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EFFECTS OF HURRICANE ANDREW ON EPIPHYTE COMMUNITIES WITHIN CYPRESS DOMES OF EVERGLADES NATIONAL PARK

Steven F. Oberbauer, Kurt von Kleist III, Kevin R. T. Whelan, and Suzanne Koptur[1]

Hurricanes routinely disturb South Florida forests, and account in part for community structure throughout the region. The epiphyte communities might be especially affected by hurricanes by virtue of their canopy exposure and wind dispersal. However, the relative infrequency of hurricanes in this century has limited information regarding how South Florida forest communities are affected by hurricanes. On 24 August 1992 Hurricane Andrew passed across our study sites in cypress domes in Everglades National Park (ENP), providing an opportunity to examine the epiphyte community response to a major hurricane in which sustained winds reached 240 km/h.

In ENP, cypress [*Taxodium distichum* (L.) Richard var. *nutans* (Ait.) Sweet] reach their greatest development in cypress domes—doughnut-shaped, nearly monospecific stands of cypress surrounding a pond (Ewel and Odum 1984, Duever et al. 1986, Ewel 1990). Cypress domes support some of the highest densities and diversities of epiphytes in the Everglades. Here, we document the short-term epiphyte community response to Hurricane Andrew in cypress domes. We attempt to answer the following questions: (1) What is the magnitude of changes in epiphyte density? (2) Were epiphyte losses related to level of tree damage within a dome? (3) Were certain epiphyte species affected more than others? (4) Can these differences be related to differences in growth characteristics? (5) Were changes in epiphyte density related to epiphyte size?

Our study sites included three cypress domes located within the Pa-hay-okee region of ENP. The domes differ somewhat in size and probable wind speed experienced during the storm. Dome 3 is largest (126 m in the longest dimension) and also was the closest to the southern eye-wall of the hurricane. Domes 1 and 2 are similar in size (70 and 58 m long, respectively) and located about 2–3 km south of dome 3 (von Kleist 1993). The epiphyte communities in each dome were distinct, but those in domes 2 and 3 were the most similar (von Kleist 1993). Of the angiosperm epiphytes present, eight bromeliad, one orchid, and one urticaceous species were represented by more than one individual among the study sites. We focus primarily on the bromeliads because they dominate the arboreal communities.

Methods

The study areas were initially inventoried in May, August, and October of 1991 for a study of cypress dome communities (von Kleist 1993). At that time, a 5-m-wide belt transect was established in each of the three domes. The transect was then divided into 3 × 5 m plots that were marked using cord. Trees, shrubs, and herbs were categorized in these 3 × 5 plots, and epiphyte ramets were enumerated in 2 × 2 m subplots up to a height of 2 m, which in cypress domes includes most of the epiphytes. Epiphyte ramets were identified to species and categorized into three relative size classes, small, medium, and large, based on the maximum size a species attains. We measured ramets rather than genets because, for most of the species, new buds produce individual rosettes that are often physiologically self-sufficient and die after flowering. Likewise, seeds may germinate in clumps, and distinguishing ramets from genets is sometimes difficult. One of the species, *Tillandsia utriculata* L., is monocarpic. This measurement technique was effective for all but *T. recurvata* L., which, because of its small size and clumpy growth form, was difficult to assign to size class. *T. usneoides* L. (Spanish moss) is a non-rosette species and was categorized on the basis of the size of the clone. We examined 81 plots: 20, 19, and 42 in domes 1, 2, and 3, respectively.

Ten months after the storm, in June 1993, we reestablished the belt transect and plots, and the same individual who did the first survey resampled the 2 × 2 × 2 m epiphyte subplots using the procedures as in the initial inventory.

Our estimates of epiphyte mortality are probably conservative for two reasons: (1) the potential for establishment and growth of smaller individuals into larger size classes between the sampling dates; (2) some epiphytes were located above the upper boundary of our plots. However, as a result of the generally slow growth rates of these plants (Benzing 1980), numbers of individuals establishing or moving into the larger size classes over the study period were probably relatively small, and mortality between the sample periods unrelated to the storm would tend to compensate some-

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what for underestimates. Although the end points of the transects and some of the plot corners were intact following the storm, resurveys in some plots were probably not conducted through identical space. In some plots epiphytes increased following the storm as a result of epiphyte-bearing trees falling or leaning into the plots.

In addition to the epiphyte measurements, we inventoried tree damage in twelve 5 × 5 m plots per dome to provide an index of the loss of attachment sites for epiphytes. Most impacted was dome 2, where 58% of the trees incurred severe damage (primary branches or crowns snapped off). Domes 1 and 3 contained fewer severely damaged trees (37% and 28%, respectively). Tree damage tracked dome size (Chi-square test, $P < 0.05$); the largest dome, dome 3, was least affected despite its close proximity to the eyewall of the hurricane.

Epiphytes occur unevenly within the domes. Any plot may contain only a fraction of the resident epiphyte species. Likewise, all of the individuals of a particular species may be found in a single plot. Twelve of the 81 plots sampled contained no epiphytes. Consequently, we compared epiphyte densities before and after the hurricane using a paired t test, excluding those plots lacking the species of interest. As a result, sample sizes were sometimes small, and significance levels were often low despite large relative changes in densities.

Results and Discussion

Although large numbers of dying epiphytes were floating in the water in the domes shortly after the storm, the overall mortality of epiphytes was relatively low. Indeed, the total number of epiphyte ramets per plot 10 mo after the storm was greater than that before Hurricane Andrew as a result of recruitment of new ramets and possibly seedlings into the small size class (14.2 vs. 20.7 ramets/plot with epiphytes; $P < 0.001$). This apparent recruitment may have resulted from the warm, wet winter of 1992–1993, in combination with opening of the canopy and improved growth conditions for the surviving plants. Considering only the large size class, density of all bromeliad species decreased 2.4 plants/plot with epiphytes ($P < 0.05$). Losses in the large size class of bromeliads were greatest in dome 2 (43%), followed by dome 1 and dome 3 at 35% and 12%, respectively, which coincides with the level of tree damage (Chi-square test, $P < 0.05$, cf. Fig. 1A). The value for dome 2 was influenced by a 54% decrease in large *Tillandsia balbisiana* Schult, the most abundant species there (Fig. 1B). This species was also abundant in domes 1 and 3, but losses were substantially lower in those sites.

Species varied in their responses to hurricane-force winds, apparently according to anchorage, substrate, and exposure, although because few statistically significant differences were found on a per-plot basis, these findings are only suggestive. For example, *T. usneoides* incurred the greatest percentage reduction (91%) in the large size class (dome 3, Fig. 1C), consistent with its lack of root attachment. In contrast, *T. utriculata,* a large species with extremely strong attachment, declined only 15% in the large size class (Fig. 1D). Interestingly, losses of medium *T. utriculata* tended to be greater than those for large plants. Seedlings of *T. utriculata* establish throughout cypress crowns, but only very large branches and trunks can support the weight of maturing plants as they attain maximum size. As a result, larger plants, although offering greater resistance to wind than juveniles, had lower losses, probably because they are attached to a more stable substrate.

Responses of the other species were intermediate. *Tillandsia fasciculata* Sw., a relatively large plant at maturity with strong attachment, sustained a 50% loss in the large size class (data not shown), while *T. recurvata,* a small species with weak attachment, lost few individuals (Fig. 1E). *T. balbisiana,* a medium-sized plant, often weakly attached to small branches, experienced high losses in all size classes in dome 2. *T. paucifolia* Baker, a small plant frequently found on small branches, declined sharply in the large size class in dome 1, but otherwise lost few individuals (Fig. 1F). Two other bromeliad species, *T. flexuosa* Sw. and *T. setacea* Sw., were rare in the study plots; *T. flexuosa* densities were unchanged, whereas all individuals (3) of *T. setacea* were lost (data not shown). *Boehmeria cylindrica* (L.) Sw., an herb typically rooted on cypress trunks just above the water line, weathered the storm unaffected. The single orchid species common to cypress domes, *Encyclia tampensis* (Lindl.) Small has very strong anchorage most commonly on tree trunks; losses of this species were minimal at all sites (data not shown).

Few other data exist on the response of epiphytes to hurricane winds. In the Luquillo forest in Puerto Rico, which was directly in the path of Hurricane Hugo, all epiphytes were removed (Migenis and Ackerman 1993). In forest 100 km south of the path of Hugo, only 17.6% of a marked population of the orchid *Comparettia falcata* Poeppig & Ednlicher was dislodged or crushed as a result of Hugo (Rodríquez-Robles et al. 1990). Our results from Everglades National Park cypress domes were intermediate despite the high storm winds. The attachment of most epiphytes low on tree trunks and the low wind resistance of the cypress probably resulted in the low mortality there.

Similar to survivorship patterns, recruitment into the small size class was greatest in the larger, less damaged domes (Chi-square, $P < 0.05$). The three species abun-

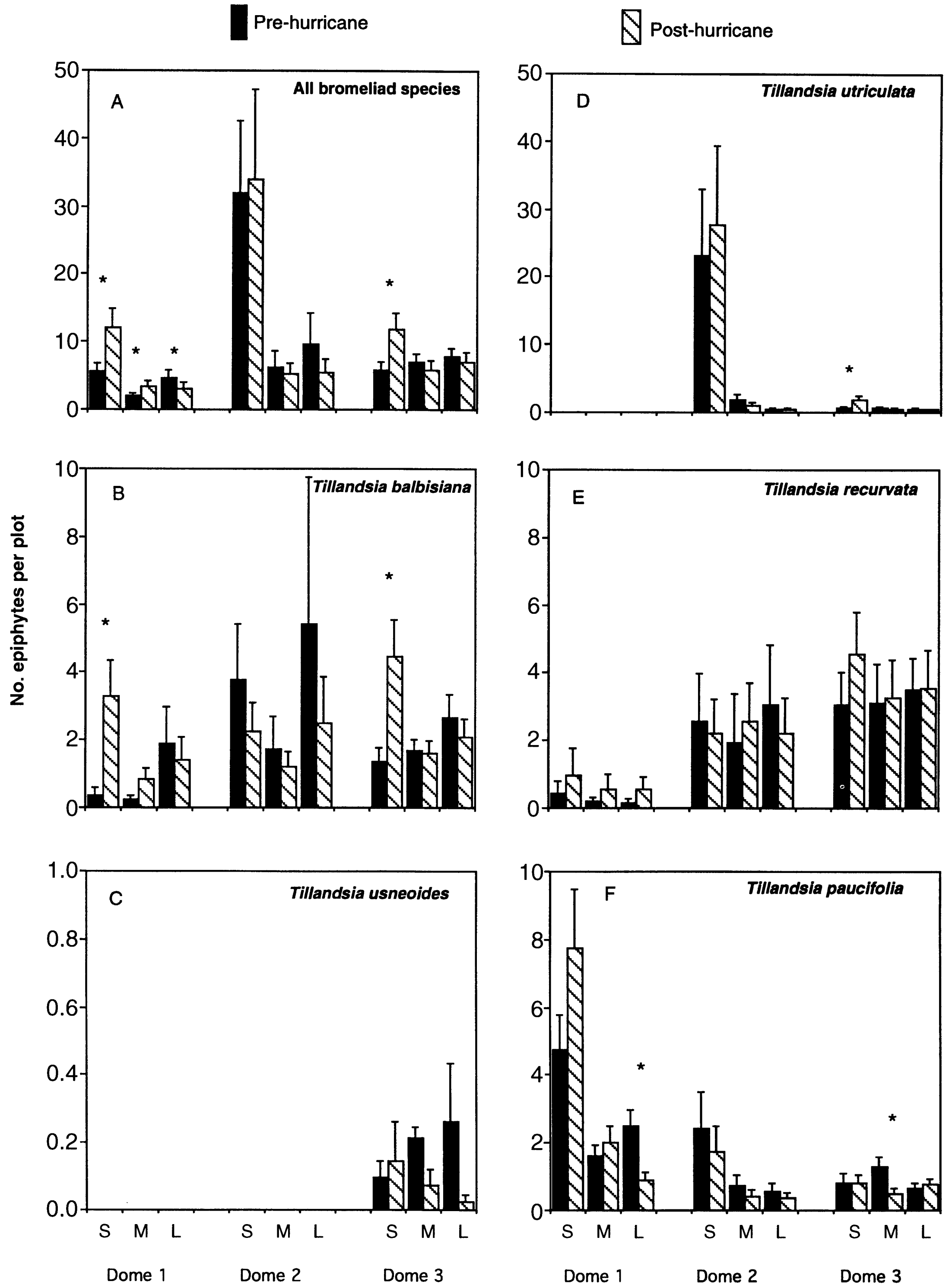

FIG. 1. Densities of epiphyte ramets by relative size class (small, medium, or large) in three cypress domes in Everglades National Park (Florida, USA) before and after Hurricane Andrew (24 August 1992). Values are number of ramets per 8-m^3 plot (mean $\pm$ 1 SE); mean values are based on all plots at a site including those without the species of interest. Asterisks indicate that differences between pre- and post-hurricane values are significant at the 2% level based on a paired t test of only those plots containing species of interest.

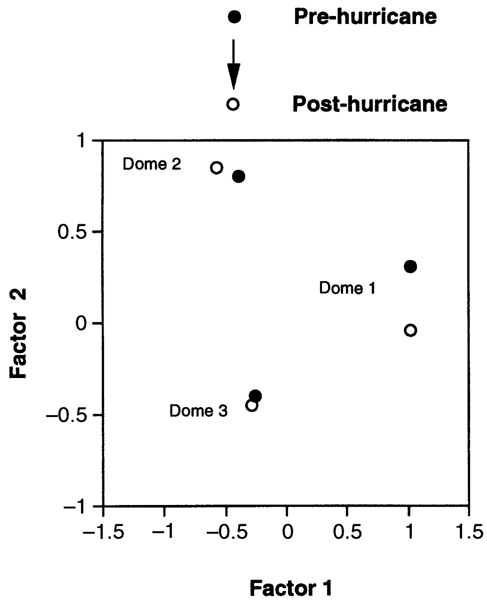

FIG. 2. Plot of the first two factor axes from factor analysis of abundances for epiphyte communities on three cypress domes in Everglades National Park before and after Hurricane Andrew.

dant in all of the domes, *T. recurvata, T. balbisiana,* and *T. paucifolia,* increased the most in domes 1 and 3, which had intermediate and lowest epiphyte mortality, respectively. Dome 2, in addition to withstanding the most damage, is dominated by *T. utriculata,* which is incapable of sprouting.

Species that lost substantial numbers in the large size class also showed recruitment in the small size class, with the exception of *T. balbisiana* in dome 2 and *T. fasciculata* in dome 3. In the case of *T. fasciculata,* small individuals were not present in the dome prior to or after the storm. Large numbers of the new recruits, however, may die and fail to contribute to the adult cohort, an idea supported by the size distributions of some of the species before the storm.

These results suggest that the epiphyte communities of cypress domes were largely unaffected by the storm. We compared the communities before and after Hurricane Andrew using a factor analysis (Tabachnick and Fidell 1983) on the abundance data without regard to size class (Fig. 2). Most (98%) of the variation in the data could be explained by factors 1 and 2, which were highly significant. The mean factor scores for communities in domes 2 and 3 were similar both before and after the storm. The mean factor scores for dome 1 shifted slightly as a result of the occurrence of a seedling of *T. utriculata,* a species not detected previously in the plots.

In summary, epiphyte mortality and post-storm recruitment corresponded to tree damage within the domes. Although large numbers of epiphytes died, post-storm recruitment is likely to compensate and perhaps increase epiphyte densities. Site preferences and rooting characteristics rather than shoot size seem to be important factors affecting differential mortality among species. Hurricanes may promote epiphyte establishment and growth by increasing light levels for these plants, which are largely light-demanding species (Craighead 1963, Benzing 1980). Overall the epiphyte community composition was largely unchanged by Hurricane Andrew. However, hurricanes possibly can affect community composition by introducing seeds of species to domes where they were not previously present.

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