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SURVIVAL AND SEED PRODUCTION OF STICKY AND VELVETY *DATURA WRIGHTII* IN THE FIELD: A FIVE-YEAR STUDY

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Abstract. Leaves of *Datura wrightii* in California (USA) are covered either with glandular trichomes (“sticky” plants) or non-glandular trichomes (“velvety” plants), and sticky plants are resistant to many insect herbivores. Theoretical models suggest that variation in resistance to herbivores may persist if resistance is costly and herbivore damage is variable. If so, then natural selection should favor resistant plants when damage is high and disfavor it when damage is low. However, without long-term equivalence between costs and benefits, then natural selection either should drive the trait to fixation if it has a net benefit or eliminate it if it has a net cost. Previously we showed that the production of glandular trichomes carried a net cost in short-term studies, suggesting that this expensive resistant trait might be eliminated from *D. wrightii* populations. To test this hypothesis we monitored survival and seed production of sticky and velvety *D. wrightii* in the presence of herbivores in 11 natural populations over four or five years. In eight populations where both types occurred, the finite rate of increase for velvety plants was 60–274% greater than for sticky plants. Plant survival averaged between two and three years and did not differ significantly between types. Because seed production consistently favored velvety plants, our prediction that the proportion of sticky plants should decline was met within five years in seven of those eight populations. If the variation in trichome morphology in *D. wrightii* is indeed maintained by variation in costs and benefits of glandular trichomes, then the periodicity of such variation extends over more than five seasons.

Key words: costs of resistance; *Datura wrightii*; demographic analysis; geographic variation; resistance polymorphism; trichomes.

INTRODUCTION

Plant populations often exhibit genetic variation for traits that confer herbivore resistance (Koricheva 2002, Strauss et al. 2002). The conventional explanation of such variation is that there is a trade-off between the costs and benefits of resistance. When the benefits are variable, then natural selection should favor resistant individuals when herbivory is intense and susceptible individuals when losses from herbivores are minimal (Simms 1992). Several theoretical models permit the persistence of intermediate values of resistance traits based upon the trade-offs between the costs and benefits of resistance (Gillespie 1975, Simms and Rausher 1987). Yet an underlying assumption of these models is that, *on average*, the costs must equal the benefits. In the absence of such equivalence, natural selection eventually should eliminate susceptible individuals if the benefits of resistance exceed its cost or resistant individuals if the costs exceed its benefits.

We study a system in which the production of a resistance characteristic is costly and the cost exceeded

its benefits in both natural and experimental populations (Elle et al. 1999, Elle and Hare 2000, Hare et al. 2003). Individual plants of *Datura wrightii* Regel (Solanaceae) are covered by trichomes, and two trichome phenotypes of this native plant occur in California, USA (Hare and Elle 2001). Some plants produce short, dense, non-glandular trichomes (“velvety” plants) while others produce longer, glandular trichomes but at a lower density (“sticky” plants). Sticky and velvety plants grow adjacently in populations, often with their branches interdigitated, indicating that microsite partitioning of the available habitat by the two types is unlikely.

Trichome phenotype in *D. wrightii* is largely controlled by a single Mendelian gene, and the sticky condition is dominant (van Dam et al. 1999). The percentage of sticky plants in California ranges from zero to 93% and increases with water availability (Hare and Elle 2001). Although the flowers have characteristics favoring pollination by night-flying hawk moths (Grant and Grant 1983), outcrossing rates are only on the order of 30% in California (Snow and Dunford 1961, Elle and Hare 2002), and interpopulation gene flow may be restricted in southern-California populations (Elle and Hare 2002).

The glandular trichomes secrete glucose esters (van Dam and Hare 1998a) that confer resistance to several insect herbivores of *D. wrightii*, including flea beetles,

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leafhoppers, and whiteflies (Hare and Elle 2002). Glandular trichomes, however, also confer susceptibility to *Tupiocoris notatus* (Distant), a mirid bug that prefers to feed on sticky plants (van Dam and Hare 1998b). Glandular trichomes have no apparent effect on a subspecies of the three-lined potato beetle, *Lema trilineata daturaphila* Kogan and Goeden (Chrysomelidae) (Hare and Elle 2002). The two trichome types of *D. wrightii* do not differ in leaf reflectance, leaf temperature, stomatal conductance, or transpiration; under certain conditions, sticky plants exhibit slightly higher photosynthetic rates (J. L. Smith and J. D. Hare, unpublished data).

In a common-garden experiment, the production of glandular trichomes was costly because the total viable seed production of sticky plants was 45% less than that of velvety plants when both were protected from herbivores (Elle et al. 1999). Exposure to herbivores reduced total viable seed production by 50–70%, but viable seed production of plants exposed to herbivores did not differ significantly between the two plant types, suggesting that the benefits of glandular trichome production equaled its costs (Elle et al. 1999, Hare and Elle 2002). In contrast to our common-garden experiment, we surveyed herbivory and seed production in four natural populations of *D. wrightii* in 1998 and found that sticky plants produced from 34% to 73% fewer seeds than velvety plants even when exposed to herbivores, suggesting that the costs of glandular trichome production exceeded its benefits in these natural populations (Elle and Hare 2000). Based upon these results, we predicted that the proportion of sticky plants should decline (Elle and Hare 2000).

Those field observations were limited only to one season, and we might have surveyed herbivory and seed production in a year when costs of glandular trichomes were high relative to their benefits. To evaluate the generality of our prediction that the proportion of sticky plants should decline, we continued our observations of survival and seed production of sticky and velvety plants in populations spanning a rainfall gradient for an additional four years. We focused particularly upon determining the average lifetime of sticky and velvety *D. wrightii* in natural populations, the total viable seed production of those plants, and how both survival and seed production might vary over a more than four-fold range of variation among sites in average annual rainfall. Finally, we attempted to detect if significant changes in the frequencies of sticky and velvety plants could be observed in as few as five seasons for this perennial species.

METHODS

We chose 11 plant populations to span the range of variation in annual rainfall that occurs among habitats of *D. wrightii* within southern California (USA). All populations were in their native habitat and at least 15 km away from any agricultural areas potentially sup-

porting insect pests of solanaceous crops. A map of these and other populations and their phenotype frequencies appears in Hare and Elle (2001).

Four populations were in the Santa Ana mountain range ("Mountain sites"). One was in Bell Canyon (BC; 33°32.5' N, 117°33.5' W) and another was near Ortega Flat Campground (OF; 33°32.0' N, 117°32.0' W), both within the Ronald W. Caspers Wilderness Park, Orange County, California. A third was in Arroyo Trabuco (AT; 33°38.5' N, 117°36.5' W) within the O'Neill Regional Park in Orange County. The fourth was within the General Thomas F. Riley Wilderness Park (RP; 33°36.0' N, 117°35.0' W), also in Orange County.

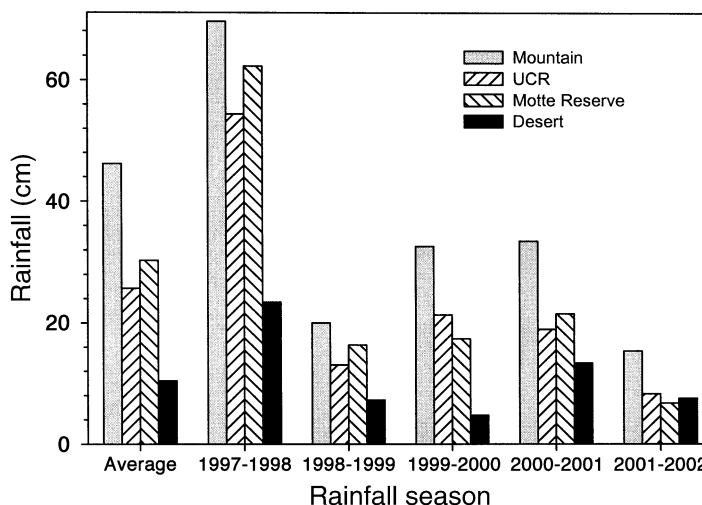
We also selected four populations in the Riversidian sage scrub habitat of western Riverside County ("Scrub sites"). One population was located at Coyote Pass (CP; 33°53.0' N, 117°8.0' W) within the boundaries of the Lake Perris State Recreation Area, and another was located near the pictographs (PT; 33°48.5' N, 117°15.0' W) in the Motte Rimrock Reserve of the University of California Natural Reserve System. A third was located on the campus of the University of California, Riverside (UCR; 33°58.5' N, 117°19.5' W), and the fourth was on undeveloped land near the intersection of Ironwood Avenue and Moreno Beach Drive within the boundaries of the City of Moreno Valley (MV; 33°57.0' N, 117°10.5' W).

We selected three populations within the Joshua Tree National Park, Riverside and San Bernardino Counties, California ("Desert sites"). One was located near the Barker Dam (BD; 34°2.0' N, 116°8.5' W), which forms a small, temporary water reservoir in years of high rainfall. Another population was located along the roadside near the White Tank campground (WT; 33°58.0' N, 116°0.5' W), ~20 km east of the BD population. The third population was in a desert wash crossing the Pinto Basin Road in Wilson Canyon (WC; 33°56.0' N, 115°58.0' W), ~4.0 km east of the WT population.

We estimated annual rainfall for the four Mountain sites from monthly data provided by the Starr Ranch Sanctuary of Audubon California (33°38' N, 117°33' W), which was between 4.1 and 10.5 km of all mountain sites. Average (1987–2002) annual rainfall was 46.19 cm and ranged during our study from 69.6 cm in 1997–1998 to 15.32 cm in 2001–2002 (Fig. 1). The 1997–1998 and 2001–2002 years were the third wettest and the driest years on record at Starr Ranch. We estimated annual rainfall for the UCR, CP, and MV sites from monthly data recorded from the National Weather Station on the grounds of the University of California Citrus Experiment Station, Riverside California (33°58' N, 117°22' W), which was between 1.6 and 20.0 km of these three sites. Rainfall records for this site were obtained online from the National Climate Data Center.³ Rainfall records for the PT site were pro-

³ URL: <http://cdo.ncdc.noaa.gov/ancsum/ACS>

FIG. 1. Annual rainfall in the Mountain, Scrub (UCR and Motte Reserve), and Desert habitats (all Southern California, USA) from 1997–1998 through 2001–2002, and long-term average rainfall for the three habitats. Averages are based on 54 years of data from the UCR (University of California, Riverside) and Desert weather stations, 29 years from the Motte Reserve, and 15 years from the Mountain weather station.



vided by the Motte Rimrock reserve. Average rainfall (1948–2002) at Riverside was 25.70 cm and ranged during our study from 54.38 cm in 1997–1998 to 8.26 cm in 2001–2002. The 1997–1998 year was the second wettest at UCR during the past 30 years, and 2001–2002 was the driest. Average rainfall (1973–2002) at the Motte Rimrock Reserve was 30.27 cm and ranged during our study from 62.26 cm in 1997–1998 to 6.71 cm in 2001–2002. The 1997–1998 year was the second wettest and was exceeded only slightly by the 63.72 cm measured in 1992–1993. The 2001–02 was the driest of the 29 years of recorded rainfall at Motte Reserve. We estimated annual rainfall for the Desert sites from the National Weather Station at Twentynine Palms, California (33°58' N, 117°22' W), which was between 12.6 and 20.2 km of all three sites. Average rainfall (1948–2002) at Twentynine Palms was 10.46 cm and ranged during our study from 23.39 cm in 1997–1998 to 4.72 cm in 1999–2000. 1997–1998 was the wettest of the past 30 years at Twentynine Palms and 1999–2000 was the fifth driest, with the lowest rainfall of 1.83 cm having been observed in 1995–1996.

Our five-year study period therefore included some of the wettest and driest years of recorded rainfall at all sites, and the study period spans most of the range of variation in rainfall to which southern California *D. wrightii* populations are normally subjected. We also examined rainfall patterns for the 10 years prior to our study and found them unremarkable; rainfall during the previous decade was nearly as likely to be above average (4 years) as below average (6 years) at all sites.

We used methods described in Elle and Hare (2000) to select individual plants for long-term observation of survival and seed production. For logistic reasons, detailed observations could be made only at 7 of the 11 populations. Within a population, we located a plant of unknown age of the rare phenotype, and then we selected a plant of the other phenotype and similar size

(±10 leaves at the time of the first census) within 2 m of the first to minimize microhabitat differences between members of each pair. We selected 10 such pairs of plants in populations where both trichome types occurred. In the Desert populations, where only velvety plants occurred, we selected 15 individual plants. We selected experimental plants in the BC, BD, and WT populations in the spring of 1998, and these are the same plants described and utilized by Elle and Hare (2000). We selected plants in the remaining populations (PT, CP, AT, and WC) in the spring of 1999.

We recorded final data on plant survival per year from all populations in late September or October each year, as surviving plants began to go dormant. Methods to estimate total viable seed production per plant were identical to those used previously (Elle et al. 1999, Elle and Hare 2000). We collected up to three mature but unopened capsules from each plant and estimated the total number of seeds as the quotient of the total mass of all seeds divided by the average seed mass as determined from a random sample of 10 seeds per capsule. We assessed seed viability at the end of the season by calculating the proportion of seeds out of 60 that germinated over three weeks in an incubator (30°C, 16-h photophase: 20°C, 8-h scotophase, constant 50% relative humidity) after an initial 10-day stratification at 10°C. We recorded the total number of capsules produced per plant and calculated total viable seed production per plant as the product of total capsule production, mean seed number per capsule, and seed germination rate. Analyses of data collected previously (Elle et al. 1999, Elle and Hare 2000) show that most (68–82%) of the variation in total number of viable seeds per plant is due to variation in the number of capsules per plant, with relatively little variation due to variation in germination rate (2–8%) or the number of seeds per capsule (1–3%).

Fewer than 20% of all plants were alive at the end of our experiment, but the longevity of those plants is

unknown so mean lifetime cannot be calculated. Therefore, we calculated survival probability distribution functions and compared the probabilities of survival of two or more groups of plants statistically. We used the log rank test of the PROC LIFETEST procedure of SAS (SAS Institute 2000) to test if survival curves differed significantly between types within populations and among populations within types.

We used demographic analyses to assess the reproductive potential of monitored plants over time. We organized our data on survival and seed production into life tables to calculate the net reproductive rate (R_0) and developed Leslie matrices for post-breeding censuses and birth-pulse reproduction to calculate the finite rate of increase (λ) for cohorts of sticky and velvety plants within each population. The net reproductive rate was calculated as $\sum l_x m_x$, where l_x and m_x are age-specific survival and viable seed production, respectively, from $x = 1999$ to $x = 2002$ for the CP, PT, AT, and WC populations, and from 1998 to 2002 for the BC, BD, and WT populations. We ignore any seed production of plants prior to the beginning of our observations. The finite rate of increase is equal to the dominant eigenvalue of the Leslie matrix (Caswell 2001). We calculated the eigenvalues of all 11 matrices (four populations with two plant types and three populations with one plant type) using Mathematica, version 4.2 (Wolfram 1999).

Because the distributions of R_0 and λ are unknown and unlikely to follow the normal distribution (Caswell 2001), ANOVA cannot be used. Therefore, we compared final R_0 and λ of sticky and velvety plants by utilizing Friedman's method for randomized blocks (Sokal and Rohlf 1995). In this analysis, the treatment was plant type, and the blocks were the AT, BC, CP, and PT populations in which the two plant types occurred.

From the life tables, we also calculated the probability of survival each year, as l_x/l_{x-1} , and the expectation of life, e_x , as $(\sum [(l_x + l_{x+1})/2])/l_x$ over all values of x . We then calculated the regression coefficient between the probability of survival or the expectation of life and annual rainfall over years and habitats pooled. We also analyzed these data by analysis of covariance to determine if the regression coefficients between rainfall and expectation of future survival differed significantly between trichome types.

To determine if there were changes in the proportion of trichome phenotypes, we classified the phenotype of a large number of plants in each population into either sticky or velvety categories in September or October each year. Most populations were sufficiently small that every individual was examined. The number of plants classified ranged between 35 and 192 with a mean of 87. We confirmed the presence or absence of glandular trichomes with a hand lens (10 \times) when necessary. We then computed the mean proportion of sticky plants and its binomial standard error as $\sqrt{\{(s)(1-s)/n\}}$,

where s is the proportion of sticky plants and n is the total number of plants examined per population. We used the sign test to evaluate our hypothesis that the proportion of sticky plants should decline over time. In this test, the null hypothesis is that the proportion of sticky plants is as likely to increase as decrease over time, while the one-tailed alternative hypothesis is that the proportion of sticky plants should decline (Sokal and Rohlf 1995).

RESULTS

Survival functions differed significantly among populations (log rank test $\chi^2 = 39.97$, $df = 6$, $P < 0.0001$, Fig. 2) but not between types within populations pooled (log rank test $\chi^2 = 0.19$, $df = 1$, $P = 0.66$). Greatest survival occurred in the PT population where at least 50% of all plants remained alive at the end of their fourth year. In contrast, survival was lowest in BC, where all sticky and 90% of the velvety plants died before the end of the third year. Plant mortality also was high in the BD and WC Desert populations, where half of the plants died before the end of the second year (Fig. 2). The high mortality in the WC population in 2000 was, in part, caused by a flash flood in late August that washed out many plants. The differences in survival among populations must be interpreted with caution, because some populations, by chance, might have had an older age structure than others at the beginning of the experiment causing plants to die sooner because of natural senescence. The similar patterns of mortality between types within populations, however, suggests that the sticky and velvety cohorts probably had similar initial age structures within populations.

The R_0 (net reproductive rate) and λ (rate of increase) values were consistently higher for velvety than sticky plants in all populations where both types occurred (Figs. 3 and 4). Because the Friedman's method for randomized blocks is based upon ranks, the results of statistical testing for differences in R_0 and λ were identical. Both R_0 and λ were significantly higher for velvety than for sticky plants (Friedman's $\chi^2 = 4.00$, $df = 1$, $P = 0.046$). The increase in R_0 ranged from 12% in the AT population to 470% in the BC population (Fig. 3). The greatest proportional difference in λ occurred in the BC population where the λ of velvety plants was 274% greater than that of sticky plants (2035 vs. 544, Fig. 4). The smallest difference was in the AT population in which λ for velvety plants was only 60% greater than that for sticky plants (353 vs. 220, Fig. 4). The Desert populations had both the lowest and the highest values of λ of those observed in this study (82 for the BD population and 14 616 for the WC population, Fig. 4).

The expectation of life increased with increasing rainfall the previous year ($b = 0.023$, $F_{1,40} = 11.07$, $P = 0.002$). This relationship did not differ between plant types ($F_{1,40} = 0.02$, $P = 0.89$). The probability of survival within any year, however, was independent of

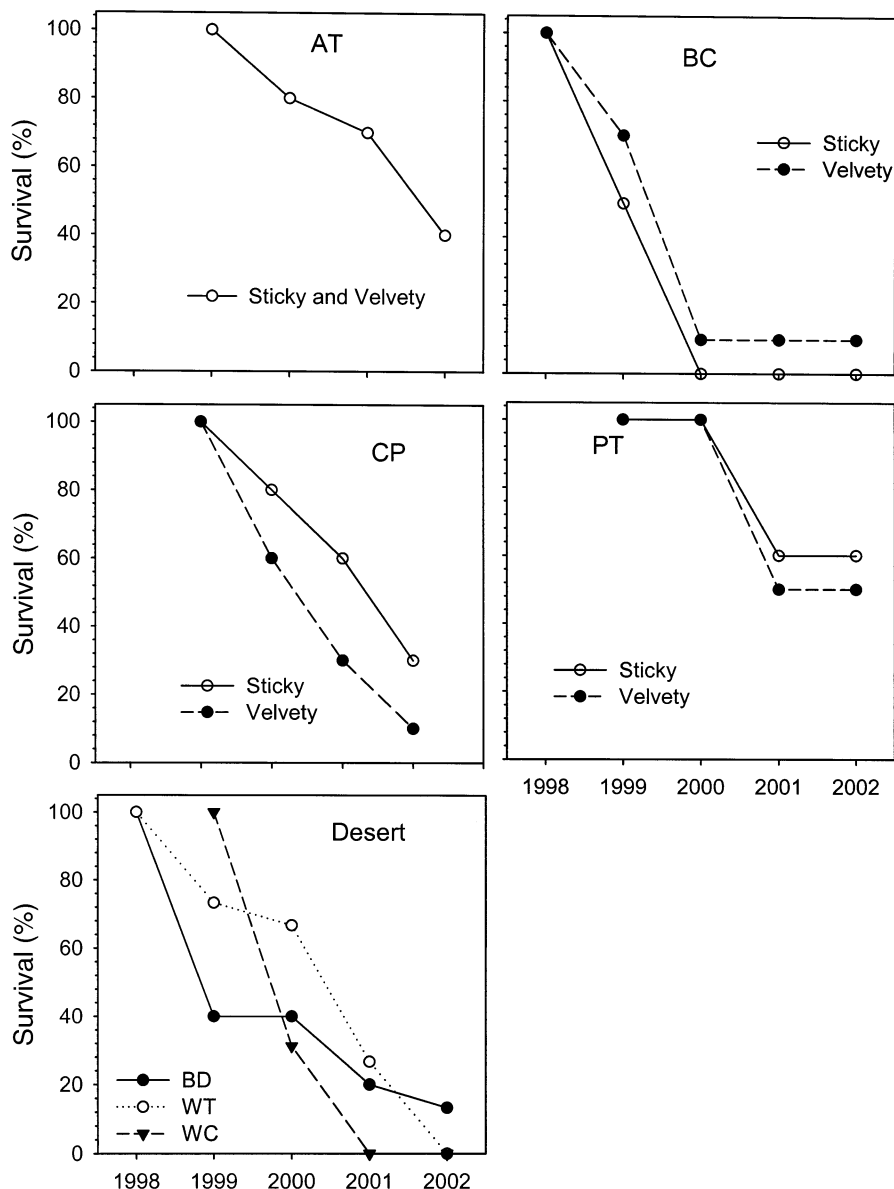


FIG. 2. Survival of sticky and velvety *Datura wrightii* over four or five years in Mountain (AT and BC), Scrub (CP and PT), and Desert (BD, WC, and WT) habitats of southern California, USA. Only velvety plants are found in the desert. Survival of sticky and velvety plants was identical in the AT population. For population codes, see *Methods*.

rainfall ($P = 0.37$). Although there was nearly a 15-fold range in annual rainfall between the wettest site and year and the driest, the high levels of plant mortality precluded any meaningful analyses on the relationship between seed production of individual plants and annual rainfall because too few plants remained alive during the relatively dry years at the end of the study.

In the eight populations with both phenotypes, the percentage of sticky plants ranged from a high of 88.6% in the RP population in 2001 to a low of 19.7% in the UCR population in 2002. The proportion of sticky plants in 2002 was lower than at the beginning of the

experiment for seven of these eight populations ($P = 0.035$) but the changes in frequency were not linear (Fig. 5). The only exception was the PT population in the Scrub habitat in which the percentage of sticky plants increased from 63.8% to 69.4% between 1998 and 2002.

DISCUSSION

The cost of producing glandular trichomes by sticky *Datura wrightii* consistently exceeded its benefits from 1998 through 2002. If variation in benefits of resistance plays a role in the maintenance of polymorphisms, then the costs of resistance should occasionally exceed its

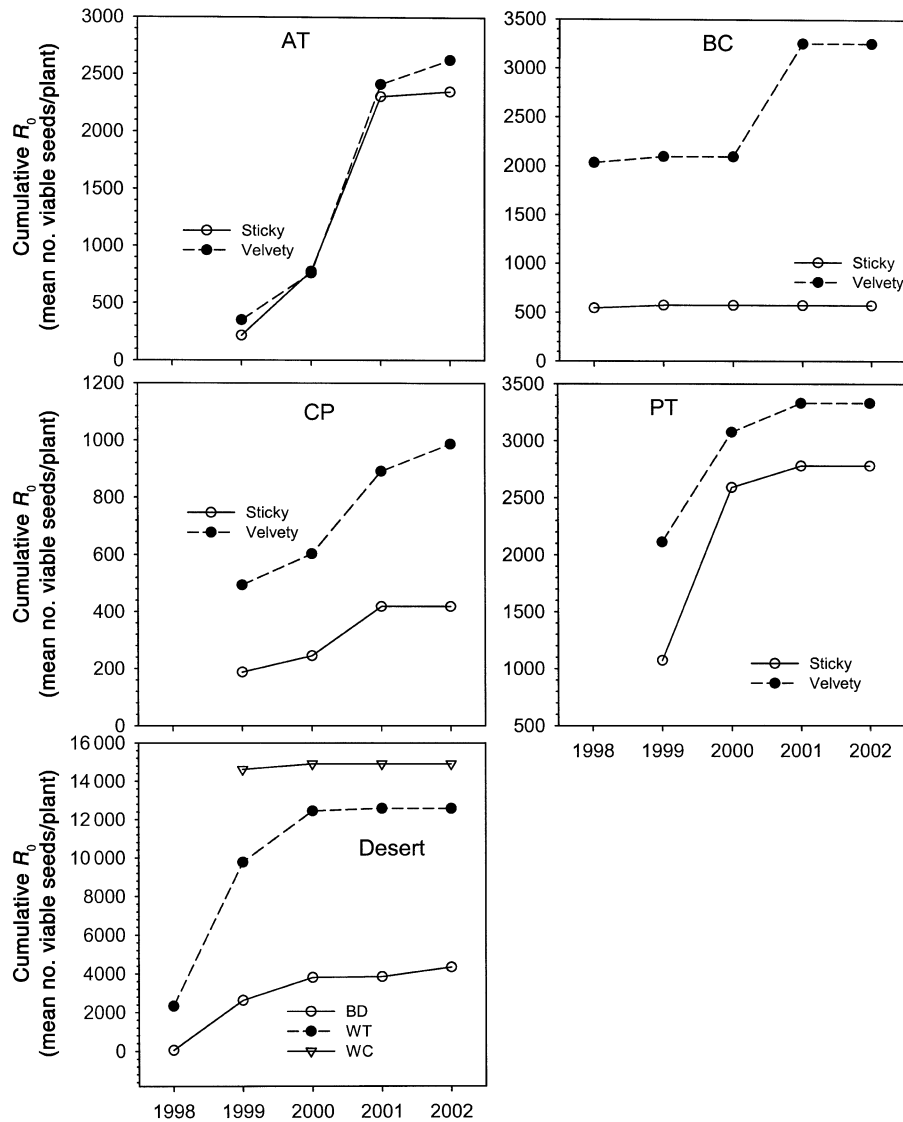


FIG. 3. Cumulative R_0 (net reproductive rate) of sticky and velvety *Datura wrightii* in southern California (USA) in Mountain (AT and BC), Scrub (CP and PT), and Desert (BD, WC, and WT) habitats of southern California. Only velvety plants are found in the desert.

benefits, and this has been observed in other systems. In *Trifolium repens*, cyanogenic forms had lower reproduction than acyanogenic forms in the presence of herbivores despite being more resistant to grazing snails (Kakes 1989). The benefits of jasmonate-induced defensive responses of *Nicotiana attenuata* varied with environment and herbivore density such that these responses were beneficial only at some field sites (Baldwin 1998). *Brassica rapa* selected to produce high levels of myrosinase, an enzyme that hydrolyzes glucosinolates in order to release their toxic components, suffered lower damage from flea beetles in the field but still had lower fitness than plants selected for low myrosinase levels (Siemens and Mitchell-Olds 1998). The cost of trichome production in *Arabidopsis thaliana*

also was greater than its benefits in a field experiment (Mauricio and Rausher 1997).

Although most of the above systems have been extensively studied, ours is the first, to our knowledge, to report consistent net costs of resistance over several seasons at several locations. Factors other than herbivores may influence selection on trichome type, although there are minimal differences in the reflectance, temperature, or physiology of leaves with glandular or non-glandular trichomes (J. L. Smith and J. D. Hare, unpublished data). The combination of the costs of producing glandular trichomes coupled with whatever unmeasured benefits there might have been to produce non-glandular trichomes resulted in consistently lower viable seed production of sticky plants in all habitats

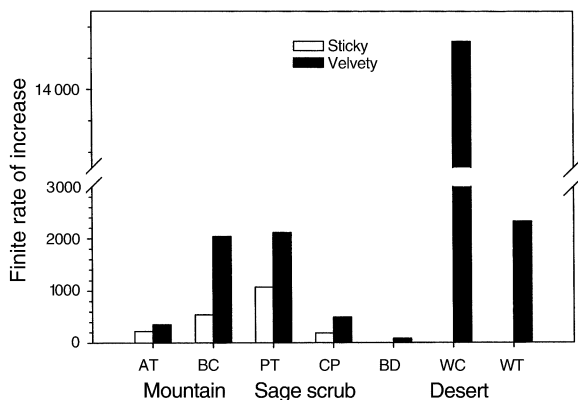


FIG. 4. Finite rate of increase (λ) of sticky and velvety *Datura wrightii* plants in Mountain, Scrub, and Desert habitats in Southern California (USA) from 1998 through 2002. Only velvety plants occur in the desert.

and years of our study. The lack of any net benefit over the large spatial scale and five years of this study suggests that if the “variable benefits” argument for the persistence of the trichome dimorphism in *D. wrightii* applies, then the periodicity when the benefits of resistance exceed its costs is longer than can be revealed by our five-year study.

Our results are consistent with previous studies on the costs and benefits of glandular trichome production by *D. wrightii* (Hare et al. 2003), although there were large differences in magnitude. In the common garden where plants were exposed to herbivores but unwatered, λ averaged 20 417, for velvety plants and 7389 for sticky plants whereas λ averaged only 1248 for velvety plants and 505 for sticky plants in the natural populations. The higher values of λ (finite rate of increase) for plants in the common garden than in natural populations probably are due to the absence of both inter- and intraspecific competition in the common garden. Although eliminating potential competitors in the common garden increased seed production compared to that in natural populations, it did not affect survival, as 58% of the velvety plants and 63% of the sticky plants died by the end of the three-year experiment, values similar to those observed after three years in the natural populations (Fig. 2).

We might expect reduced seed production in the Desert populations because of low rainfall, but the WC desert population had the highest λ of 14 161. In contrast to the populations in the Mountains and Scrub habitats, each of the three Desert populations was located in an area of relatively high moisture availability. The BD population was located around an ephemeral water reservoir, and the WC population was in a wash that was occasionally flooded by runoff from thunderstorms. Similarly, plants in the WT population probably benefited from runoff from the surface of the asphalt road immediately adjacent. In the Mojave Desert we have only found *D. wrightii* populations in such

sites, suggesting that plants only occur in relatively wet areas within the Desert habitat. Seed production was extremely high for the WC population in 1999, but most plants were killed by a flash flood in the summer of 2000. Because of the sensitivity of λ to early reproduction, the high seed production in 1999 was sufficient to give this population the highest λ of all populations over the five-year period despite the high mortality in 2000.

One potential limitation to our conclusion, that velvety plants have a higher potential for population growth than sticky plants, is that we did not measure germination or seedling survival in nature. The possibility therefore exists that seedlings of sticky plants may survive better until establishment than seedlings of velvety plants under natural conditions and potentially offset some of the advantage of seed production by velvety plants. We believe that the likelihood of this being the case is low for two reasons. First, all seedlings express the sticky phenotype until at least 10 true leaves are produced (van Dam et al. 1999), so there is little reason to expect variation in trichome morphology to affect seedling survival directly. Second, we previously examined seedling mortality in field experiments (Elle et al. 1999). Seedling mortality was low and did not differ between types when plants were protected from herbivores. In the presence of herbivores,

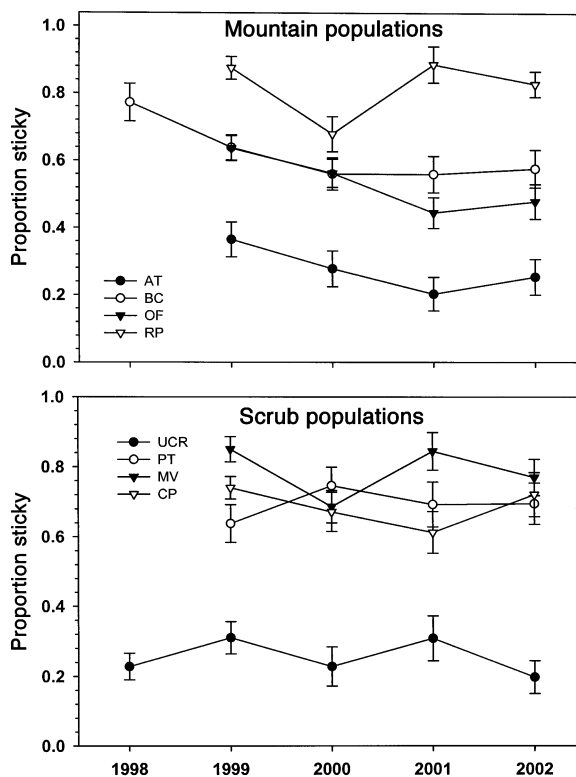


FIG. 5. Mean proportion and binomial standard errors of sticky *Datura wrightii* plants in eight populations in southern California (USA). For population codes, see *Methods*.

significantly more plants from sticky families died than plants from velvety families. The data above run counter to the hypothesis that the reduced reproduction of sticky plants might be offset by higher survival of seedlings that ultimately express the “sticky” adult phenotype.

Similarly, our conclusion of no differences in survival of sticky and velvety plants may be limited by the relatively small sample sizes used to determine long-term survival. Larger sample sizes might have allowed a significant difference to be observed, although the biological significance of such a difference is unclear. Any significant difference is likely to be of relatively small magnitude (Fig. 2), and the small size of most populations (often <200 individuals) suggests that the expression of those differences often may be obscured by random sources of mortality.

If the cost of glandular trichome production consistently exceed its benefits, then we would expect to see a reduction in the frequency of sticky plants. We did indeed see such reductions in frequency in seven of eight populations by the end of the study. We can only speculate as to the factors that might have promoted the initial high frequencies of sticky plants in these populations, and additional time will be required to determine if the sticky type is always at a selective disadvantage. Studies lasting longer than five years seem to be necessary to fully understand the dynamics of the trichome dimorphism in *D. wrightii*.

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