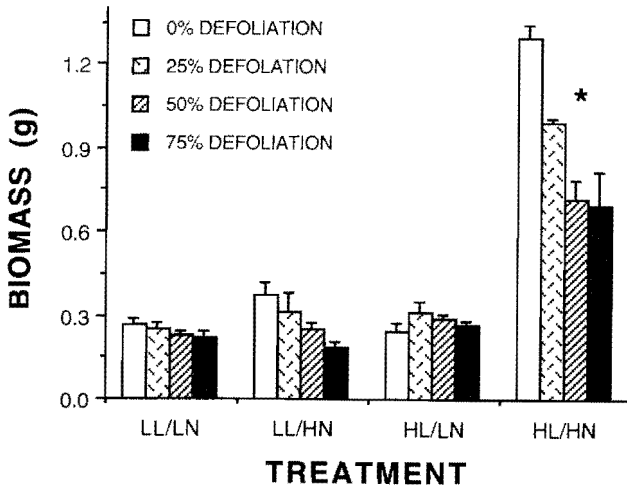


Figure 2. Final biomass (g) of plants receiving four levels of defoliation and grown under conditions of LL/LN, LL/HN, HL/HN, and HL/LN. Means and standard errors are presented for six replicates of each treatment. The * indicates a significant effect of defoliation from 1-way ANOVAs within treatment groups.

the fact that the F-value was 25 times greater than for defoliation and 6 times greater than for light. The significant interactions between defoliation and light, defoliation and nutrients, and light and nutrients (Table 1), emphasize that the effect of each of these factors depended on the magnitude of other factors. Growth rates of defoliated and control plants did not significantly differ under conditions of LL/LN, HL/LN, or HL/HN ($P > .05$ for all comparisons). Only under conditions of LL/HN did defoliation significantly decrease plant growth rate (Fig. 1; $F = 13.6$, $df = (3, 17)$, $P < .001$). Thus, it appears that when light is limiting, damaged plants can not attain the same height as control plants, even when high levels of nutrients are available.

Final biomass of plants was also significantly affected by defoliation level, light, nutrients, and all possible interactions (Table 1). The highly significant light X nutrient interaction is evident from the 3.5–5.4-fold greater biomass of control plants in the HL/HN treatment than in any of the other three treatments (Fig. 2). Biomass of defoliated and control plants did not differ under conditions of LL/LN, LL/HN, or HL/LN ($P > .05$ for all comparisons). However, defoliation significantly decreased biomass under HL/HN ($F = 14.7$, $df = (3, 19)$, $P < .001$); thus plant compensation occurred under all conditions except under high light and high nutrients.

DISCUSSION

Results from this study clearly demonstrate that resource levels strongly influence the ability of tomato plants to re-grow following defoliation by *Manduca sexta*. Plants showed growth compensation for damage under low resource conditions, but not under high resource conditions. Under all sets of

conditions in which levels of one or both resources were low, final biomass of defoliated and control plants did not differ; only under high levels of both resources did defoliation significantly decrease biomass. However, the non-significant trend of decreasing biomass with increasing defoliation under low light and high nutrients was similar to that observed for the high light and high nutrient conditions (see Fig. 2). Thus, it appears that: (1) light and nutrients interact to influence plant growth compensation and (2) nutrients were more important than light in influencing plant compensatory ability.

It was interesting that the two aspects of above-ground growth measured in this study, height growth and biomass, exhibited different responses to nutrient levels and different regrowth responses following defoliation. In general, height growth seemed to be mostly nutrient-limited, whereas biomass production seemed to be both nutrient-limited and light-limited. In addition, defoliated plants added as much height as control plants under high resource conditions (see Fig. 1), but did not attain as great a mass as control plants (see Fig. 2). It appears that defoliated plants put more energy into height growth rather than into development of lateral branches under high resource conditions.

The result that plants compensated for herbivory, in terms of biomass, only under low resource levels is in contrast to results from several studies (Cox and McEvoy 1983, Pierson et al. 1990, Hjalten et al. 1993). In fact, Maschinski and Whitham (1989) found overcompensation in *Ipomopsis arizonica* only with nutrient supplementation. However, our results agree with several other studies reporting compensation under low resource conditions (Georgiadis et al. 1989, Oosterheld and McNaughton 1991). Meyer and Root (1993) report that goldenrod plants compensated for herbivory in terms of seed production only under low soil fertility. They further suggest that plants growing under conditions of low soil resource levels would more likely be nitrogen-limited rather than carbon-limited, and thus reduced leaf area would not affect seed production; on the other hand, under high soil resource conditions, plants would be carbon-limited and defoliation would strongly affect seed production. If this line of reasoning is applied to growth compensation in tomato plants, then the lack of compensation at high nutrient levels may result from carbon-limitation. Tomato plants growing at high resource levels appear to be growing so quickly that regrowth can not compensate for damage.

If Coley et al.'s (1985) predictions about the strength of herbivory as a selective force on different plant species growing under different resource levels can be extended to comparisons within plant species, then one would predict that herbivores would have stronger effects on plant fitness when resources are scarce. Maschinski and Whitham's (1989) model also predicts that the degree to which a plant can compensate for herbivory decreases as nutrient availability decreases. Results from this study do not support these predictions; instead, herbivory appears to exert the strongest differential impact on plant growth when resources are abundant. However, conclusions about compensation in terms of reproductive output, the most meaningful measure of plant fitness, can not be made from this preliminary study, because reproduction was not measured.

In conclusion, it appears that herbivore impacts on plant growth are strongly condition-dependent. Many studies report significant negative effects of herbivory on plant growth, survivorship, and fecundity (Louda et al. 1990, Huntly 1991). In a study similar to ours, Welter (1991) found a significant negative correlation between growth of tomato plants and percentage defoliation; this study only found negative effects of herbivory on biomass under high levels of both resources. Further research is needed to determine if the preponderance of studies showing negative effects of herbivory result

partly from the fact that most studies are conducted with vigorous plants growing under conditions of high resources.

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