BIOTROPICA 34(4): 547–554 2002

Herbivore-Free Time? Damage to New Leaves of Woody Plants after Hurricane Andrew[1]

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ABSTRACT

All broadleaf woody plants of pinelands and hammocks (upland areas) in the northern parts of Everglades National Park were defoliated by the strong winds of Hurricane Andrew in August 1992. Most plants re-leafed within two months of the storm, at which time we tagged newly produced leaves of eight species (five species in two hardwood hammocks and four in two pineland sites; one species was studied in both habitats), and monitored individual leaf area lost or damaged monthly for three months. We marked a second cohort of new leaves on the same individuals four months later and monitored these for three months. Herbivory rates in leaves of the first cohort were lower than observed in pre-hurricane studies on two of the species, and lower in the first cohort than in the second cohort in six of the eight species studied, indicating that most insect herbivores were virtually absent for the first few months after the storm. Additionally, most species produced significantly larger leaves in the first cohort than the second cohort, and leaves of the second cohort were not significantly different in size from pre-hurricane leaves in one species for which pre-hurricane data were available. The large disturbance of the hurricane defoliated and reduced the above-ground biomass of the plants, but apparently also eliminated most herbivores and competition for light, facilitating the recovery of the plants.

RESUMEN

Todas las plantas de hojas anchas que se encontraban en los pinares rocosos y en los bosques de madera dura en el área norte del Parque Nacional de los Everglades fueron defoliadas por los vientos fuertes del huracán Andrew en agosto de 1992. En muchas de estas plantas las hojas renacieron en los dos meses posteriores al huracán; durante este periodo se marcaron las hojas nuevas en ocho especies (cinco especies en dos bosques de madera dura y cuatro especies en dos sitios de pinares, una de dichas especies se estudió en los dos habitats). Se registró el área foliar perdida o dañada de cada hoja cada mes durante tres meses. Un segundo grupo de hojas nuevas se marcó en los mismos individuos cuatro meses después y se muestreó durante tres meses. La tasa de herbivoría en las hojas del primer grupo fue más baja que la observada en estudios anteriores al huracán en dos de las especies, y más baja en el primer grupo que en el segundo en seis de las ocho especies estudiadas, lo cual indica que muchos de los insectos herbívoros estuvieron ausentes en los meses posteriores al huracán. Adicionalmente en el primer grupo muchas de las especies produjeron hojas significativamente más grandes que las del segundo. El tamaño de las hojas del segundo grupo no fue significativamente diferente del de hojas previas al huracán en una de las especies de la que se tenían mediciones. La defoliación masiva y la reducción de biomasa causada por el huracán en las plantas eliminó la mayoría de insectos herbívoros y la competencia por la luz lo que ayudó a la recuperación de las plantas.

Key words: *compensation; defoliation; disturbance; Florida Everglades; herbivory; hurricane; leaves; rocklands; timing; trees.*

The timing of leaf production can affect the amount of herbivore damage that leaves sustain. Herbivory is influenced by how the seasonality of leaf production corresponds to herbivore abundance (Aide 1988, Mopper & Simberloff 1995), whether or not leaf production is synchronized with conspecifics (Aide 1991, 1993), and when an individual plant leafs in relation to the peak leaf production by conspecifics (Murali & Sukamar 1993). The degree of herbivore impact can depend on the timing of grazing (Maschinski & Whitham 1989). Clipping can delay the phenology of certain species (Juenger & Bergelson 1997), and altering the phenology of leafing can have a negative effect on herbivore populations (Lawrence *et al.* 1997). Some plants may experience compensatory growth following herbivory to their vegetative parts (Paige 1992, Lowenberg 1994, Singh & Thompson 1995), and the removal of photosynthetic "sink" tissues (flowers, immature fruit) may also stimulate

[1] Received 18 March 2002; revision accepted 23 September 2002.

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growth (Honkanen *et al.* 1994). Leaf quality often improves after clipping/browsing and regrowth (Pullin 1987, Landsberg 1988, du Toit *et al.* 1990), although there are some cases when resprouts are more highly defended chemically than similar leaves on non-damaged plants (Schultz & Baldwin 1982; Bryant *et al.* 1985, 1991). Leaf fall from hurricane damage also creates a pulse of nutrients that can promote regrowth (Oberbauer & Koptur, pers. obs.).

Few studies have examined the influence of catastrophic events on herbivory. After a tornado damaged beech–hemlock forest, recruitment of hemlock seedlings was thwarted by deer browsing followed by drought (Peterson & Pickett 1995); treefall mounds also created refugia from browsing mammals, allowing hemlock to regenerate atop the mounds (Long *et al.* 1998). Outbreaks of many Lepidoptera were observed (Torres 1992) in the Luquillo Mountains of Puerto Rico seven or more months after Hurricane Hugo, presumably based on the flush of new foliage that developed after the passage of the hurricane. Post-hurricane regrowth, however, may not be correlated with leaf area missing or herbivore abundances (Schowalter & Ganio 1999).

Herbivory is best studied by repeated measures on leaf cohorts over time (Sand-Jensen *et al.* 1994), since discrete (one-time) measures generally underestimate herbivory by half (Filip *et al.* 1995). Most folivory occurs within a restricted period of leaf availability, usually within the first month or two of the leaf's life (Coley 1982, Aide 1993). One study done after Hurricane Hugo examined canopy invertebrate communities with one-time measures of herbivory (Schowalter 1994, Schowalter & Ganio 1999), and compared leaf area missing in dry and wet season samples during the five years following in forests with light versus severe hurricane disturbance (using leaf harvest methods). To our knowledge, no studies have yet compared cumulative damage to leaves produced at different times following a hurricane, or leaves produced before and after a hurricane.

On 24 August 1992, Hurricane Andrew swept across south Florida, causing severe damage to pinelands and hammocks in the Long Pine Key region of Everglades National Park (Loope *et al.* 1994). The hurricane broke and toppled many trees; this changed the environment considerably, especially in hammocks where the characteristic tree-sheltered, shady understory was exposed and open after the hurricane. Late August is the middle of the wet season in this subtropical climate, and most species (all of the ones included in this study) are normally fully leafed at that time of year. All broadleaf plants lost their leaves, and produced new leaves within two months of the hurricane. While setting up plots and beginning to assess damage and recovery to plants in the various upland habitats (Koptur & Oberbauer, pers. obs.), we noticed that the environment was exceptionally quiet, with neither the humming of mosquitos typical of the wet season months nor noticeable activity of any other insects. We reasoned that a lack of insect activity may provide the plants with a respite from herbivory. Since the major part of insect damage occurs early in a leaf's life, it is important to follow leaves from early in their development to observe major increases in damage (Coley 1982, Aide 1993). We therefore compared damage in two cohorts of leaves: those produced immediately after the hurricane and those produced four months later. Our goal was to use leaves of some common species to monitor loss of leaf area to herbivores, and indirectly, herbivorous insect activity following this major environmental disturbance.

Total defoliation of evergreen plants, or of deciduous plants at a time earlier than their leaves would normally be lost, may lead either to plant death (Koptur 1991) or re-leafing (depending on water availability, nutrient status of the plant, and the competitive environment). Within a plant genotype, there is flexibility, or plasticity, of certain traits in response to environmental variation, including the size of vegetative parts (such as leaves). In this study, we also observed the effects of hurricane defoliation on leaf size.

METHODS

We used two sites (intended as replicates) from each habitat, hammock and pineland, all in the Long Pine Key region of Everglades National Park, Florida. Both of these habitats are upland forests of the Everglades: pinelands are maintained by fires and succeed to hammocks if they go unburned for many years (Snyder *et al.* 1990). We chose four common species typical of each habitat and chose nine individuals of each species per site. The idiosyncratic nature of hardwood hammocks resulted in the absence of one of the species (tagged in the first site) from the second site and so two species were not replicated (see below).

All species studied (Table 1) are common in the habitats. Taxonomy follows Wunderlin (1998) and names are listed with authors, synonyms, and common names. Vouchers are deposited at Fair-

TABLE 1. *Leafing, flowering, and fruiting of species studied. Months are abbreviated by their first three letters. Taxonomy follows Wunderlin (1998). Sources are Tomlinson (1980); Pascarella (1997); M. Ross, J. Redwine, J. H. Geiger (pers. comm.); and S. Koptur and S. F. Oberbauer (pers. obs.).*

Species and authority	Family and Common Name	Leafing	Flowering Season	Fruiting Season
Ardisia escallonioides Scheide & Deppe ex Schldl. & Cham.	Myrsinaceae marlberry			
Exothea paniculata (Juss.) Radlk. ex T. Durand	Sapindaceae inkwood	Evergreen	Jan–Apr	May–Jun
Guettarda scabra (L.) Vent.	Rubiaceae rough-leaved velvetseed	Deciduous	May–Jul	Aug–Jan
Lysiloma latisilquum (= *L. bahamense* (Benth.)	Fabaceae: Mimosoideae wild tamarind	Deciduous	Mar–Aug	Mar–Mar
Ocotea coriacea (Swartz) Britton (= *Nectandra coriacea* [Sw.] Griseb.)	Lauraceae lancewood	Evergreen	Mar–Sep	Sep–Jan
Psychotria nervosa Sw.	Rubiaceae wild coffee	Evergreen	Mar–Aug	May–Mar
Rapanea punctata (= *Myrsine floridana* A. DC.)	Myrsinaceae myrsine	Evergreen	Nov–Jan	Apr–Dec
Tetrazygia bicolor (Mill.) Cogn.	Melastomataceae tetrazygia	Evergreen	Mar–Aug	May–Mar

child Tropical Garden (FTG), Everglades National Park (ENP), and Florida International University. Information about leafing, flowering, and fruiting has been summarized from our observations and several other sources (Table 1) to aid interpretation of results. We only studied leaves at a height less than 2 m from the ground. All species have simple leaves except for the two species that were monitored in one of each hammock site (*Lysiloma* and *Exothea*). These two species were chosen to contrast with simple-leaved species, but the compound-leaf species tagged in the first hammock was not found in the second hammock. Rockland hammocks in the Everglades are renowned for their high beta diversity, or individual character (Snyder *et al.* 1990; Koptur & Oberbauer, pers. obs.).

In summary, *Ardisia* was studied in all four sites used in this project, two pineland and two hammock sites. We studied all other species in two sites of the same habitat (pineland or hammock), except for *Exothea* and *Lysiloma*, which were each studied in one hammock site.

Individuals were located in a stratified random fashion: three individuals within each of our three 10 x 20 m damage and recovery study plots at each site. We located study individuals haphazardly within the plots, choosing plants that had re-leafed and appeared robust. On each individual plant, we tagged and monitored damage to 5 leaves (making a total of 45 leaves per species per site per cohort). We used thin, yellow, plastic ring bird bands around the petiole of each leaf monitored. Cohort 1 was established in October 1992 and monitored monthly for six months (we only report on the first three months data here); cohort 2 was established in January 1993 and monitored for three months, at which time the study ended.

For each species (except *Lysiloma*; see below), we collected 20 undamaged leaves and in the laboratory measured their length, width, and area using a leaf-area meter, and used the data to obtain regressions of these three variables. We measured leaf length and width of each tagged leaf in the field and estimated their area from the appropriate regression. We measured damage monthly by counting the number of squares at least 50 percent damaged in clear plastic grids (with squares of 0.09 cm^2), providing a measure of damage for each leaf.

A comparative study of insect herbivory on *Lysiloma* in pineland and hammock habitats was conducted in this area prior to the hurricane (Rodriguez 1995). Because of this species' many small leaflets (<0.5 cm^2 each) and the methods used in the previous study, we simply counted the number of leaflets with damage rather than using the plastic grid method for this species. We did not measure leaf area of this species in our study.

We considered three ways of presenting the data: actual damage, the percent damage (damage/leaf area), and leaf area remaining. The latter two measures were confounded by differences in leaf area between the two cohorts (see Results), and so we chose to compare actual area damaged. We analyzed cumulative damage, rather than damage since last census.

We averaged all leaves on an individual to pro-

TABLE 2. *Mean leaf size (area of individual leaves in square cm) ± standard error of the two cohorts of leaves for each study species. Leaf size of 5 tagged leaves was averaged over individuals.* N = *36 individuals for* Ardisia, *9 for* Exothea, *and 18 for all other species.* F *and* P *from analysis of variance.*

Species	Cohort 1	Cohort 2	Difference
Ardisia escallonioides			Habitat:
pineland	7.1 ± 1.4	2.0 ± 1.4	$F(1, 68) = 15.5$, $P = 0.0002$
A. escallonioides			Cohort:
hammock	25.2 ± 1.0	15.6 ± 1.0	$F(1, 68) = 24.4$, $P < 0.001$
Exothea paniculata	91.8 ± 22.7	157.7 ± 75.7	Student's $t = 2.5$, $P = 0.03$
Guettarda scabra	12.7 ± 0.5	7.5 ± 0.5	$F(2, 35) = 28.66$, $P = 0.0001$
Ocotea coriacea	24.4 ± 0.9	21.1 ± 0.8	$F(2, 34) = 13.71$, $P = 0.0001$
Psychotria nervosa	54.0 ± 4.0	23.2 ± 4.0	$F(2, 35) = 21.09$, $P = 0.0001$
Rapanea punctata	22.0 ± 1.4	11.8 ± 1.4	$F(2, 35) = 23.11$, $P = 0.0001$
Tetrazygia bicolor	22.0 ± 1.0	20.8 ± 0.9	$F(2, 33) = 0.57$, $P = 0.5723$

vide one measure of area or damage per individual at each sampling time (to avoid pseudoreplication). We analyzed data using analysis of variance to compare leaf areas of the different cohorts (for *Ardisia*, we used two-way ANOVA, testing for habitat differences and interaction between cohort and habitat). For all species, differences between sites were not significant, and so we combined data from both sites within each habitat. We used repeated measures analysis of variance to compare damage over time to marked leaves in the two cohorts (GLM procedure; SAS 1990). For *Ardisia*, we used two between-subject factors, habitat and cohort, and probability was determined using the Greenhouse–Geisser adjustment because the test for sphericity was significant (SAS 1990).

RESULTS

LEAF SIZE COMPARISONS BETWEEN COHORTS.—For six of the seven species measured in this study, leaf size (area of individual leaves; all the leaflets of a compound leaf combined) differed significantly between cohort 1 (leaves produced directly following the hurricane) and cohort 2 (produced three months later; Table 2). For all species, except *Exothea* and *Tetrazygia*, mean leaf size was substantially greater in the first cohort than the second cohort. *Exothea* leaves were substantially larger in the second cohort, whereas *Tetrazygia* leaves did not differ in size between cohorts.

Leaf size of *Ardisia* differed significantly between the two habitats, with leaves in hammocks larger than those in pinelands. Two-way ANOVA showed no interaction between cohort and habitat ($F_{1, 68} = 2.27$, $P = 0.13$), but both sources of variation were significant (for cohort, $F_{1, 68} = 24.41$, $P < 0.001$; for habitat, $F_{1, 68} = 15.5$, $P = 0.0002$).

DAMAGE COMPARISONS BETWEEN COHORTS.—For six of the eight species in this study, damage differed significantly between the two cohorts (Fig. 1). For all species except *Psychotria nervosa* and *Tetrazygia bicolor*, damage was substantially greater to cohort 2 leaves than cohort 1, from two to five times greater. (We consider *Guettarda scabra*, with $P = 0.06$, close enough to 0.05 [the generally accepted level of significance], with the averaging over individuals.) *Psychotria* leaves experienced major damage the second month of the study, with substantial herbivory to cohort 1 leaves from their specialized leaf-rolling herbivore, but differences between the two cohorts were not significantly different due to high interindividual variation. *Tetrazygia* leaves showed a mean damage trend like most of the species, but differences between the two cohorts were not significant due to high variation among individuals.

Damage to *Ardisia escallonioides* did not differ substantially between the two habitats ($F_{1, 68} = 0.65$, $P = 0.4216$). Damage between cohorts was substantially different ($F_{1, 68} = 7.69$, $P = 0.0071$), but differences in cohorts were moderated by a significant interaction between damage and cohort ($F_{2, 136} = 5.00$, $P = 0.0224$). There was no three-way interaction ($F_{2, 136} = 2.19$, $P = 0.1385$).

DISCUSSION

The wet season (May/June through November/December) is a time when woody plants are in full leaf in Everglades hammocks and pine rocklands. After hurricane defoliation, the common woody plants of pinelands and hammocks involved in our study re-leafed in a window of minimal insect activity. Leaves of most of these species developed fully with very little damage.

In six out of seven species measured, leaves in

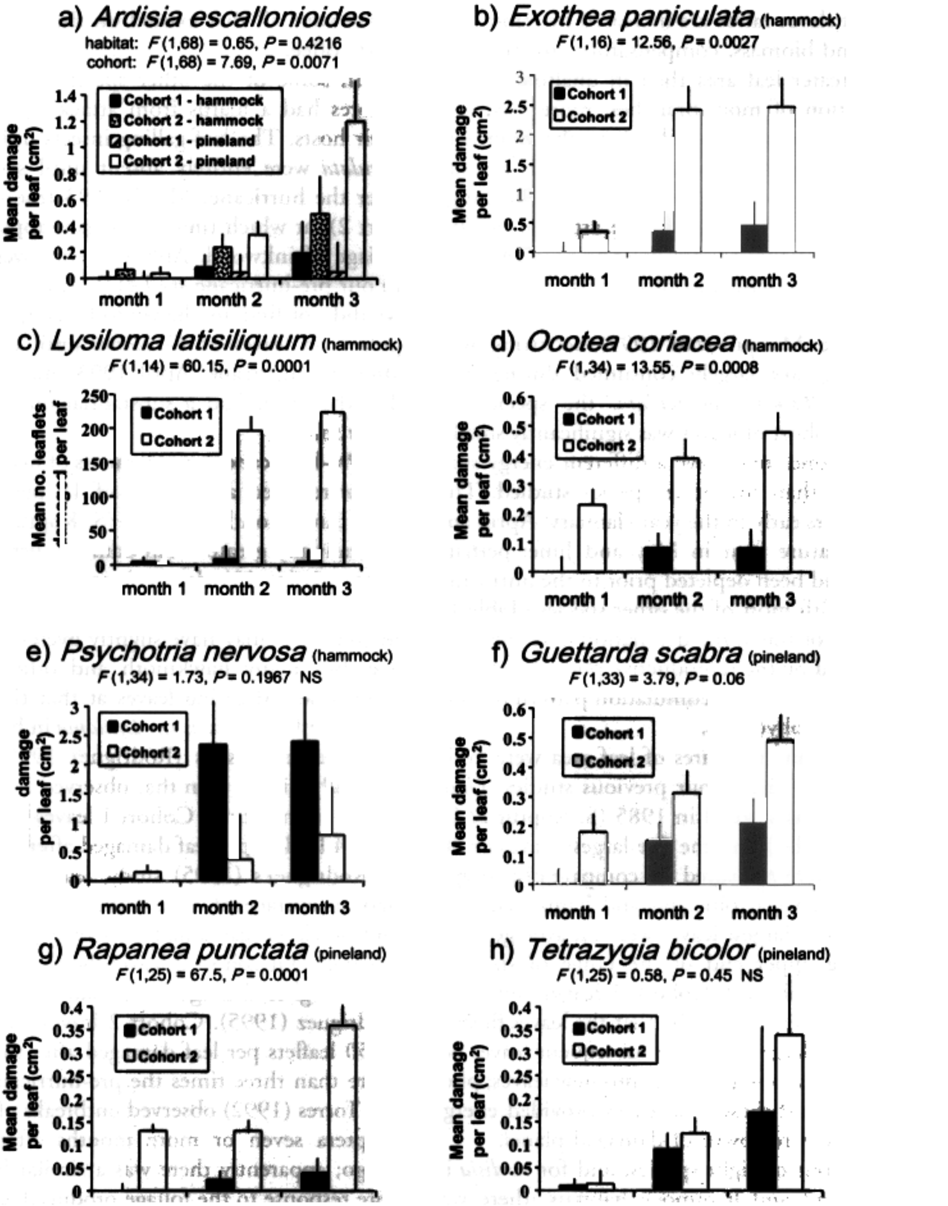

FIGURE 1. Mean area damaged per leaf (in cm²) of the two cohorts of leaves for each study species: hammock species first, pineland species second. Damage of 5 tagged leaves was averaged over individuals for each sample date. Missing values were not included in the analyses. Error bars are 1 SE from the mean. Sample sizes are as in Table 2. For *Lysiloma*, we report the mean number of leaflets damaged rather than the mean area damaged. *F* and *P* are from repeated measures analysis of variance.

the first flush were significantly larger in size than leaves produced later. This may reflect the strong plant response to balance the large discrepancy between leaf and root area. Root:shoot ratios of wind-pruned, totally defoliated plants were large compared to plants before the hurricane, and the energy to make new leaves could only be channeled into a limited number of leaves, as plant heights were greatly reduced and branches were considerably shortened (Koptur & Oberbauer, pers. obs.).

When root:shoot ratios are increased by removal of aboveground biomass, compensatory growth could produce greater leaf area than in unaltered plants by production of more branches, more leaves, or larger leaves. Numerous studies have shown growth enhancement or compensatory growth as a result of severe defoliation (Shabel & Peart 1994, Singh & Thompson 1995), and future artificial defoliation experiments with these Everglades plants may provide some insight into this phenomenon. Carbon accumulation can be seasonal even in an aseasonal climate (Marquis *et al.* 1997), occurring prior to flowering and largely consumed during fruit maturation. *Exothea paniculata*, the species for which first cohort of leaves was significantly smaller than the second, may have a different energy storage strategy than the other species studied. This species flowers early in the year (January–April) and produces mature fruit in May and June; perhaps its energy had been depleted prior to the hurricane, compared with most of the other species (Table 1). The impact of hurricane defoliation may therefore be influenced by the reproductive phenology of the plant species and the accumulation pattern of nonstructural carbohydrates.

Pre-hurricane measures of leaf area were available from only one of our previous studies. *Guettarda scabra* was studied in 1985 (S. Koptur & D. Garcia, pers. obs.) and the five largest leaves on 30 individuals were measured (to compare phenotypic differences between pineland and hammock individuals). These largest leaves were on average *ca* 17 cm^2, at the upper end of the range of sizes we measured in cohort 1 (cohort 2 leaves were substantially smaller). It may be that the leaves flushed initially were larger than the subsequent leaves because resources were put only into new leaves; photosynthesis from these first leaves provided energy for subsequent regrowth of damaged plants.

For six out of eight species, and for *Ardisia* in both pineland and hammock habitats, there was relatively little damage to the first leaves produced after the hurricane. Only *P. nervosa* showed higher damage to this cohort of leaves, and this damage was exclusively due to the specialized leaf-tying tortricid moth caterpillar *Desmia ploralis.* It may be that the life history of the moth enabled the insects to reestablish within a month of the hurricane's defoliation; this species moves from branch to branch, tying and feeding as it develops, but eventually drops from the plant to pupate in the litter or hammock soil (S. Koptur & A. Peterson, pers. obs.). Perhaps some pupae remained undisturbed, and eclosed after the hurricane, when fresh new leaves were all that existed on the branches of the wild coffee.

In some of the other species, specialized herbivores had a hiatus from attacking the leaves of their hosts. The leaf-galling insects utilizing *E. paniculata* were entirely absent until seven months after the hurricane, March 1993 (month 2 in cohort 2), at which time many galls appeared on the foliage of inkwood. Although they were common in our pre-hurricane studies (S. Koptur, pers. obs.), we did not find any hawkmoth caterpillars (Sphingidae) on leaves of *G. scabra* until eight months after the hurricane, April 1993 (month 3, cohort 3), when they had a substantial impact on *Guettarda* foliage.

Pre-hurricane measurements of herbivory on *G. scabra* revealed an average of 18 percent damage after three months in 1986 (S. Koptur, pers. obs.), substantially greater than damage sustained by our cohort 1 (*ca* 1% damage) and cohort 2 (*ca* 5% damage). Previous data were collected in a different manner that may have slightly overestimated damage, but many hawkmoth and other caterpillars were observed eating leaves at that time. Pre-hurricane herbivory rates on *Lysiloma* in both pineland and hammock sites (Rodriguez 1995) were substantially higher than that observed in *Lysiloma* cohort 1 in this study. Cohort 1 leaves had an average of *ca* 4 leaflets per leaf damaged after three months; in Rodriguez's (1995) study, leaves in hammocks had an average of 12.2 leaflets per leaf damaged, and pineland leaves had an average of 11.8 leaflets per leaf. Our cohort 2 leaves, however, experienced much higher damage rates than leaves studied by Rodriguez (1995). Cohort 2 leaves had an average of 50 leaflets per leaf damaged after three months, more than three times the pre-hurricane levels.

Torres (1992) observed outbreaks of many Lepidoptera seven or more months after Hurricane Hugo; apparently there was a similar lag in herbivore response to the foliage produced after the hurricane. Our study revealed substantial insect damage seven months after Hurricane Andrew (*e.g.*, in *Guettarda* and *Lysiloma*, previous paragraph), suggesting that for most species, there is a window in time that is relatively free from insect herbivore pressure. Since most folivory by insects takes place in the first few months of a leaf's life, the leaves produced in response to hurricane defoliation are likely to remain fairly undamaged for the remainder of their lives. Schowalter and Ganio (1999) found that leaf area missing from five species in Puerto Rico peaked in the wet season each year following Hurricane Hugo. Our cohort 1 leaves flushed in September and were monitored for three months through the wet season; cohort 2 leaves were produced and monitored during the dry season. The mostly greater damage seen in cohort 2 (during the dry season) was unlikely to be attributable to normal seasonal variation, but further study is needed for comparison.

The hurricane interrupted and in some cases disrupted plant/insect interactions. The specialized herbivores on *P. nervosa* attacked their hosts within two months of Hurricane Andrew's defoliation. The obligate interaction between fig trees (*Ficus* spp.) and their pollinators reestablished within five months to pre-hurricane levels (Bronstein & McKey 1995). The less specific but mutualistic interactions between *A. escallonioides* and its generalist pollinator array were similar before and after the hurricane, whereas populations of a specialist flower galling moth on this species declined following the hurricane, with some local populations taking two years to recover from extirpation (Pascarella 1998). It seems that the hurricane affected different interactions differently, depending on the particular stage of the life cycle of the insect or plant at the time of the environmental perturbation.

Large disturbances like hurricanes can disrupt the balance of plant/herbivore interactions in favor of the plants. The general elimination of insect populations allows plants to releaf, photosynthesize without much competition for light, and recover using the photosynthate stored in their roots and woody parts. In contrast, smaller disturbances (such as drought, patchy fires, or tornados) may actually give insects the advantage. After these disturbances, foliage may be more palatable, and insects can take full advantage of the plants under stress. A large-scale disturbance may destroy or severely reduce insect populations, and so it takes the insects longer to return. With smaller disturbances, insects (and other herbivores) are more likely to find refuge and attack the first flush of regrowth.

ACKNOWLEDGMENTS

We thank Ann Weekley, Rhonda Herndon, Caroline Hooper, Linda Evans, and Kirk Rawson for field assistance, and Yvon Mon for assistance in the lab. John Geiger, Jed Redwine, and Mike Ross augmented our observations on phenology. The manuscript was improved by constructive comments from Anne Cox, John Geiger, Paul Granville, Suzanne Kennedy, Lauren Linares, Hong Liu, John Palenchar, Cathy Bach, Paulo Oliveira, and anonymous reviewers. This research was supported by NSF grant DEB-9224776.

LITERATURE CITED

AIDE, T. M. 1988. Herbivory as a selective agent on the timing of leaf production in a tropical understory community. Nature 336: 574–575.

———. 1991. Synchronous leaf production and herbivory in juveniles of *Gustavia superba*. Oecologia 88: 511–514.

———. 1993. Patterns of leaf development and herbivory in a tropical understory community. Ecology 74: 455–466.

BRONSTEIN, J. L., AND M. HOSSAERT-MCKEY. 1995. Hurricane Andrew and a Florida fig pollination mutualism: Resilience of an obligate interaction. Biotropica 27: 373–381.

BRYANT, J. P., I. HEITKONIG, P. KUROPAT, AND N. OWEN-SMITH. 1991. Effects of severe defoliation on the long-term resistance to insect attack and on leaf chemistry in six woody species of the southern African savanna. Am. Nat. 137: 50–63.

———, G. D. WIELAND, T. CLAUSEN, AND P. KUROPAT. 1985. Interactions of snowshoe hare and feltleaf willow in Alaska. Ecology 66: 1564–1573.

COLEY, P. D. 1982. Rates of herbivory on different tropical trees. *In* E. G. Leigh Jr., A. S. Rand, and D. M. Windsor (Eds.). The ecology of a tropical forest: seasonal rhythms and long-term changes, pp. 123–132. Smithsonian Institution Press, Washington, D.C.

DU TOIT, J. T., J. P. BRYANT, AND K. FRISBY. 1990. Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. Ecology 71: 149–154.

FILIP, V., R. DIRZO, J. M. MAASS, AND J. SARUKHAN. 1995. Within- and among-year variation in the levels of herbivory on the foliage of trees from a Mexican tropical deciduous forest. Biotropica 27: 78–86.

HONKANEN, T., E. HAUKIOJA, AND J. SUOMELA. 1994. Effects of simulated defoliation and debudding on needle and shoot growth in Scots pine (*Pinus sylvestris*): implications of plant source/sink relationships for plant/herbivore studies. Funct. Ecol. 8: 631–639.

JUENGER, T., AND J. BERGELSON. 1997. Pollen and resource limitation of compensation to herbivory in scarlet gilia, *Ipomopsis aggregata*. Ecology 78: 1684–1695.

KOPTUR, S. 1991. Extrafloral nectaries of herbs and trees: modeling the interaction with ants and parasitoids. *In* C. R. Huxley and D. F. Cutler (Eds.). Ant–plant interactions, pp. 213–230. Oxford Scientific, Oxford, England.

LANDSBERG, J. 1988. Dieback of rural eucalypts: tree phenology and damage caused by leaf feeding insects. Aust. J. Ecol. 13: 251–268.

Lawrence, R. K., W. J. Mattson, and R. A. Haack. 1997. White spruce and the spruce budworm: defining the phenological window of susceptibility. Can. Entomol. 129: 291–318.

Long, Z. T., W. P. Carson, and C. J. Peterson. 1998. Can disturbance create refugia from herbivores: an example with hemlock regeneration on treefall mounds. J. Torrey Bot. Soc. 125: 165–168.

Loope, L., M. Duever, A. Herndon, J. Snyder, and D. Jansen. 1994. Hurricane impact on uplands and freshwater swamp forest. BioScience 44: 238–246.

Lowenberg, G. J. 1994. Effects of floral herbivory on maternal reproduction in *Sanicula arctopoides* (Apiaceae). Ecology 75: 359–369.

Marquis, R. J., E. A. Newell, and A. C. Villegas. 1997. Non-structural carbohydrate accumulation and use in an understorey rain-forest shrub and relevance for the impact of leaf herbivory. Funct. Ecol. 11: 636–643.

Maschinski, J., and T. G. Whitham. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. Am. Nat. 134: 1–19.

Mopper, S., and D. Simberloff. 1995. Differential herbivory in an oak population: the role of plant phenology and insect performance. Ecology 76: 1233–1241.

Murali, K. S., and R. Sukumar. 1993. Leaf flushing phenology and herbivory in a tropical dry deciduous forest, southern India. Oecologia 94: 114–119.

Paige, K. N. 1992. Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. Ecology 73: 2076–2085.

Pascarella, J. B. 1997. Pollination ecology of *Ardisia escallonioides* (Myrsinaceae). Castanea 62: 1–7.

———. 1998. Hurricane disturbance, plant–animal interactions, and the reproductive success of a tropical shrub. Biotropica 30: 416–424.

Peterson, C. J., and S. T. A. Pickett. 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. Ecology 76: 763–774.

Pullin, A. S. 1987. Changes in leaf quality following clipping and regrowth of *Urtica dioica*, and consequences for a specialist insect herbivores, *Aglais urticae*. Oikos 49: 39–45.

Rodriguez, M. C. 1995. Interactions between *Lysiloma bahamensis* Benth. (Fabaceae: Mimosoideae) and herbivorous insects in the Everglades. M.S. thesis. Florida International University, Miami, Florida.

Sand-Jensen, K., D. Jacobsen, and C. M. Duarte. 1994. Herbivory and resulting plant damage. Oikos 69: 545–549.

SAS. 1990. SAS/STAT user's guide. Version 6. SAS Institute, Cary, North Carolina.

Schowalter, T. D. 1994. Invertebrate community structure and herbivory in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. Biotropica 26: 312–319.

———, and L. M. Ganio. 1999. Invertebrate communities in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. Ecol. Entomol. 24: 191–201.

Schultz, J. C., and I. T. Baldwin. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. Science 217: 149–151.

Shabel, A. B., and D. R. Peart. 1994. Effects of competition, herbivory, and substrate disturbance on growth and size structure in pin cherry (*Prunus pensylvanica* L.) seedlings. Oecologia 98: 150–158.

Singh, K. A., and F. B. Thompson. 1995. Effect of lopping on water potential, transpiration, regrowth, super(14)C-photosynthate distribution and biomass production in *Alnus glutinosa*. Tree Physiol. 15: 197–202.

Snyder, J. R., A. Herndon, and W. B. Robertson. 1990. South Florida rockland. *In* R. L. Myers and J. J. Ewel (Eds.). Ecosystems of Florida, pp. 230–277. University of Central Florida Press, Orlando, Florida.

Tomlinson, P. B. 1980. The biology of trees native to tropical Florida. Harvard University Printing Office, Allston, Massachusetts.

Torres, J. A. 1992. Lepidoptera outbreaks in response to successional changes after the passage of Hurricane Hugo in Puerto Rico. J. Trop. Ecol. 8: 285–298.

Wunderlin, R. P. 1998. Guide to the vascular plants of Florida. University Press of Florida, Gainesville, Florida.