

## POLYMORPHIC BUTTONWOOD: EFFECTS OF DISTURBANCE ON RESISTANCE TO HERBIVORES IN GREEN AND SILVER MORPHS OF A BAHAMIAN SHRUB<sup>1</sup>

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We studied consequences of storm damage on buttonwood (*Conocarpus erectus*) shrubs and their herbivores in the Bahamian islands. Buttonwood is polymorphic, with green shrubs producing few leaf trichomes and silver shrubs covered in dense trichomes. We first characterize traits of green vs. silver shrubs relevant for herbivores, and then assay damage by two prominent insects. Next, on replicated islands, we experimentally address how different types of storm damage (simulated hurricane surge damage vs. simulated intense wind) affected phenotypic traits of both buttonwood morphs and subsequent herbivory over a one-year sampling period. Our results show that although leaves produced by green shrubs are 21% tougher than leaves produced by silver shrubs, green leaves have 16% higher nitrogen concentrations and greater levels of herbivory. Consistent with previous observational studies of a natural hurricane at our study site, we found stronger effects of simulated surge damage than simulated wind damage. Experimental pruning of shrubs resulted in reduced toughness, higher nitrogen concentration, fewer trichomes, and greater herbivory compared to controls and compared to shrubs with their leaves stripped. The results were stronger for the silver compared to the green morph. Morph differences in buttonwood have strong consequences for herbivores, and these effects are modified by disturbance.

**Key words:** *Biopsyche thoracica*; *Combretaceae*; *Conocarpus erectus*; Great Exuma Bahamas; herbivory; hurricane disturbance; leaf nitrogen content; plant-insect interactions; polymorphism; sprouting; trichomes.

The role of abiotic storm damage in affecting plants, their resistance traits, and food web dynamics has recently been receiving increased attention (Hunter and Forkner, 1999; Schowalter and Ganio, 1999; Hirsh and Marler, 2002; Koptur et al., 2002; Spiller and Agrawal, 2003). In this study we experimentally simulate two types of storm damage affecting island vegetation and study their ecological consequences. In October 1996, we had just finished our annual survey of the biota inhabiting small islands located on both sides of the very large island Great Exuma, when the eye of Hurricane Lili passed directly over our study site with sustained winds approximately 185 km/h and a 5-m storm surge (Spiller et al., 1998). The surge removed most of the standing biomass of vegetation on the exposed islands, but left other protected islands less damaged; protected islands were affected by high winds that stripped many leaves off the plants. Since then, we have been studying the natural pattern of recolonization of the islands (Spiller et al., 1998), herbivory on plants, and experimentally dissecting the mechanisms by which the hurricane disturbance affected the food web (Spiller and Agrawal, 2003).

To investigate herbivory, we have been focusing on buttonwood, *Conocarpus erectus* L. Combretaceae, one of the most common shrubs on our study islands. Buttonwoods that produce primarily glabrous (green) or heavily trichomed (silver) leaves co-occur in the Bahamas, frequently within meters of each other (Fig. 1) (Semple, 1970; Correll and Correll, 1982; Schoener, 1987). Although intermediates are fairly common, most plants are distinctly green or silver (Semple, 1970;

Schoener, 1987, 1988). Polymorphism in trichome production appears to be common among plant species (Semple, 1970; Flanders et al., 1992; Westerbergh, 1992; van Dam et al., 1999) and production of trichomes is frequently associated with resistance to herbivores (Schoener, 1987; van Dam and Hare, 1998; Agrawal, 1999; Haddad and Hicks, 2000).

On exposed islands, shrubs that regenerated by sprouting from stumps during the year after the hurricane had high levels of herbivory. Shrubs with silver leaves before the hurricane, sprouted green leaves the year after, and then reverted to producing silver leaves the following year. In addition, the sprouted foliage appeared to be very vigorous, possibly increasing susceptibility to herbivory (Price, 1991; Roininen et al., 1997). These observations suggested that foliage sprouting on severely damaged shrubs was more susceptible to herbivores than new foliage on undamaged shrubs. We confirmed this hypothesis using a controlled field experiment in which severe storm surge damage was simulated by pruning shrubs on replicated islands (Spiller and Agrawal, 2003). Enhanced herbivory on exposed islands following Hurricane Lili was caused, at least in part, by increased susceptibility of the sprouted foliage to herbivores.

In contrast, on protected islands we did not detect such changes in the appearance of shrubs or measured levels of herbivory that had their leaves stripped by hurricane winds. However, other abiotic and biotic factors present on protected islands might have prevented the herbivores from responding to increased susceptibility following the hurricane (Spiller and Agrawal, 2003). Previous studies of areas exposed to primarily wind damage by severe storms had mixed results. Increased herbivory was found by Hunter and Forkner (1999) following Hurricane Opal in North Carolina, United States and by Hirsh and Marler (2002) following Typhoon Paka in Guam, whereas decreased herbivory was found by Schowalter and Ganio (1999) following Hurricane Hugo in Puerto Rico and by Kop-

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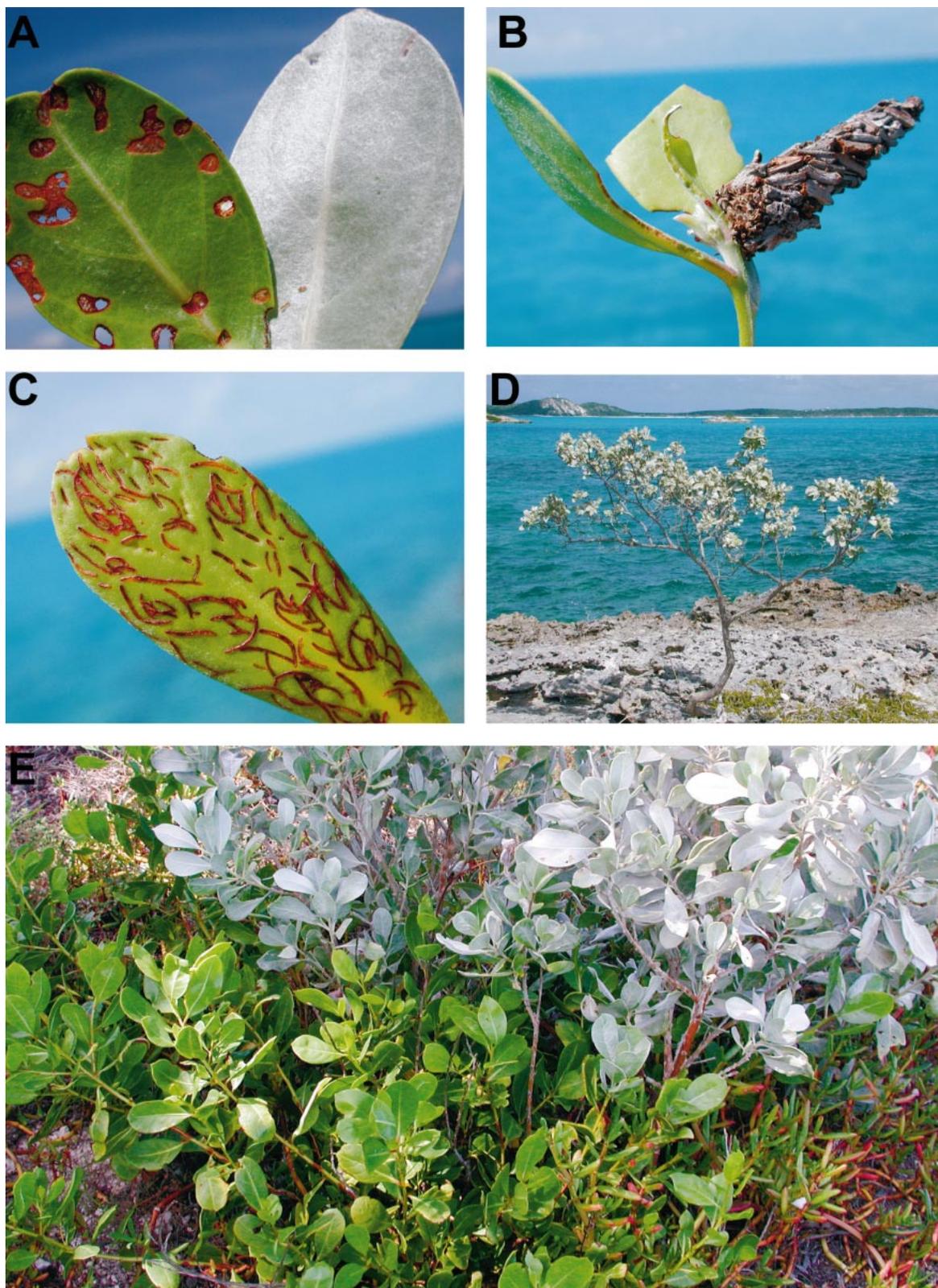


Fig. 1. (A) The green and silver morph leaves of buttonwood, *Conocarpus erectus*, (B) a major herbivore on buttonwood, the bagworm lepidopteran (*Biopsyche thoracia*), (C) brown scars caused by leaf damage of a major coleopteran herbivore, *Chaetocnema brunnescens*, (D) a single reproductive silver shrub, (E) juvenile green and silver shrubs growing side by side near Regatta Point, Great Exhuma, Bahamas.

tur et al. (2002) following Hurricane Andrew in Florida, United States. Hence, we hypothesized that different types and intensities of damage may have contrasting effects on regrowth foliage, with both positive and negative effects on herbivory.

In the current study we address the effects of experimentally simulating storm surge (pruning branches), and wind (leaf stripping) damage on phenotypic traits and subsequent herbivory on green and silver morphs of buttonwood. Taking an island biogeographic and correlational approach, Schoener (1987, 1988) suggested that pubescence in buttonwood is a defense against defoliation. In our previous study (Spiller and Agrawal, 2003), we only investigated the effect of storm surge and did not separate the effects on the different morphs. Because polymorphic plants may not only vary in their responses to herbivores, but also to abiotic factors (Daday, 1965; Tallamy and Krischik, 1989; van Dam et al., 1999), we were particularly interested in differential responses of the two morphs to the two types of storm damage. We predicted that although the silver morph may be more resistant to herbivores compared to the green morph, this difference may be reduced under stressful conditions such as hurricane damage.

Thus, on replicated islands in the Bahamas, we specifically asked the following questions: (1) How do green and silver shrubs differ in foliar carbon and nitrogen content, leaf toughness, and herbivory? (2) Do the most abundant herbivores of buttonwood prefer green leaves over silver leaves in choice and no-choice experiments? (3) How do two kinds of simulated storm damage (loss of leaves vs. loss of all aboveground biomass) influence leaf traits and herbivory?

## MATERIALS AND METHODS

**Comparison of traits on green vs. silver shrubs**—To test for phenotypic differences in green and silver leaves that may be relevant to herbivory, we collected leaves from a total of 53 shrubs (27 green and 26 silver) from eight different small islands (exposed) that each had both green and silver shrubs (October 2001). In addition to the differences in trichomes, we assayed leaf carbon, nitrogen content, and toughness. In particular, leaf nitrogen content and toughness are among the best predictors of herbivory in the field (Mattson, 1980; Coley, 1983; Kauser et al., 1999; Marquis et al., 2001). For consistency, we chose the youngest fully expanded leaves without herbivore damage. A map of the site showing the study islands is provided in Spiller et al. (1998). Leaves were dried, ground to a fine powder, and analyzed for their total leaf nitrogen and carbon concentration using a LECO 600 elemental analyzer (St. Louis, Missouri, USA).

A single leaf from 88 bushes (42 green and 46 silver) from the same eight islands was measured for leaf toughness. Toughness was estimated twice for each leaf, using a force gauge penetrometer (Type 516, Chatillon Corp., New York, USA); the grams of force required to punch a hole in each leaf was recorded and the two estimates for each leaf were averaged to generate a single data point. Data on leaf carbon, nitrogen, and toughness were analyzed using *t*-tests. To assay natural levels of herbivory on green vs. silver leaves, we located 16 pairs of shrubs near Regatta Point (Great Exuma), that were growing in close proximity, but producing green and silver leaves (Fig. 1E). This paired design allowed us to control for potential microclimatic differences between green and silver shrubs. On a single branch from each shrub, we counted the proportion of leaves (out of at least 10 leaves) that showed any signs of herbivory. We employ a paired *t*-test to examine levels of attack on green versus silver branches.

**Laboratory bioassays of resistance to herbivores**—To determine differences in plant resistance of the two leaf morphs, we tested for effects on two of the most abundant herbivores of buttonwood, an adult flea beetle (*Chaetocnema brunnescens*, body length ~1–2 mm) and a bagworm lepidopteran (most likely *Biopsyche thoracica*, although it could be *B. apicalis*; middle to

late instar larvae ~10–20 mm) (Fig. 1), in choice and no-choice tests (Agrawal, 1999, 2000). Our no-choice tests consisted of placing single leaves in 30-mL plastic vials with a single field-collected herbivore (total  $N = 78$  for beetles;  $N = 23$  for caterpillars). Choice tests for caterpillars ( $N = 76$ ) were conducted in the same type of vials with a single leaf of each plant morph. Because flea beetles are much more mobile, choice tests with the flea beetles were conducted in 20-L buckets (total  $N = 8$ ), each with a small sprig (with five leaves) of the silver and green morph in separate cups of water; five beetles were introduced to each bucket. All assays were conducted for 3–4 d and leaves remained turgid for this period; all leaves were pressed and then digitally photographed. Leaves from single plants were used for each replicate and the plant material was collected from Regatta Point. Total percent damage area was measured digitally using Sigma Scan Pro Image Analysis System and differences were analyzed with a *t*-test (no-choice) or a nonparametric equivalent of a paired *t*-test, Wilcoxon signed-rank test (choice). The nonparametric test was employed in the choice test because of the highly skewed data (many zero values). Here, we used one-tailed tests based on our own a priori observational data and that of Schoener (1987, 1988).

**Field experiment simulating abiotic disturbance**—To test the hypothesis that different abiotic disturbances would modulate plant responses that affect herbivores, and potentially in a differential fashion on the two morphs of buttonwood, we established an experiment employing replicated small islands. The experiment was conducted on islands exposed to Hurricane Lili, rather than on protected islands, because we suspected that other abiotic and biotic factors present on protected islands may prevent the herbivores from responding to the manipulation (Spiller and Agrawal, 2003).

In a  $2 \times 3$  factorial design (two morphs, three treatments), we established five replicate blocks on four islands. One island had two blocks of the six treatment/morph combinations; these blocks were on the opposing sides of the island separated by a narrow passage. The treatments were (1) unmanipulated controls, (2) pruned shrubs: these plants were treated to resemble the condition immediately following Hurricane Lili on the exposed islands (Spiller and Agrawal, 2003); the shrubs were reduced to stumps by pruning virtually all apical meristems and aboveground mass, (3) stripped shrubs: these plants were treated to simulate the high wind damage experienced on the protected islands (Spiller et al., 1998; Spiller and Agrawal, 2003); all leaves were removed on the shrubs, without destroying apical meristems or dormant buds. These three treatments were randomly assigned within each block containing three green and three silver shrubs, growing intermixed on the islands. Treatments were randomly assigned to shrubs that were matched according to size, foliage color, and location (members within each of the five blocks were 2–6 m apart).

Prior to the establishment of the treatments, in October 2001, we took four random samples from each shrub, each sample containing ~20 leaves. Leaves were obtained by looking away, reaching towards the shrub, and collecting leaves on the first branch contacted. Only young fully expanded leaves were used in the analyses. Leaves were pressed, photographed, and damage was assessed as described above. Percent leaf area damaged on each shrub was computed by summing the total and damaged areas of all the leaves sampled. We also obtained carbon, nitrogen, and toughness data on these samples as described above. In addition, trichomes were examined under a dissection microscope and leaves were classified as silver ( $\geq 30$  trichomes/mm transect) or green ( $< 30$  trichomes/mm) as in (Schoener, 1988). Ten randomly selected leaves were examined from each experimental shrub and the proportion of leaves that were silver was considered the trichome index (Spiller and Agrawal, 2003). Samples were again taken as described above in December 2001, May 2002, and October 2002.

Because susceptibility to herbivory may vary with leaf age, when all the leaves on treated shrubs were relatively young (December 2001), only correspondingly young leaves located on the distal ends of branches were collected on control shrubs. To control for leaf age more precisely four randomly chosen branches were tagged on each shrub, and the most distal leaves present were marked with ink in December 2001. Only leaves that emerged after December 2001 were collected in May 2002. The same procedure was performed in May 2002 to control for leaf age in the October 2002 samples.

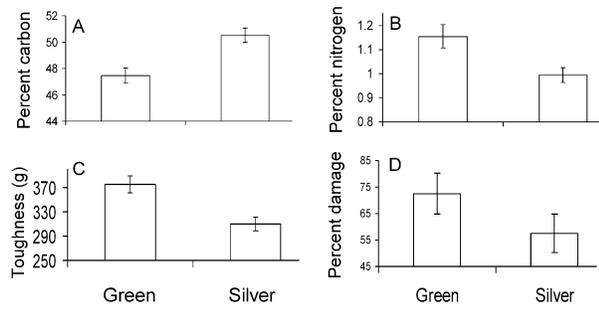


Fig. 2. A comparison of phenotypic differences between the green and silver morph of buttonwood leaves: (A) percent leaf carbon, (B) percent leaf nitrogen, (C) leaf toughness measured in grams, (D) percent leaf damage in a paired analysis. Bars are means  $\pm$  1 SE.

Data were statistically analyzed by performing repeated-measures analyses of variance in SAS version 8 (PROC GLM; SAS, 1999). This analysis was employed because of our design, in which we repeatedly sampled the same shrubs. The experimental units were individual shrubs; morph, treatment and block were between subjects factors and sampling date was the within subjects factor. Our data generally met the assumptions of ANOVA, although mean leaf damage was arc sine square-root transformed, which improved the distribution of the residuals. We only report sampling date effects in the Figs because, although sampling date was always significant, sampling date did not interact with any of the other factors. None of the pretreatment samples differed by treatment groups, although there were some pre-existing block and morph differences that are noted.

RESULTS

In our survey of resistance-related traits of the green and silver morphs of buttonwood, we found that green leaf morphs had 6% lower carbon content ( $df = 51, t = 3.978, P < 0.001$ ), 16% higher nitrogen content ( $df = 51, t = 2.83, P = 0.007$ ),

and were 21% tougher ( $df = 86, t = 3.632, P < 0.001$ ) than leaves from silver shrubs (Fig. 2). In addition, our survey of paired green and silver bushes revealed that green branches had higher levels of herbivory (72 vs. 57% of leaves showed damage,  $df = 15$ , paired  $t = 2.598, P = 0.020$ , Fig. 2).

Choice and no-choice experiments with two abundant herbivores, a flea beetle and a bagworm lepidopteran, revealed that leaves from green morph plants were generally preferred over that from silver shrubs (beetle choice: nonparametric paired Wilcoxon  $N = 8, Z = 2.028, P = 0.021$ ; beetle no choice:  $df = 38, t = 2.929, P = 0.003$ ; bagworm choice: paired Wilcoxon test  $N = 38, Z = -1.932, P = 0.027$ ; Fig. 2). The exception was the no-choice test we conducted with the bagworm caterpillar, where we found no difference in the amount of feeding on each type ( $df = 21, t = 0.042, P = 0.483$ , Fig. 3).

In our manipulative experiments, we imposed two types of simulated abiotic disturbance (surge damage by pruning branches, wind damage by stripping leaves off branches) to assess the consequences for leaf quality and resistance traits. The percent carbon in leaves was unaffected by our treatments (Fig. 4, all  $P_s \gg 0.3$ ). Conversely, leaf nitrogen concentration was strongly affected by the treatments (Table 1, Fig. 4), with pruning increasing nitrogen concentrations compared to controls, but only in silver shrubs (see interaction term in Table 1). Stripped silver shrubs had intermediate concentrations of nitrogen (Fig. 4, contrasts, pruned vs. stripped:  $P = 0.044$ , control vs. stripped:  $P = 0.069$ ). Although green leaves were tougher than silver leaves ( $F_{1,19} = 9.92, P = 0.005$ ) and both treatments generally decreased leaf toughness compared to controls, neither overall treatment ( $F_{2,19} = 1.84, P = 0.186$ ), nor an interaction between morph and treatment ( $F_{2,19} = 0.22, P = 0.805$ ) was statistically detectable (Fig. 4). Despite the treatment effects, most effects were strongest in the months

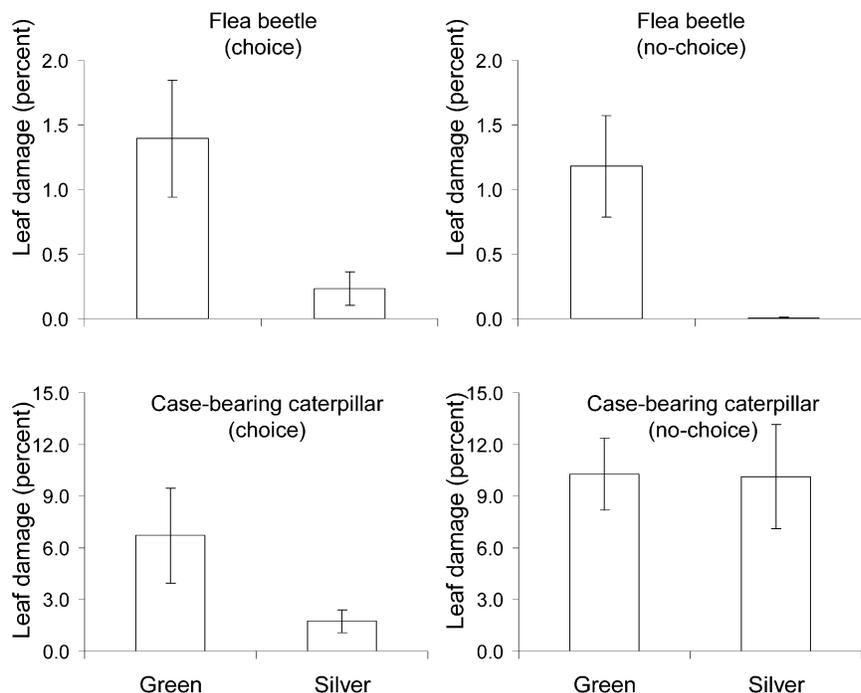


Fig. 3. Effects of the green vs. silver morph of buttonwood leaves for two abundant folivores in choice and no-choice experiments. Bars are means  $\pm$  1 SE.

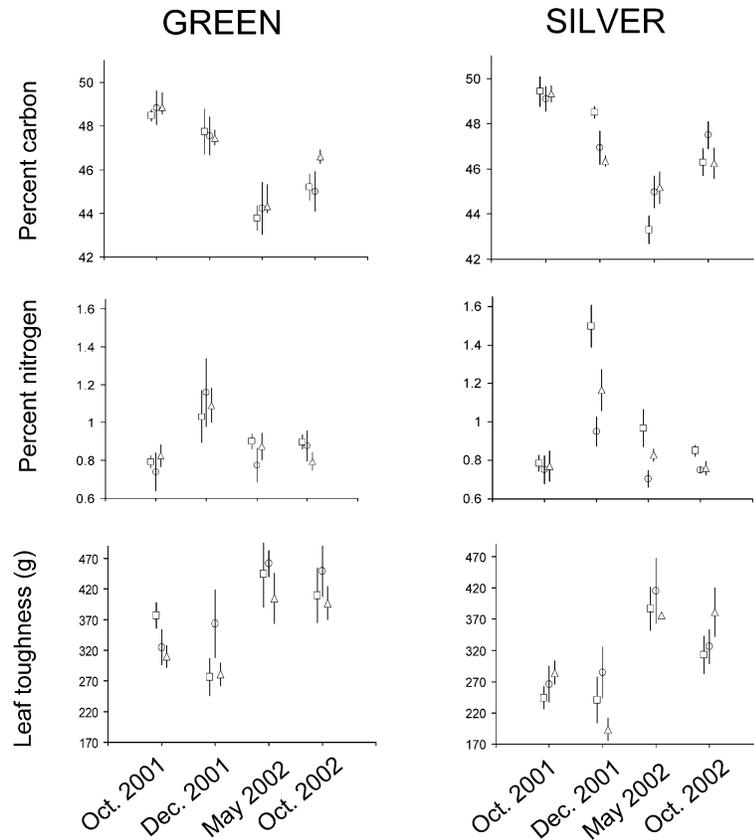


Fig. 4. Effects of disturbance treatments (squares = pruned, circles = control, triangles = stripped) on green and silver buttonwood shrubs over one year following the imposition of treatments. October 2001 represents the pretreatment values. Points are means  $\pm$  1 SE.

directly after the treatments were imposed, and high levels of seasonal variation persisted for most traits (Fig. 4).

Effects of our disturbance treatments on leaf trichome production could only be assessed on silver shrubs, as green leaves do not produce measurable trichomes. Pruning reduced the trichome production by nearly 80% for up to a year following the treatment (Fig. 5, treatment:  $F_{2,7} = 16.42$ ,  $P = 0.002$ , block:  $F_{4,7} = 1.61$ ,  $P = 0.273$ , contrast of pruned shrubs vs. controls,  $P < 0.001$ , and pruned vs. stripped shrubs,  $P = 0.005$ ). Stripping did not have a significant effect compared to controls (contrast  $P = 0.364$ ).

Ultimately we were interested in the net effects of our treatment on subsequent herbivory by naturally colonizing herbivores. In general, green shrubs received two-fold more natural herbivory than silver shrubs and our pruning treatment (storm surge simulation) increased herbivory levels on both morphs of buttonwood compared to controls and stripped plants (Fig.

6, Table 2, pruned vs. control contrast,  $P = 0.026$ , pruned vs. stripped contrast  $P = 0.039$ ). However, our simulation of wind damage, stripping of leaves, had no effect compared to controls (contrast  $P = 0.923$ ). The treatment by morph interaction was not significant (Table 2).

DISCUSSION

**Green versus silver shrubs**—Plant trichomes come in a variety of forms and are frequently posited to be involved in resistance to herbivory, ecophysiological water relations of leaves, and protection from ultraviolet light (Baur et al., 1991; Woodman and Fernandes, 1991; Ågren and Schemske, 1993; Fernandes, 1994; Karabourniotis et al., 1995). For *C. erectus*, which shows a dramatic polymorphism in the production of trichomes, these leaf hairs appear to serve a defensive function. We found that although glabrous “green” leaves were

TABLE 1. Repeated-measures analysis of variance for effects of plant morph (green vs. silver) and treatment (control, leaves stripped, branches pruned) on percent leaf nitrogen content over three samples, starting one year after the treatments were imposed. The only pretreatment difference in nitrogen content was according to block ( $P < 0.001$ ). All terms and interactions associated with the repeated measures were included in the analysis, but only sample date was significant ( $P < 0.001$ )

Source	df	Type III SS	MS	F	P
Morph	1	0.010	0.010	0.260	0.617
Treatment	2	0.316	0.158	4.130	0.036
Morph $\times$ Treatment	2	0.293	0.146	3.820	0.044
Block	4	0.438	0.109	2.860	0.058
Error	16	0.613	0.038		

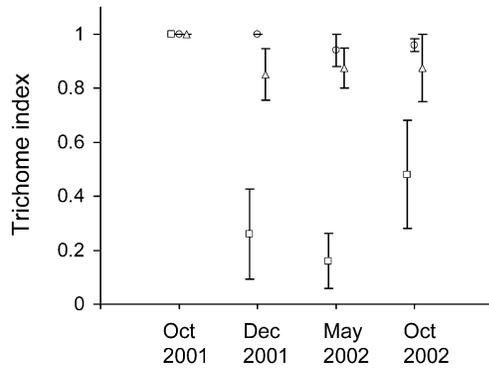


Fig. 5. Effects of disturbance treatments (squares = pruned, circles = control, triangles = stripped) on leaf trichomes of silver buttonwood shrubs over one year following the imposition of treatments. October 2001 represents the pretreatment values. Points are means  $\pm$  1 SE.

tougher than “silver” leaves, greater levels of herbivory on green leaves were associated with high levels of nitrogen and the lack of trichomes. Indeed, in our bioassays with flea beetles, insects preferred to feed on green over silver leaves. This effect was consistent with bagworm choice, but not in the no-choice test, indicating that small flea beetles may be more sensitive to trichomes than the larger chewing caterpillars. Although there is a qualitative difference between the morphs in trichomes, other differences (nitrogen, toughness) confound this distinction. Further work, perhaps involving a manipulation of trichomes (Schmitz, 1994; Haddad and Hicks, 2000) is needed to directly implicate the role of trichomes in defense.

In previous island biogeographic studies, Schoener (1987, 1988) showed that (1) larger islands, (2) islands closer to the mainland, and (3) islands without top predator lizards all had a higher proportion of the silver morph of buttonwood compared to green morph. These effects of island size, distance, and trophic structure were correlated with herbivore levels: larger islands have more leaf damage than smaller islands, islands close to the mainland have more leaf damage than farther away islands, and islands with top predator lizards have less leaf damage than islands without lizards. If herbivores are strong selective agents, as is widely believed (Marquis, 1992; Hawkes and Sullivan, 2001), then these biogeographic and trophic correlates suggest that there is predictability in the morph frequencies due to natural selection. Mechanistically we have now shown that the green morph is, in fact, favored by some herbivores, providing a mechanism by which herbivory may have a selective impact on the plant polymorphism.

**Effects of storm damage on phenotypic traits and herbivory**—After Hurricane Lili hit our study site in 1996, we began

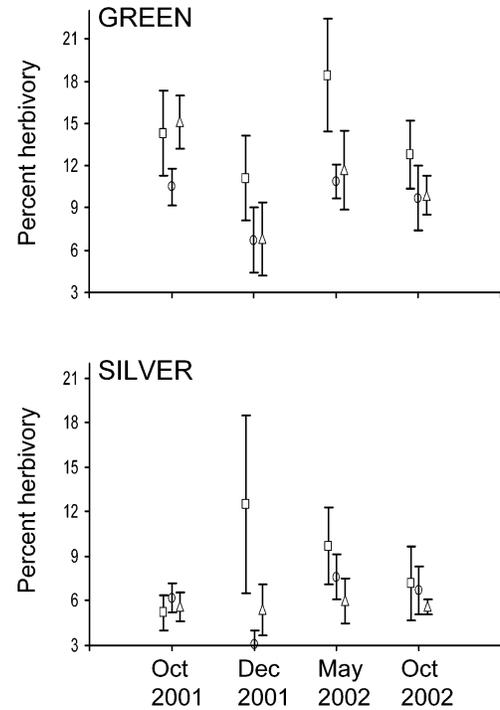


Fig. 6. Effects of disturbance treatments (squares = pruned, circles = control, triangles = stripped) on percent herbivory of green and silver buttonwood shrubs over one year following the imposition of treatments. October 2001 represents the pretreatment values. Points are means  $\pm$  1 SE.

to notice general shifts in the levels of herbivory on exposed islands compared to protected islands (Spiller and Agrawal, 2003). Shrubs exposed to the storm surge, as simulated by our pruning treatments, which removed all meristems, produced resprouts with higher nitrogen, fewer trichomes, and less tough leaves than control plants (Spiller and Agrawal, 2003). In the current study, we extended these results to examine the consequences of two types of storm damage (leaf loss vs. loss of all aboveground stems). High winds and the loss of leaves are perhaps more common than surge damage, and also represents a very different type of physiological effect, since meristems are not removed (Honkanen and Haukioja, 1998). Our results showed that simulated wind damage (leaf loss) had no significant effect on herbivory or traits related to herbivore susceptibility. Apparently, in our system severe damage caused by storm surge, which removes most of the plant biomass (including meristems), is required to have a detectable effect on resprouting foliage and herbivory.

We generally found that silver shrubs were more responsive to severe abiotic disturbance than green shrubs. This effect was

TABLE 2. Repeated-measures analysis of variance for effects of plant morph (green vs. silver) and treatment (control, leaves stripped, branches pruned) on percent leaf herbivory over three samples, starting one year after the treatments were imposed. The only pretreatment difference in herbivory levels was according to plant morph ( $P < 0.001$ ). All terms and interactions associated with the repeated measures were included in the analysis, but only sample date was significant ( $P = 0.010$ )

Source	df	Type III SS	MS	F	P
Morph	1	310.820	310.820	5.920	0.025
Treatment	2	381.631	190.816	3.630	0.046
Morph $\times$ Treatment	2	3.832	1.916	0.040	0.964
Block	4	411.599	102.900	1.960	0.142
Error	19	997.952	52.524		

particularly clear for leaf nitrogen content. Green shrubs did not respond to treatments (Table 1, Fig. 4), whereas silver shrubs dramatically increased nitrogen content following pruning for a full year, resulting in a significant morph  $\times$  treatment interaction. We note, however, that the effect of pruning on herbivory (leaf damage) was not significantly different for the two morphs (Table 2, Fig. 6). One possible explanation for this inconsistency is that the direct response by plants to pruning (increase nitrogen) was less variable than the indirect response by herbivores to pruning. Multiple factors, including several plant traits, determine herbivore attack. Furthermore, our measures of leaf nitrogen content may not reflect plant quality for most of the preceding period when herbivory was occurring. Responses to leaf stripping were weaker than responses to pruning and did not persist. The ecophysiological correlates of changes in leaf nitrogen will be addressed in future studies. Although higher nitrogen leaves may be consumed more by herbivores, they may also have greater photosynthetic capabilities. For example, the green morph may be primarily allocating to growth and photosynthesis, and therefore may not respond strongly to environmental stress, such as hurricane damage. Conversely, because of the apparent allocation to defense in the silver morph, environmental stress may affect these plants more, thereby causing the plants to shift allocation strategies.

Differences in leaf trichomes are only relevant for silver shrubs, and the pattern here was the same as for nitrogen; the strong and lasting effects we detected were only in response to pruning, not leaf stripping. These results are consistent with the pattern of herbivory we observed following the hurricane in 1996 (Spiller and Agrawal, 2003); all islands were subjected to strong winds, but trichomes were only reduced on islands exposed to the storm surge and not on islands protected from the surge. Thus, the strong effects of disturbance apparently caused a shift away from defense in the silver shrubs. Again, there may be additional consequences of reduced trichome density than increased herbivory. Reduced microshading in leaves with fewer trichomes may increase photosynthetic capacity, increasing the recovery of silver shrubs.

Each of the effects of pruning on leaf traits related to increased herbivory was weak but consistent across the two morphs. This suggests that no one factor (nutritive content, leaf toughness, trichomes) is likely responsible for the observed changes in resistance following damage (Agrawal, 1998). In particular, we have thus far not measured potential chemical defenses of buttonwood shrubs, including its partially characterized phenolics and terpenes (Hayashi and Thomson, 1975; Rafii et al., 1996). The positive effect that certain types of stem damage can have on herbivores has been widely recognized (Honkanen and Haukioja, 1998). In particular, grazing by large mammals, which results in loss of apical dominance, has been shown to increase plant susceptibility to herbivores in numerous study systems (Danell and Huss-Danell, 1985; Hjalten and Price, 1996; Roininen et al., 1997; Martinsen et al., 1998; Olofsson and Strengbom, 2000). In one study with Scandinavian mountain birch shrubs, plants with damaged meristems produced new foliage with increased nitrogen, larger leaves, and other chemical and ecophysiological changes (Haukioja et al., 1990). The apparent differences we observed in trees with leaf loss (simulated wind damage) and stem damage (simulated surge damage) are consistent with previous findings (Honkanen and Haukioja, 1998) and suggests a common mechanism by which different types of biotic

or abiotic plant damage may influence subsequent ecological interactions.

The effect of storms on plant communities and on interactions with herbivores has recently received increasing attention. The four other studies that have compared herbivory on plants in areas affected or unaffected by tropical storms, found mixed results, with storm damage causing positive (Hunter and Forkner, 1999; Hirsh and Marler, 2002) to negative effects (Schowalter and Ganio, 1999; Koptur et al., 2002) on herbivores. Differences in the results of these studies may be caused by variation in the severity of damage on the plants and variation in the magnitude of the storm's direct impact on herbivore populations. Our studies on the hurricane influences on Bahamian buttonwoods have combined observational and experimental work to attempt to identify ecological mechanisms of the effects of storms on food webs.

In conclusion, our studies indicate that variation in the severity of damage caused by storms, which result in different disturbances to the plant community, may predictably alter plant quality for herbivores. For buttonwood, polymorphism in foliar trichomes appears to partially modify herbivore resistance strategies and also how the plants respond to abiotic disturbance. Specifically, this experiment shows that silver morphs are affected phenotypically by simulated storm surge damage more than green. In addition to a reduction of trichomes, such damage resulted in higher nitrogen in silver leaves but not green. Silver morphs are more common than green on protected islands, whereas green are more common than silver on exposed islands (unpublished data), suggesting that the green morph may have a selective advantage in the disturbed environment on exposed islands.

#### LITERATURE CITED

- AGRAWAL, A. A. 1998. Induced responses to herbivory and increased plant performance. *Science* 279: 1201–1202.
- AGRAWAL, A. A. 1999. Induced responses to herbivory in wild radish: effects on several herbivores and plant fitness. *Ecology* 80: 1713–1723.
- AGRAWAL, A. A. 2000. Benefits and costs of induced plant defense for *Lepidium virginicum* (Brassicaceae). *Ecology* 81: 1804–1813.
- ÅGREN, J., AND D. W. SCHEMSKE. 1993. The cost of defense against herbivores: an experimental study of trichome production in *Brassica rapa*. *American Naturalist* 141: 338–350.
- BAUR, R., S. BINDER, AND G. BENZ. 1991. Nonglandular leaf trichomes as short-term inducible defense of the gray alder, *Alnus incana* (L.), against the chrysomelid beetle, *Agelastica alni* L. *Oecologia* 87: 219–226.
- COLEY, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53: 209–233.
- CORRELL, D. S., AND H. B. CORRELL. 1982. Flora of the Bahamian Archipelago. Cramer, Vaduz.
- DADAY, H. 1965. Gene frequencies in wild populations of *Trifolium repens* L. IV. Mechanism of natural selection. *Heredity* 20: 355–365.
- DANELL, K., AND K. HUSS-DANELL. 1985. Feeding by insects and hares on birches earlier affected by moose browsing. *Oikos* 44: 75–81.
- FERNANDES, G. W. 1994. Plant mechanical defenses against insect herbivory. *Revista Brasileira de Entomologia* 38: 421–433.
- FLANDERS, K. L., J. G. HAWKES, E. B. RADCLIFFE, AND F. I. LAUER. 1992. Insect resistance in potatoes sources evolutionary relationships morphological and chemical defenses and ecogeographical associations. *Euphytica* 61: 83–111.
- HADDAD, N. M., AND W. M. HICKS. 2000. Host pubescence and the behavior and performance of the butterfly *Papilio troilus* (Lepidoptera: Papilionidae). *Environmental Entomology* 29: 299–303.
- HAUKIOJA, E., K. RUOHOMAKI, J. SENN, J. SUOMELA, AND M. WALLS. 1990. Consequences of herbivory in the mountain birch (*Betula pubescens* ssp. *tortuosa*): importance of the functional organization of the tree. *Oecologia* 82: 238–247.

- HAWKES, C. V., AND J. J. SULLIVAN. 2001. The impact of herbivory on plants in different resource conditions: a meta-analysis. *Ecology* 82: 2045–2058.
- HAYASHI, T., AND H. THOMSON. 1975. New lignans in *Conocarpus erectus*. *Phytochemistry* 14: 1085–1087.
- HIRSH, H., AND T. MARLER. 2002. Damage and recovery of *Cycas micro-nesica* after Typhoon Paka. *Biotropica* 34: 598–602.
- HJALTEN, J., AND P. W. PRICE. 1996. The effect of pruning on willow growth and sawfly population densities. *Oikos* 77: 549–555.
- HONKANEN, T., AND E. HAUKIOJA. 1998. Intra-plant regulation of growth and plant-herbivore interactions. *Ecoscience* 5: 470–479.
- HUNTER, M. D., AND R. E. FORKNER. 1999. Hurricane damage influences foliar polyphenolics and subsequent herbivory on surviving trees. *Ecology* 80: 2676–2682.
- KARABOURNIOTIS, G., D. KOTSABASSIDIS, AND Y. MANETAS. 1995. Trichome density and its protective potential against ultraviolet-B radiation damage during leaf development. *Canadian Journal of Botany-Revue Canadienne De Botanique* 73: 376–383.
- KAUSE, A., V. OSSIPOV, E. HAUKIOJA, K. LEMPA, S. HANHIMAKI, AND S. OSSIPOVA. 1999. Multiplicity of biochemical factors determining quality of growing birch leaves. *Oecologia* 120: 102–112.
- KOPTUR, S., M. C. RODRIGUEZ, S. F. OBERBAUER, C. WEEKLEY, AND A. HERNDON. 2002. Herbivore-free time? Damage to new leaves of woody plants after Hurricane Andrew. *Biotropica* 34: 547–554.
- MARQUIS, R. J. 1992. Selective impact of herbivores. In R. S. Fritz and E. L. Simms [eds.], *Plant resistance to herbivores and pathogens*, 301–325. University of Chicago Press, Chicago, Illinois, USA.
- MARQUIS, R. J., I. R. DINIZ, AND H. C. MORAIS. 2001. Patterns and correlates of interspecific variation in foliar insect herbivory and pathogen attack in Brazilian cerrado. *Journal of Tropical Ecology* 17: 127–148.
- MARTINSEN, G. D., E. M. DREIBE, AND T. G. WHITHAM. 1998. Indirect interactions mediated by changing plant chemistry: beaver browsing benefits beetles. *Ecology* 79: 192–200.
- MATTSON, W. J., JR. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11: 119–161.
- OLOFSSON, J., AND J. STRENGBOM. 2000. Response of galling invertebrates on *Salix lanata* to reindeer herbivory. *Oikos* 91: 493–498.
- PRICE, P. W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62: 244–251.
- RAFI, Z. A., R. S. DODD, AND F. FROMARD. 1996. Biogeographic variation in foliar waxes of mangrove species. *Biochemical Systematics and Ecology* 24: 341–345.
- ROININEN, H., P. W. PRICE, AND J. P. BRYANT. 1997. Response of galling insects to natural browsing by mammals in Alaska. *Oikos* 80: 481–486.
- SAS INSTITUTE. 1999. SAS/STAT users guide, version 8. SAS Institute Inc., Cary, North Carolina, USA.
- SCHMITZ, O. J. 1994. Resource edibility and trophic exploitation in an old-field food web. *Proceedings of the National Academy of Sciences, USA* 91: 5364–5367.
- SCHOENER, T. W. 1987. Leaf pubescence in buttonwood: community variation in a putative defense against defoliation. *Proceedings of the National Academy of Sciences, USA* 84: 7992–7995.
- SCHOENER, T. W. 1988. Leaf damage in island buttonwood, *Conocarpus erectus*: correlations with pubescence, island area, isolation and the distribution of major carnivores. *Oikos* 53: 253–266.
- SCHOWALTER, T. D., AND L. M. GANIO. 1999. Invertebrate communities in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. *Ecological Entomology* 24: 191–201.
- SEMPLE, J. C. 1970. The distribution of pubescent leaved individuals of *Conocarpus erectus* (Combretaceae). *Rhodora* 72: 544–547.
- SPILLER, D. A., AND A. A. AGRAWAL. 2003. Intense disturbance enhances plant susceptibility to herbivory: natural and experimental evidence. *Ecology* 84: 890–897.
- SPILLER, D. A., J. B. LOSOS, AND T. W. SCHOENER. 1998. Impact of a catastrophic hurricane on island populations. *Science* 281: 695–697.
- TALLAMY, D. W., AND V. A. KRISCHIK. 1989. Variation and function of cucurbitacins in *Cucurbita*: an examination of current hypotheses. *American Naturalist* 133: 766–786.
- VAN DAM, N. M., AND J. D. HARE. 1998. Differences in distribution and performance of two sap-sucking herbivores on glandular and non-glandular *Datura wrightii*. *Ecological Entomology* 23: 22–32.
- VAN DAM, N. M., J. D. HARE, AND E. ELLE. 1999. Inheritance and distribution of trichome phenotypes in *Datura wrightii*. *Journal of Heredity* 90: 220–227.
- WESTERBERGH, A. 1992. The genetic basis of hairlessness in *Silene dioica* (Caryophyllaceae). *Hereditas* 117: 287–291.
- WOODMAN, R. L., AND G. W. FERNANDES. 1991. Differential mechanical defense: herbivory, evapotranspiration, and leaf hairs. *Oikos* 60: 11–19.