Journal of Agricultural Science and Technology A 6 (2016) 255-260
doi: 10.17265/2161-6256/2016.04.005

Predicting Compensatory Growth and Reproduction in Agricultural Weeds Using a Plant's Growth Rate Trajectory: A Test with Defoliation of *Abutilon theophrasti*

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Abstract: A plant's capacity to compensate for pest damage as a function of resource availability needs to be predictable in order to apply biocontrol agents effectively. In this research, it was hypothesized that a weedy plant species' capacity to compensate for defoliation is related to how resource availability affects a plant's growth trajectory. Growth rate trajectory is defined as the percent change in relative growth rate or the slope of a plant's relative growth rate. 90 *Abutilon theophrasti*, a common weed species, in cultivated fields of corn and soybean, grew in a greenhouse for 70 d under three nitrogen (N) fertilization treatments. "Unfertilized" plants were not fertilized, "bulk" fertilized plants received 0.6 g N on day 15 and "exponential" fertilized plants received a total of 0.6 g N supplied at an exponential rate of 10% per day with a starting concentration of 0.02 g N on day 15. On day 25, 15 plants in each N treatment had 75% of total leaf area removed. Biomass and reproductive compensation were determined after 50 d and 70 d of growth. Results showed that bulk plants had the greatest absolute growth, but also the greatest decline in growth rates and the least capacity for compensation. Unfertilized plants had the lowest absolute growth, but declines in growth rates were similar to bulk plants with only a slightly greater compensatory capacity. Exponential plants had intermediate absolute growth, but the least decline in growth rates and the greatest capacity for compensation. This experiment indicates that a plant's growth rate trajectory, and not high or low relative growth rates or N availability *per se*, can be used to predict a weedy plant's capacity to compensate for herbivory, and has implications for biocontrol of weedy species.

Key words: Biocontrol, compensatory growth, herbivory, nitrogen fertilization, relative growth rate, reproductive allocation.

1. Introduction

Predicting plant compensation responses for herbivore damage is complicated by variability in nutrient availability [1], but is required to understand the interaction between crops and weed species when biocontrol is used to reduce the negative effects of a weed [2]. It has been commonly assumed that plants growing in high rather than low nutrient conditions are better able to compensate for herbivory [3], because replacing a fixed amount of herbivory requires a larger fraction of the net production of a plant at low rather than high nutrient availability [4]. However, a number of studies have shown greater compensatory growth and/or reproduction in plants growing at low rather than high nutrient availability [3]. Hypotheses, such as the "compensatory continuum hypothesis" [5] suggest that this occurs because plants growing in high resource conditions are more likely than plants growing in low resources conditions to be growing at or near their potential maximum relative growth rate (RGR), so any increase in RGR to compensate would be less at the high than that at low resource condition.

One explanation for the opposite predictions presented above is that endogenous and exogenous factors that affect compensatory growth and reproduction are taxon specific [3]. Another

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explanation is that nutrient availability affects compensatory growth as a function of the rate of change in growth rate. Because biological control of a weed species must consider the fertilization regime being used for growing the crop [2, 6], compensatory responses of the weed need to be predictable.

The RGR of a plant describes the rate at which biomass is accumulated on a daily basis as a proportion of the total plant biomass. The growth rate trajectory of a plant is a combination of the magnitude of RGR and the direction (slope of RGR vs. time) of RGR. Because RGRs are driven by the supply of N in relation to the growth demands set by plant size (the N supply and demand ratio) [4], plants with negative growth rate trajectory have a declining N supply relative to demands of growth. *Abutilon theophrasti* was used to test the hypothesis, because it causes significant economic loss and is often controlled by insects [7, 8]. This study was conducted to test the hypothesis that plants with a negative growth rate trajectory have a diminished capacity to compensate for damage.

2. Materials and Methods

A. theophrasti seeds were obtained from Caribbean Garden (Pottstown, PA, USA) and grown for 70 d in the Missouri State University greenhouse in 6%-70% Canadian sphagnum moss with perlite, vermiculite and dolomite limestone (SunGrow, Agawam, MA, USA) in 1 L pots. Three N-addition treatments were utilized: "unfertilized", "bulk" fertilized (6 g N all on day 15) and "exponential" fertilized (N supplied at an increasing rate 10% per day with initial N = 0.02 g and total N = 6 g). Seventy five percent of total leaf area was removed using scissors on day 25 (20 d prior to flowering). Five periodic harvests for biomass occurred every 10-15 d, and measurements of leaf area every 4-10 d. The growth rates were calculated as Eq. (1):

$$\text{Growth rate} = [(\ln x_2 - \ln x_1)/(t_2 - t_1)] \quad (1)$$

where, x is biomass or leaf area at time t_1 or t_2, respectively. Growth rate trajectories were derived by fitting third order polynomials to ln leaf area over time and solving the equation for the second derivative. Relative compensation was defined by the percent difference between defoliated and control (not defoliated) for a given growth or reproductive variable. A two-way analysis of variance (ANOVA) was used to test significant difference in means of all growth and reproduction variables followed by pairwise comparisons of means (Tukey's test).

3. Results

The ability of *A. theophrasti* to compensate for 75% defoliation was related to growth and reproduction (Table 1, Fig. 1). Unfertilized and bulk fertilized plants were not able to compensate for defoliation, and growth rates were reduced by 30% and 33%, respectively. Growth of exponentially fertilized plants was reduced only by 7%. Patterns in total biomass, total reproductive mass and reproductive allocation were similar. For example, total reproductive mass was reduced by 58% in unfertilized plants, 68% in bulk fertilized plants, but only 7% in exponentially fertilized plants. Reductions in bulk fertilized plants of total biomass, flower and pod mass, and seed mass were statistically significant, but for unfertilized and exponentially fertilized were only significant for seed mass (Fig. 1).

The ability of exponential plants to compensate for 75% defoliation was clearly related to relative growth rates and the rates of change in leaf area growth rates (i.e., growth rate trajectories) (Fig. 2). The decline in growth rate over the time period of growth in undefoliated plants was the greatest in bulk fertilized plants (Fig. 2) and was clearly related to significant reduction in growth and reproductive mass (Fig. 1).

Table 1 Effects of N supply on ability of plants to compensate for defoliation.

N supply treatment	Compensatory ability (% difference from undefoliated plants)					
	Change of RBGR (%)	Slope of RLAGR (cm^2/d)	Total biomass (g)	Total reproductive mass (g)	Seed mass (g)	Reproductive allocation (g/g)
Unfertilized	-30	-0.000420	-48	-58	-42	-18
Bulk	-33	-0.000520	-41	-68	-58	-35
Exponential	-7	-0.000012	-5	-7	-34	-8

RBGR: relative biomass growth rates; RLAGR: relative leaf area growth rates.

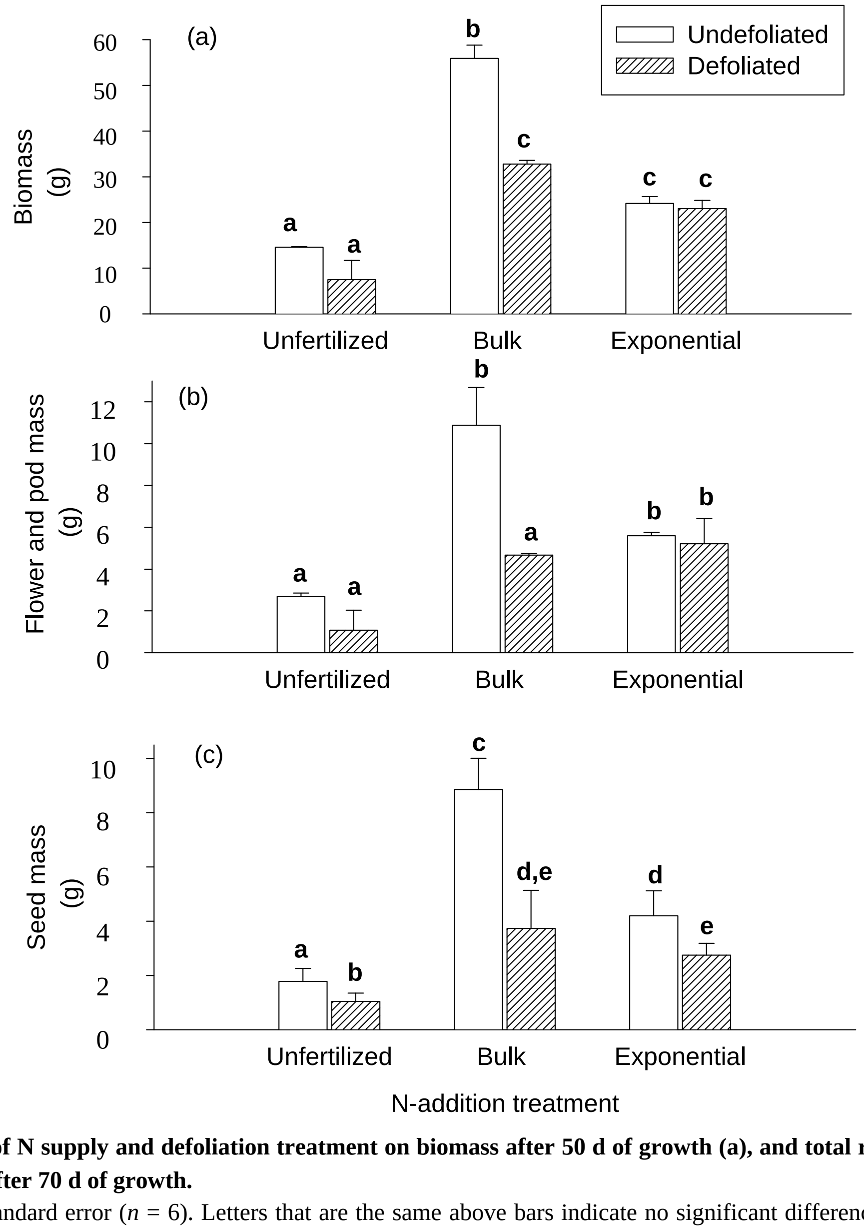

Fig. 1 The effect of N supply and defoliation treatment on biomass after 50 d of growth (a), and total reproductive mass (b) and seed mass (c) after 70 d of growth.

Bars are means ± standard error (n = 6). Letters that are the same above bars indicate no significant difference in means ($P < 0.05$, Tukey's test).

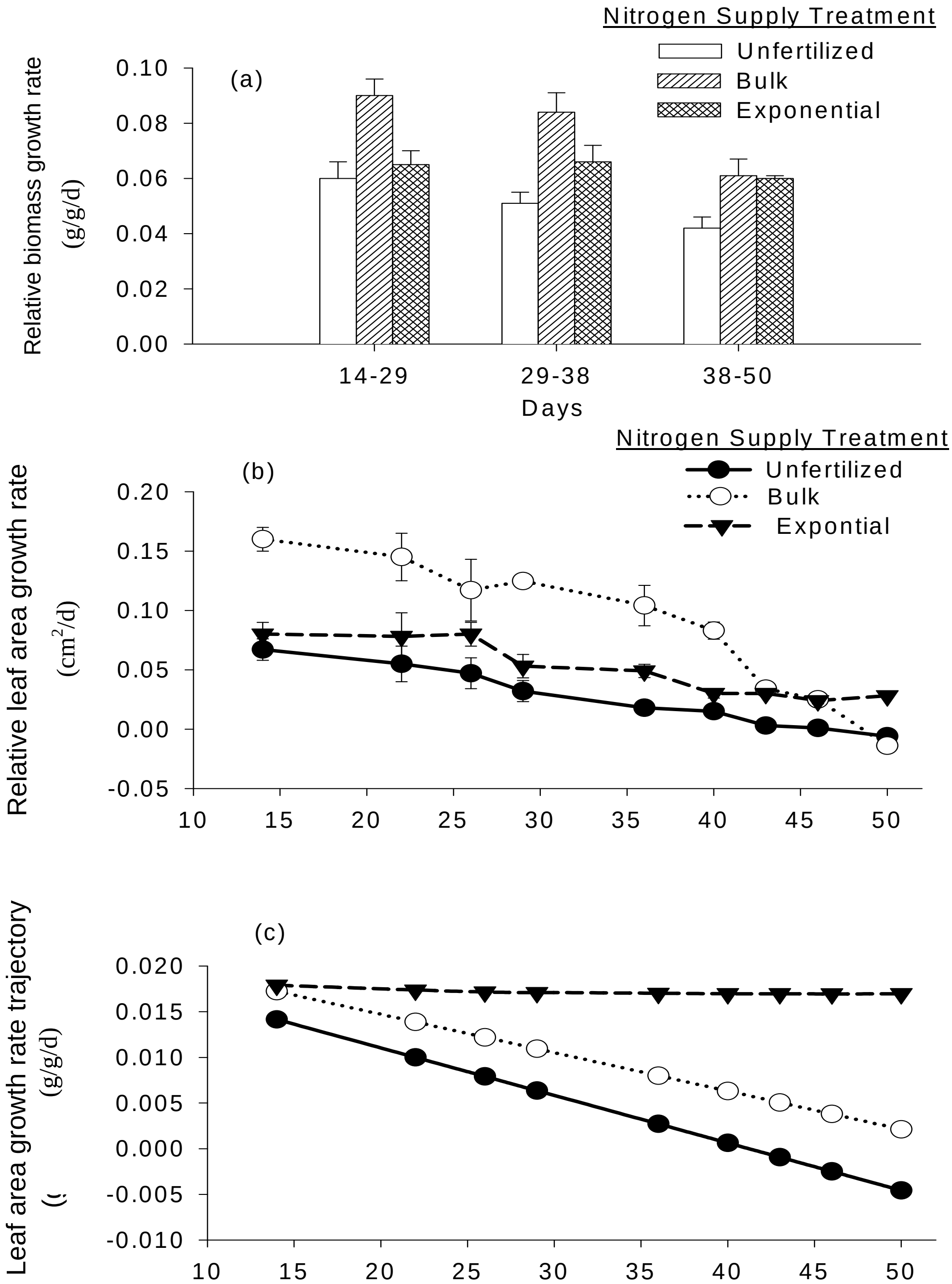

Fig. 2 The effect of N supply on relative biomass growth rates (a), relative leaf area increment rates (b) and leaf area growth rate trajectories (c) (slope of RLAGR) for undefoliated plants.

RLAGR: relative leaf area growth rates. In Fig. 2a, bars are means ± standard error (n = 6), in Fig. 2b and 2c, points are means ± standard error (n = 12).

4. Discussion

Compared to a low resource level (0 g N), a high resource level (0.6 g N) applied early in the growth period had no positive effect on compensatory capacity, while that same resource level applied at exponential rates had a positive effect on compensatory capacity. The plants receiving a high resource level applied once (bulk) were significantly negatively affected by defoliation, while the plants receiving the same amount of N supplied exponentially (exponential) were not significantly affected by defoliation. The results of this study provide a potential solution to the difficulty of controlling soil nutrient dynamics that support crop growth over weed growth, which have been identified by Wortman et al. [2]. Given that compensatory growth in weeds can negate the effects of biological control agents [9], this study illustrates a mechanism and growth variables that need to be measured to predict compensatory responses in weed species as a function of environmental resource levels.

The relative growth rate trajectory in *A. theophrasti* was clearly related to relative compensatory ability. Bulk and unfertilized plants had the fastest decreases in relative biomass growth rates (RBGR) and relative leaf area growth rates (RLAGR) and the least capacities to compensate, while exponential plants had the slowest decrease in relative biomass growth rates and relative leaf area growth rates and the greatest capacity to compensate. Therefore, compensatory growth responses can be predicted by knowing how resource supply affects growth rate trajectories. Plants with the greatest decrease in rate of change in relative growth through time (e.g., most negative slope of relative growth rate) have the least ability to compensate. This hypothesis can be tested in the field with biocontrol agents as a means of decreasing the negative effects of weed species, via competition for resources, on crop species. The results do not necessarily contradict the limited resource model of plant compensatory responses [10], or the compensatory continuum hypothesis [5], but rather provide a reason that variables, such as net assimilation rate and leaf area ratio, are related to compensatory responses, and why compensatory growth is not always positively related to resource level [11].

5. Conclusions

This study was carried out to better understand the compensatory growth of weed species as a function of resource supply in cropped systems, and relate directly to the use of biocontrol agents for controlling *A. theophrasti*. The results suggest that biocontrol methods for weeds need to consider both the amounts and timing of fertilization in a way that optimizes N fertilizer rates to increase competitive advantage of crop species. Most significantly, the study shows that a plant's relative growth trajectory better predicts the compensatory responses in plants than the amount of nitrogen supplied, and how nitrogen supply can be modified to meet various management need.

Acknowledgments

This study was supported by a Missouri State University Faculty Research Grant to David Alexander Wait. Thank Cindy Austin for help in maintaining plants in the greenhouse.

References

[1] Trumble, J. T., Kolodnyirsch, D. M., and Ting, I. P. 1993. "Plant Compensation for Arthropod Herbivory." *Ann. Rev. Entom.* 38: 93-119.

[2] Wortman, S. E., Lindquist, J. L., Schutte, B. J., and Davis, A. S. 2011. "Integrating Management of Soil Nitrogen and Weeds." *Weed Sci*. 59 (2): 162-70.

[3] Wise, M. J., and Abrahamson, W. G. 2007. "Effects of Resource Availability on Tolerance of Herbivory: A Review and Assessment of Three Opposing Models." *Am. Nat.* 169 (4): 443-54.

[4] Wait, D. A., Jones, C. G., and Schaedle, M. 1996. "Controlling Growth and Chemical Composition of Saplings by Iteratively Matching Nutrient Supply to Demand: A Bootstrap Fertilization Technique." *Tree Physiol.* 16 (3): 359-66.

[5] Pirk, G. I., and Farji-Brener, A. G. 2013. "Can the Nutrient-Rich Soil Patches Created by Leaf Cutting Ants Favor Plant Compensation for Foliar Damage? A Test of the Compensatory Continuum Hypothesis." *Plant Ecol.* 214 (8): 1059-70.

[6] Mabry, C. M., and Wayne, P. W. 1997. "Defoliation of the Annual Herb *Abutilon therophrasti*: Mechanisms Underlying Reproductive Compensation." *Oecologia* 111 (2): 225-32.

[7] Spencer, N. R. 1988. "Inundative Biological Control of Velvetleaf, *Abutilon theophrasti* (Malvaceae) with *Niesthrea louisianica* (Hem.: Rhopalidae)." *Entomophaga* 33 (4): 421-9.

[8] Spencer, N. R., and Sankaran, T. 1985. "Prospects for

Biological Control of Velvet Leaf (*Abutilon theophrasti*)." In *Proceeding of the VI International Symposium on Biological Control of Weeds*, 167-75.

[9] Lu, X., and Ding, J. 2010. "Flooding Compromises Compensatory Capacity of an Invasive Plant: Implications for Biology Control." *Biol. Inv*. 12 (1): 179-89.

[10] Van Staalduinen, M. A., Dobarro, I., and Begonna, P. 2010. "Interactive Effects of Clipping and Nutrient Availability on the Compensatory Growth of a Grass Species." *Plant Ecol.* 208 (1): 55-64.

[11] Brody, A. K., and Irwin, R. E. 2012. "When Resources Don't Rescue: Flowering Phenology and Species Interactions Affect Compensation to Herbivory in *Ipomopsis aggregate*." *Oikos* 121 (9): 1424-34.