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Journal

Ecology, 86(2)

Authors

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Publication Date

2005

Peer reviewed

COMPETITION, HERBIVORY, AND REPRODUCTION OF TRICHOME PHENOTYPES OF *DATURA WRIGHTII*

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Abstract. The trichome dimorphism of *Datura wrightii* is intriguing because glandular trichome production has a high fitness cost. Plants producing glandular trichomes (“sticky” plants) are resistant to many insect herbivores that attack plants producing nonglandular trichomes (“velvety” plants). When protected from herbivores, sticky plants initially produce fewer seeds than velvety plants but grow to a larger size. In a three-year field experiment, we tested the hypothesis that sticky plants acquire a competitive advantage through greater vegetative growth. In the absence of herbivores, sticky and velvety plants grew to similar sizes in their first year, but sticky plants grew larger in the second and third years. Seed production of sticky plants was 46–60% less than velvety plants in their first year, and this caused a 13% reduction in their finite rate of increase overall, even though sticky plants produced more seeds than velvety plants did in later years. The impact of herbivory varied with plant density, and herbivores reduced plant fitness more at low plant density than at high plant density. The differences in growth associated with trichome morphology occurred too late to provide a competitive advantage to sticky plants and probably contribute little to the maintenance of *D. wrightii*’s trichome dimorphism.

Key words: competition; *Datura wrightii*; herbivory; polymorphism; resistance; trichomes.

INTRODUCTION

It has been difficult to develop generalizations concerning the combined effects of competition and herbivory on plant fitness despite extensive research on each factor individually. One hypothesis is that competition and herbivory should affect plant performance independently (Reader and Bonser 1998), and many studies indeed find such independence (Parker and Salzman 1985, Rees and Brown 1992, Karban 1993, Maron 2001). Independence is not universal, and damage by herbivores also can exacerbate (Lee and Bazzaz 1980) or mitigate the effects of competition (Parmesan 2000, Haag et al. 2004).

The lack of pattern may be influenced by details of the experimental design. The effect of herbivory on competition will depend upon how herbivory is distributed over the superior and inferior competitors. If damage were concentrated on the inferior competitor, then herbivory should increase the asymmetry of competition favoring the superior competitor. If damage were concentrated on the superior competitor, then herbivory should reduce the superior competitor’s advantage. If herbivores attack superior and inferior competitors similarly, then herbivory may mitigate the effects of competition overall (Gurevitch et al. 2000). Similarly, no interaction is expected between competition and herbivory if competition and resistance mechanisms are independent (Uriarte et al. 2002), and

synergistic interactions are expected when resistance and competitive ability are positively associated (Siemens et al. 2002). When resistance occurs at the expense of competitive ability, a number of outcomes are possible; competition may either amplify the costs of resistance, especially on early growth under asymmetric competition with low levels of damage, or amplify the benefits of resistance under symmetric competition at high plant density and high levels of damage to susceptible plants (Weis and Hochberg 2000).

We studied competition and herbivory using *Datura wrightii* Regel (Solanaceae). In this species, herbivore resistance is costly and is correlated with plant growth traits that may be beneficial in a competitive environment. All plants produce leaf trichomes, and two phenotypes occur (van Dam et al. 1999). “Velvety” plants are densely covered with short, nonglandular trichomes while “sticky” plants are less densely covered with glandular trichomes. Glandular trichomes secrete acyl-sugars (van Dam and Hare 1998) that confer resistance to many of *D. wrightii*’s insect herbivores (Hare and Elle 2002). Trichome phenotype is controlled by a single Mendelian gene, the sticky condition is dominant (van Dam et al. 1999), and the frequency of sticky plants ranges from 0 to 93% among populations (Hare and Elle 2001).

The production of glandular trichomes is correlated with increased vegetative growth at the expense of early seed production (Hare et al. 2003). Although sticky plants initially produce fewer seeds than velvety plants, sticky plants may accrue a competitive advantage over velvety plants by virtue of greater size at high densities.

Manuscript received 15 June 2004; revised 13 September 2004; accepted 15 September 2004. Corresponding Editor: A. R. Zangerl.

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The cost of producing glandular trichomes might be reduced or eliminated when sticky and velvety plants are grown under sufficiently high competition.

We carried out a competition experiment in the field over three years where sticky and velvety plants were grown in pure or mixed stands at three different densities (Marshall and Jain 1969, Gurevitch et al. 1990, Goldberg and Scheiner 1993), and exposed to, or protected from herbivores to test the following hypotheses:

- 1) Because sticky plants eventually grow larger than velvety plants, the sticky type may be the better competitor, and the advantage that velvety plants have over sticky plants should decline when plants are grown at increasing densities.
- 2) If the sticky type is the superior competitor, then the seed production of sticky plants should be relatively greater, and that of velvety plants should be relatively less, when grown in mixed than in pure stands.
- 3) Herbivory and competition will act independently upon plant fitness.

METHODS

The life history of *D. wrightii* in southern California has been described previously (Elle et al. 1999). In brief, plants are found in sandy or gravelly disturbed sites in the southwestern United States and Mexico (Avery et al. 1959). Seeds germinate during the winter rainy season, and plants flower and produce seeds from April through December. The large white flowers are open for one night, and, despite obvious characteristics favoring pollination by hawk moths (Grant and Grant 1983), outcrossing averaged only 29% in previous experiments (Elle and Hare 2002). Leaves and stems senesce during the winter, and new foliage is produced from a storage root each spring. Plant leaf canopies often reach 1–2 m in diameter and 1 m in height (Mira and Bernays 2002, Hare et al. 2003).

Experimental conditions were similar to those used previously (Hare et al. 2003), except that plants were never irrigated after establishment. Seedlings were utilized from three randomly selected families originating from crosses between a randomly selected velvety pollen donor and heterozygous sticky pollen acceptor from two local populations. Because the sticky phenotype is inherited as a dominant Mendelian character, the expected ratio of sticky and velvety offspring from these crosses is 1:1. Seedlings were germinated in the greenhouse in the winter of 2000–2001 and reared until adult trichome type could be assessed. Plants were transplanted to a field at Agricultural Operations, University of California, Riverside, on 19 and 20 April 2001, after the field had been furrow irrigated for 20 h.

Plants were arrayed in hexagonal plots of 19 plants (Harper 1977: Fig. 8/1). The center plant was surrounded by a hexagon of six data, or focal, plants and the data plants were surrounded by an outer hexagon of 12

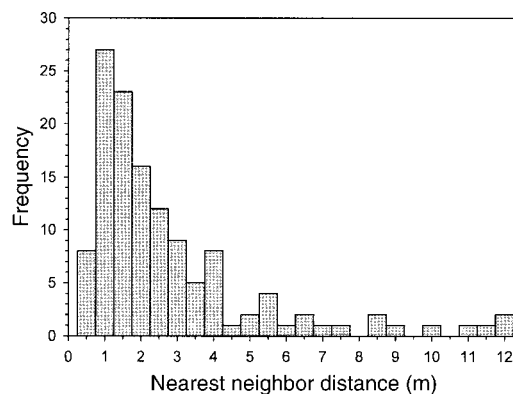


FIG. 1. Distribution of nearest-neighbor distances between individual *Datura wrightii* plants. Data were obtained from four populations (two sites from University of California, Riverside, California, USA: Pictograph Trail and Mill Creek; see van Dam et al. [1999] and Hare and Elle [2004] for more detailed population descriptions).

competitors. Each data plant was in direct competition with six adjacent plants: the center plant, two adjacent data plants, and three nondata competitors in the outside ring. We used three stand types: pure velvety, pure sticky, and mixed. The mixed stand utilized three data plants of each type, each of which was surrounded by three sticky and three velvety competitors. To determine relevant plant densities for our experiment, we surveyed 131 plants from four local populations. The nearest-neighbor distances between plants yielded a skewed distribution ranging from 0.5 m to 12 m with a mean of 2.9 m but a mode of 1.0 m (Fig. 1). On the basis of this information, we replicated our stands at three plant spacings: 3 m, 1 m, and 0.5 m between plants.

We also included an herbivory treatment in which half of the plots were exposed to herbivorous insects and the other half were protected from herbivory by twice-monthly applications of acephate (0.63 kg/ha active ingredient), an insecticide that does not affect plant growth (Elle et al. 1999). Applications were made between 24 May and 27 September 2001, 3 April and 13 October 2002, and 3 April and 16 October 2003. Weeds were controlled by hoeing and treatment with glyphosate when needed.

There were a total of 54 plots (three densities \times three stand types \times three families \times two herbivore treatments), 324 data plants, and 1026 plants in total. Plots were separated by at least 5 m of bare soil and the whole field site was 0.6 ha in size.

A fully expanded leaf from each data plant protected from herbivores was collected in July 2001. The numbers of glandular and nonglandular trichomes on the abaxial midrib of each leaf were tallied under a dissecting microscope using standard procedures (van Dam et al. 1999). Densities of glandular and nonglandular trichomes were analyzed by analyses of variance

(ANOVA) to determine if the densities of either trichome type varied among plant families.

Data on plant size and herbivory were collected weekly from 10 May to 1 November 2001, from 3 April to 3 November 2002, and from 1 April to 23 October 2003 using nondestructive methods (Hare and Elle 2002). On each census date, a branch with 10–20 leaves was chosen at random and the number of leaves on the branch was recorded, as well as the total number of branches on the plant. The product of these two values estimates the number of leaves per plant. The total leaf area per plant was estimated by multiplying the total number of leaves per plant by the mean leaf area determined monthly with a Li-Cor model 3000 leaf area meter (Li-Cor Inc., Lincoln, Nebraska, USA) from a sample of fully expanded leaves from each data plant in each low-density protected plot. We estimated herbivore damage as the proportion of the leaf area removed from the selected branch by herbivores and multiplied this by the total leaf area to estimate the total leaf area removed or damaged by herbivores per plant. We combined variation in both the size and the persistence of leaf canopies by integrating the weekly leaf area estimates over time, in units of $\text{cm}^2\text{-d}$, hereafter, leaf area days. We also calculated season-long total removal of leaf area days by herbivores by integrating the weekly damage estimates over time (Hare and Elle 2002).

We analyzed data on leaf area days by the PROC MIXED procedure of SAS (SAS Institute 2000) using a repeated-measures model with year as the repeated factor. Family and its interactions were “random” effects, whereas the factors of herbivory treatment, trichome type, density, and stand type and their two-way and higher-order interactions were “fixed” effects. The cube root transformation was used to ensure normality of residuals, and the Satterthwaite method was used to calculate degrees of freedom.

We estimated total viable seed production per plant per year as described previously (Hare et al. 2003) as the product of the number of seed capsules per plant, the mean number of seeds per capsule, and the germination rate of seeds from each plant. We recorded the number of surviving plants and determined the number of viable seeds that each had produced. Competition will be reduced when a competitor dies, so differential survival may affect the intensity of competition. To evaluate this, we compared analyses on unadjusted viable seed production per plant with viable seed production adjusted for the death of competitors. For example, when one of the six competitors dies leaving five, we multiplied the unadjusted seed production by 5/6 to calculate adjusted seed production. Because of the high survival of plants (see *Results*), these adjustments changed viable seed production only by 3% overall and did not alter the pattern of significant differences. Accordingly, we only report unadjusted viable seed production.

We calculated age-specific survivorship (l_x) and age-specific reproduction (m_x) for each of the 72 groups of plants in each combination of herbivory treatment, density, type, stand, and family. We constructed separate life tables for the sticky and velvety plants within mixed stands. We determined age-specific survivorship from the survival of all 19 plants within each plot in order to obtain more precise survival estimates. In neither the protected nor the exposed plots did survival of data plants differ from that of nondata plants ($G = 0.348$, $df = 1$, $P = 0.56$ for protected plots and $G = 1.794$, $df = 1$, $P = 0.18$ for exposed plots). From the l_x and m_x values, we formed Leslie matrices for post-breeding censuses and birth-pulse populations. We calculated the finite rate of increase (λ) as the dominant eigenvalue of the Leslie matrix using PROC IML of SAS (SAS Institute 2000). We analyzed the λ values using PROC MIXED, as above, after applying the square root transformation to ensure normality and homogeneity of residuals. In these analyses, we were more interested in the interactions than the main effects. For example, our first working hypothesis, that sticky plants are the superior competitor, would be supported by a significant interaction between trichome type and density showing that the differences in fitness between types declined with increasing density. Our second working hypothesis, that competition is asymmetrical, would be consistent with an interaction between trichome type and stand type, especially at higher densities (e.g., trichome type \times stand type \times density interaction). Our third hypothesis, that competition and herbivory act independently, would be rejected by a significant interaction between herbivory and density.

RESULTS

The density of glandular trichomes on sticky plants averaged 86.97 ± 1.84 trichomes/ mm^2 (mean \pm 1 SE) and did not vary among families, plant density treatments or their interaction (all $P \geq 0.26$). The density of nonglandular trichomes on velvety plants averaged 211.02 ± 9.27 trichomes/ mm^2 and also was independent of family, density treatment, and their interaction (all $P \geq 0.12$). These trichome densities are typical of *D. wrightii* (van Dam et al. 1999). Plant survival after three years averaged 79.7% overall. Survival was higher when protected than when exposed to herbivores (89.2% vs. 73.9%, $P < 0.0001$), and sticky plants had higher survival than velvety plants (85.7% vs. 78.4%, $P = 0.023$).

Leaf area days differed significantly due to the main effects of herbivory ($F_{1,284} = 26.61$, $P < 0.0001$) and density ($F_{2,229} = 111.16$, $P = 0.0052$, Fig. 2). Herbivores reduced leaf area days by 15% overall. Proportional damage to each plant, however, did not vary with density ($F_{2,144} = 1.50$, $P = 0.23$) or type ($F_{1,136} = 0.27$, $P = 0.60$, data not shown). Leaf area days were reduced 30% overall by reducing plant spacing from 3 m to 1 m and by 47% by reducing plant spacing from 3 m to

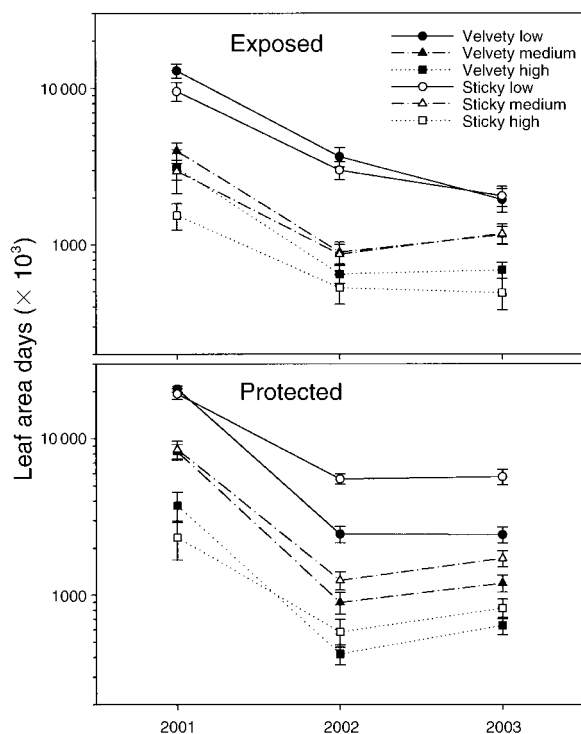


FIG. 2. Least-squares mean (± 1 SE) leaf area days (log scale) of sticky and velvety *D. wrightii* exposed to, or protected from, herbivores at low, medium, or high density over three years after pooling over families and stand types.

0.5 m. Leaf area days also differed due to the interactions of herbivory with trichome type ($F_{1,286} = 8.67$, $P = 0.0035$) and with density ($F_{2,284} = 6.358$, $P = 0.0016$, Fig. 2). The herbivory by type interaction occurred because sticky plants had greater leaf area days than velvety plants when protected from herbivores but not when exposed to herbivores (Fig. 2). The herbivory by density interaction occurred because the differences in leaf area days between protected and exposed plants declined with increasing plant density. Low-density plants had 20% fewer leaf area days when exposed to herbivores than when protected, medium-density plants had 14% fewer leaf area days, but high-density plants had only 4% fewer leaf area days when exposed to herbivores than when protected. Some of these differences varied among years (Fig. 2), but the differences were largely in magnitude and not in direction. A notable exception was the difference in leaf area days between sticky and velvety plants over time as shown by the year \times trichome type interaction ($F_{2,270} = 9.85$, $P < 0.0001$). In 2001, sticky plants had 9.9% fewer leaf area days than velvety plants, but sticky plants had 6.0 and 9.4% more leaf area days in 2002 and 2003. Neither stand type, family, nor any of their interactions were statistically significant (all $P \geq 0.13$).

Viable seed production varied among years, and with several treatment effects and interactions with year, and was strongly influenced by the number of seed capsules

(81.0% to 87.7% of the variation in total viable seed production within years over all plants pooled). Variation in seeds per capsule and germination rate contributed little to the variation in total viable seeds per plant (seeds per capsule, 1.9–4.5%; germination rate, 1.0–2.5%). Germination rates ranged from 75.8% to 84.7% and did not differ between types or due to any other factors in any year. Because λ accounts not only for variation in total viable seed production but also for variation in survival and the timing of reproduction, λ provides a more revealing summary of overall plant reproduction than analyses on seed production in any given year.

The finite rate of increase was strongly affected by three of the four main effects in our experimental design: herbivory ($F_{1,46} = 7.09$, $P = 0.0107$), trichome type ($F_{1,31.9} = 5.41$, $P = 0.0266$), and density ($F_{2,46} = 43.96$, $P < 0.0001$, Fig. 3). Herbivores reduced λ by 46% overall, and λ of velvety plants was 13% greater than that of sticky plants overall. Decreasing plant spacing from 3 m to 1 m reduced λ by 76% and decreasing plant spacing from 3 m to 0.5 m reduced λ by 89%. Our first working hypothesis that the sticky type would be the superior competitor was not supported because there was no significant interaction between density and trichome type ($F_{1,46} = 0.31$, $P =$

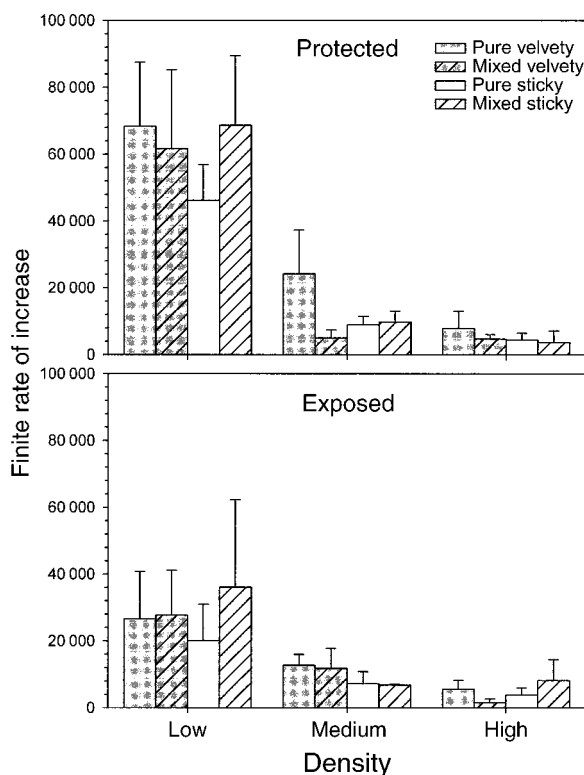


FIG. 3. Least-squares mean (± 1 SE) finite rate of increase of sticky and velvety *D. wrightii* exposed to, or protected from, herbivores at low, medium, or high density over three years after pooling over families.

0.58). Our second hypothesis, that competition would be asymmetrical, also was not supported because neither the main effect of stand type, nor any of its interactions, was statistically significant (all $P \geq 0.11$). Our third hypothesis, that competition and herbivory were independent, was rejected because we observed a significant herbivory \times density interaction ($F_{2,46} = 4.49$, $P = 0.0165$, Fig. 3). The reduction in λ due to herbivory was 55% at the low density, 20% at the medium density, and only 7% at the highest density. These differences were similar for both trichome types because the herbivory \times density \times trichome type interaction was not significant ($F_{2,46} = 0.94$, $P = 0.40$). There was no significant variation in λ due to plant family or any interaction with family (all $P \geq 0.28$).

DISCUSSION

Although sticky plants grew larger than velvety plants in the second and third years of the study, these size differences emerged too late to provide a competitive benefit to sticky plants overall. Herbivory affected the outcome of competition, however, and the impact of herbivory was greatest for plants at the lowest density. As competition squeezed plant fitness toward zero then the additional fitness losses due to herbivory also tended toward zero.

The time course of plant growth and seed production in the current experiment was similar to patterns seen in a prior study (Hare et al. 2003), especially for the low-density treatment, whose plant spacing replicates the earlier study. In both studies, sticky plants became progressively larger than velvety plants over time but sticky plants suffered a 45% (Hare et al. (2003) and 46% (this study) reduction in seed production in the first year of life. The effects of herbivory also were similar in the two studies. In the prior study, herbivory reduced λ by 69–83% (Hare et al. 2003), whereas in the current study, herbivory reduced λ of these plants by 55% overall.

Although most studies on competition and herbivory show either independent effects, or herbivory being more debilitating at high levels of competition than at low (reviewed by Gurevitch et al. 2000), our finding that herbivory is less debilitating at high plant density than at low is not unprecedented (Parmesan 2000). Haag et al. (2004) also found that herbivory was more debilitating at low plant density than at high, but herbivore densities varied between focal and competing plants. They suggested that their results were caused by systematic differences in herbivory on focal vs. competing plants at different densities. We can rule out any effect of differential herbivory on focal vs. competing plants because focal plants and competitors were similarly attacked by herbivores. Additionally, because the proportional damage level was independent of density, we can exclude density-related variation in herbivore damage as the cause of our herbivory \times density interaction. Plants in our outer ring of competitors were

substantially larger than our data plants in the medium and high-density treatments, probably because plants in the outer ring were competing with only three or four other plants and not six. Focal and competing plants were most similar in size in the low-density treatment. We speculate that the reduction in the effect of herbivory from low to high plant density was because herbivores reduced the intensity of plant competition as herbivores reduced not only the size of the focal plants but also the size of their competitors in the higher-density treatments.

It may be possible that sticky plants might have had an advantage if the experiment were run for a longer time. However, previous studies on the survival of *D. wrightii* in the field show that the probability of future survival in natural conditions is approximately two years (Hare and Elle 2004), so three seasons is a reasonable amount of time to study competition in this perennial species. Additionally, because of the sensitivity of λ to early reproduction, it becomes progressively more difficult to offset the initial fitness deficit of sticky plants with advantages in later years. Thus, we feel it unlikely that a study of longer duration would yield qualitatively different outcomes.

Despite the fact that the increased vegetative growth of sticky plant did not confer an advantage to sticky plants when in competition with velvety plants, our results contribute toward understanding the natural trichome dimorphism in *D. wrightii*. The absence of any growth-related advantage to sticky plants re-emphasizes our previous conclusion that the fitness costs of glandular trichome production often exceeds its benefits and is consistent with recent observations of declines in the frequency of sticky plants in established populations (Hare and Elle 2004).

ACKNOWLEDGMENTS

We thank E. Elle, A. Gassmann, and N. M. van Dam for comments on previous drafts of the manuscript and C. Siguenza, J. Schlax, and many undergraduates for field and laboratory assistance. This research was funded by the National Science Foundation (NSF DEB 00-89519 to J. D. Hare).

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