

Windthrow in South Florida Pine Rocklands: Pit-and-Mound Features and Plant Microhabitat Associations Following Hurricane Andrew

Report to Everglades National Park

by

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[Abstract](#)

[Introduction](#)

[Methods](#)

[Study Area](#)

[Sampling Method](#)

[Vegetation Analysis](#)

[Results](#)

[Discussion](#)

[Plant Assemblages](#)

[Background Variation](#)

[Conclusion](#)

[Literature Cited](#)

Appendix 1 ([available upon request](#))

Appendix 2 ([available upon request](#))

Appendix 3 ([A](#), [B](#), [C](#), [D](#), [E](#), & [F](#))



ABSTRACT

We examined the effect of environments created by the uprooting of adult trees during Hurricane Andrew (August 1992) on spatial patterning in the pine forest understory. Our two study areas --- a wet site in Big Cypress National Preserve and a more xeric one in Everglades National Park --- differed markedly in morphology and substrate dynamics in pit and mound environments during the post-hurricane period. At BCNP, where pine roots occupied continuous marl soils, tipup pits were shallow, wide, and filled in rapidly after the hurricane. At ENP, trees were rooted in limestone bedrock, pits were

deeper, and infilling with limestone fragments was irregular. The two sites also differed in the relative favorability of the two major tipup habitats for plant establishment. Following the high water conditions of 1995-96, species richness on BCNP mounds was about 60% higher than in pits. In contrast, pits in ENP were about twice as speciose as mounds. Pit and mound species composition (especially the former) were distinct from background vegetation during the immediate post-hurricane period. However, these relationships did not appear to persist; old tipup features which were still recognizable in the rockland landscape did not differ from undisturbed terrain with respect to plant species composition. Spatial analyses indicated that pine forest understory vegetation was strongly structured at distances between 0.3 and 15 meters. Within that range, units of relatively homogeneous vegetation of all sizes were present at both sites. Our results suggest that the uprooting of pine trees during periodic hurricanes creates ecologically significant substrate variation in the rockland surface, thereby contributing to fine-scale structuring in understory species assemblages.

INTRODUCTION

Forests in interior Dade County were not inundated by tides or excessive rainfall during Hurricane Andrew (August 24, 1992), but were impacted by sustained winds which have been estimated at about 62 m/sec (139 mph) in some areas (Powell and Houston 1996). By damaging or killing resident trees, such events release resources which may stimulate the establishment of new individuals from a range of growth forms, and initiate a relatively predictable sequence of species replacement, or succession. When trees are uprooted entirely, fresh, relatively persistent niches in the physical environment are created --- the pit-and-mound features previously described by a series of soil scientists (e.g., Shaler 1891; Lutz 1940; Denny and Goodlett 1956; Stephens 1956; Lyford and Maclean 1966; Koop 1981) --- and these may be rapidly occupied by specially adapted plants. From these perspectives, hurricanes may be forces which contribute to habitat and ultimately biological diversity in rockland forests. We examined pit-and-mound topography created by Hurricane Andrew in two South Florida pine forests, how it developed over a two-year period, and what plants took advantage of the newly-exposed substrates. More generally, we examined variation in pine rockland understory species composition against the background of these gradually infilling breaks in the local landscape.

METHODS

Study Area

After reconnaissance of a number of South Florida pine forests, we selected a single stand in which uprooted trees were common in Pine Island (Everglades National Park) and in Lostman's Pines (Big Cypress National Preserve) ([Figure 1](#)). Both stands were located inside a ca 45 km swathe in which hurricane winds were the strongest, Pine Island south of the eye of the storm and Lostman's Pines to its north. However, the two sites represent opposite poles among South Florida pine forests in terms of site history, substrate characteristics, and hydrology.

Pine Island (PI), an isolated upland in easternmost ENP (25°22'57"N, 80°35'34"W), is situated between the much more extensive Long Pine Key pine forest and the agricultural (formerly pine-covered) Redland area of southwest Dade County. Logging began in the Redland about 1905 and generally proceeded toward the west through the mid-1940's (Robertson 1955). PI was logged in the early 1930's (Robertson pers. comm.) according to logging practices of the day, which included the retention of a substantial component of residual trees deemed too small or poorly formed to harvest. Maintenance facilities and residences for Park employees were established within the recovering pine forest at PI soon after the creation of Everglades National Park in 1947. In contrast, Lostman's Pines (LP), located in southern BCNP (25°41'20"N, 81°03'58"W), has never been logged (Doren et al. 1993)

and bears no evidence of permanent structures. However, both sites had been used regularly by hunters and recreationists for centuries before the establishment of ENP or BCNP, and LP continues to receive considerable off-road vehicle traffic today. Over the last few decades, both sites have been included in active fire management programs carried out by the respective Parks.

The geologic and hydrologic settings at Pine Island and Lostman's Pines differ. Geologically, the two are dissimilar in the age and type of limestone exposed at the surface, the thickness of mineral soils, and in broad topographic relief. Pine Island is part of a larger regional outcropping of the Miami Limestone which forms the east coast ridge, and is important in defining Everglades flow patterns (Figure 2). The surficial limestones (Miami Formation) at PI are nearly pure carbonate and are late Pleistocene in age. The lack of silicates, especially quartz sand, has resulted in a paucity of mineral soil and a rough surface topography. In contrast, exposed limestones at LP are older Pliocene, quartz-rich limestones of the Tamiami Formation (Duever et al, 1979). As a result of phreatic and vadose dissolution, the quartz component of the Tamiami limestones is the primary source of the thin, more or less continuous mineral soils at LP. In the southeastern portion of the BCNP, pine forests like the LP site are found on isolated limestone outcroppings surrounded by wetlands, usually marl prairies (Figure 2). The relief of the exposed limestone in respect to adjacent wetland soils is much less at LP than at Pine Island. Hydrologic data from PI and LP are not available, but our own experience suggests that the latter is a much wetter site. In the winter of 1995-96, LP was inundated for at least three months by as much as 30 cm of water. During the same period, we never observed water above the surface at PI for more than a few days. Such differences in the type of substrate available and in hydrologic regime have the potential to affect vegetation and its response to disturbance dramatically.

Sampling Methods

Sampling of pine uprooting and its consequences was directed at several features of the hurricane-impacted forests: (a) distribution and characteristics of trees uprooted during Hurricane Andrew, (b) extent, morphology, and development of pits and mounds associated with uprooting occurrences, (c) plant species composition on these substrates four years after Hurricane Andrew, and (d) vegetation and topographic variation along transects representative of the pine forests as a whole.

Tip-up occurrence. The distribution and significance of uprooting occurrences in relation to other types of hurricane-induced mortality were assessed in a one-hectare (50 x 200 meter) plot established at each site in May 1994. Using a tape, right angle prism, and theodolite, we subdivided the plot into one hundred 10 x 10 m cells, and determined the elevation of each cell's midpoint relative to an arbitrary benchmark. In June and July 1994, we assigned a grid coordinate (nearest 0.5 m) to each live and dead tree (stem greater than 1 cm diameter at 1.45 m, or DBH). At both sites, we recorded the DBH and mode of death (broken, uprooted, standing intact) of each dead tree, and the direction of treefall of uprooted and broken stems. Where dead stems were sufficiently intact, we estimated pre-disturbance bole length for uprooted (PI and LP), broken (PI only), and standing dead trees (PI only). We also estimated the DBH and crown characteristics (total height, crown length and width, crown fill percentage) of all live trees at Pine Island. At LP, we measured the DBH of all live individuals, but crown measurements were confined to trees located within a 10 x 200-meter band bisected by the plot midline.

Tip-up extent, morphology, and development. Concurrent with the surveys described above, we measured the length, width, and maximum depth of the pits created by each uprooted tree in the one-ha plots at Pine Island and Lostman's Pines. We calculated pit area as one-half of an ellipse, or $\pi(a*b)/2$, where a = one-half the pit length and b = the pit width. More extensive observations were made on six tipups at each site. These were randomly chosen to document temporal change along transects which

profiled the disturbed substrates at the base of uprooted trees. Two transects were established which originated in the undisturbed substrate below the pit, crossed the pit and mound, and paralleled the tree bole on either side for several meters beyond the root ball. Relative elevation, soil depth, and substrate type were recorded at 10 cm intervals in May 1994 and January 1996. Between the first and second geomorphic surveys, both sites were burned under prescription by park fire crews (PI, July 7, 1995; LP, May 18, 1995). A mid-day shower resulted in a very patchy fire at Pine Island, while the burn at Lostman's Pines was hotter and more complete (Snyder et al. in prep.). The fires were followed by a very wet summer and fall (Orians et al. 1996), during which all but the highest microsites at LP were inundated through most of the winter. Flooding at PI was localized and of short duration during the same period.

Plant species composition in tip-up environments. Plant surveys were carried out in May/June of 1996, ca four years after Hurricane Andrew. A random subset of treefalls in each stand (PI, 26 trees; LP, 17 trees) were selected for analysis of post-hurricane vegetation dynamics. The affinity of plant species for environments created by treefalls was assessed on the basis of their occurrence in pits and mounds compared to adjacent undisturbed terrain. In May and June 1996, we recorded the presence of all taxa rooted in (1) the mound (i.e., the two surfaces presented by the uprooted tree slab itself, plus the smaller area of soft sediments which had begun to accumulate at the base of the slab), (2) the pit (i.e., the ground surface exposed by the uprooted slab), and (3) a circular control plot adjacent to the pit and equal in area to it.

Background compositional and topographic variability. Our examination of compositional and substrate variation in the pine forest understory utilized small contiguous plots sampled along relatively long transects. In June 1996, three transects were established perpendicular to the long axis of the one-hectare plots at PI and LP. Transects were established at locations selected haphazardly in each third of the plots (Figure 3). Transects ranged in length from 35 to 50 meters. Elevations relative to an arbitrary benchmark were determined at 30 cm intervals along the transects. Sediment depth and type were also recorded. These points served as the midpoints for contiguous 0.3 x 0.3 m vegetation quadrats in which the presence of all plant taxa were recorded. We also searched for old tip-up features along the transect and recorded their location.

Vegetation Analysis

Species-microhabitat relationships. We used Detrended Correspondence Analysis (DCA) (Jongman et al. 1995) to examine overall compositional relationships between the two study areas and among microhabitats in 1996. DCA analyses were run on a combined data set from Pine Island and Lostman's Pines, as well as on individual data sets from each study area. Species were coded 1 (present) or 0 (absent), and relativized within plots (i.e., tree-microhabitat combinations).

Analysis of variance procedures were used to examine differences among microhabitats in the occurrence of several plant growth forms in 1996. Species were categorized as fern, forb, graminoid, shrub, tree, or vine, and the number of species of each growth form present in each plot was determined. Data were analyzed as a complete block design within each site, with habitat and growth form as fixed treatment effects, and tipup tree as a random blocking variable. In order to homogenize the variance among groups for analysis, species numbers were transformed by adding 0.5 and taking their square-root. Our interest was primarily in the microhabitat x growth form interaction. Where this interaction was significant ($\alpha = 0.05$), we examined the effect of habitat independently within each growth form, with tree again as a blocking variable. For growth forms which exhibited significant effects of habitat, we examined two individual contrasts ---Control v. Pit and Control v. Mound --- using $\alpha = 0.025$ as the significance criterion.

We also examined species-microhabitat associations individually by constructing separate 2 x 2 contingency tables for Control v. Pit and Control v. Mound comparisons for each species at each study area. G-statistics were calculated and tested against the Chi-square value for 1 degree of freedom (Sokal and Rohlf 1981). Species-microhabitat relationships identified in this manner should be considered cautiously, since they were drawn from 474 individual comparisons, each with a discrete probability of Type I error.

Background variation in species composition. Our analytical strategy for the transect data was three-phased: for each transect we (a) examined vegetation spatial structure and its environmental correlates, (b) identified sharp discontinuities or breaks in species composition along the transect, and (c) described species-environment relationships among the units of relatively uniform composition between breaks.

In our examination of spatial structure in plant species composition, we first computed Percent Dissimilarity (PD) (Gauch 1982) for each pair of plots along the transect, where:

$$PD = 2 * (\text{number of species common to both plots}) / (\text{the total number of species occurrences})$$

We calculated the mean PD (PD_{mean}) for each lag distance (h) among plots on this basis, and fitted the data according to an exponential model:

$$PD_{\text{mean}}(h) = C_0 - C * \exp(-3h/a),$$

using the STATISTICA Non-linear Curve-fitting module (StatSoft Inc, 1995). In order for all PD_{mean} values to represent a minimum of fifty data pairs, the fitted data were limited to lag distances of 60 units (20 meters) or less. While these variograms are based on dissimilarities rather than semivariances, we retained the terminology of Isaaks and Srivastava (1989), defining the following terms: the *nugget* was the value indicated by the exponential model at a lag of 1 unit, the *sill* was the model value at lag 60, and the *practical range* was the lag at which the model PD_{mean} equaled the nugget plus 95% of the difference between nugget and sill.

We used a moving split-window method introduced by Whittaker (1960) and developed further by others (Webster 1973, Ludwig and Cornelius 1987, Wierenga et al. 1987) to identify discontinuities along transects. The method involves the calculation of dissimilarity between two halves of a window, where the window contains data from a fixed block of contiguous quadrats, followed by movement of the window one quadrat further along the transect, and repetition of the process. After trying window sizes between 16 and 64, we settled on a window of 40 0.3 x 0.3 m units, because it seemed to produce the best definition in dissimilarity peaks. In this case, we calculated dissimilarity as Euclidean Distance (Pielou 1977), based on species' frequencies among the 20 quadrats on either side of the window, according to the formula:

$$d_{ij} = \left[\sum_{t=1}^s (x_{ti} - x_{tj})^2 \right]^{1/2}$$

where d_{ij} was the dissimilarity between window halves i and j , and species t was one of s species present in at least two quadrats in i and/or j .

Canonical correspondence analysis (CCA) (ter Braak 1986) was used to quantify species-environment relationships within each study area. CCA analyses were applied to two separate data matrices extracted from the transect data. In the first, sites were the individual 0.3 X 0.3 m quadrats,

species abundances were "1" (present) or "0" (absent), and environmental variables were the measured elevation and soil depth at each quadrat center. In the second data matrix, sites were groups of quadrats between the peaks identified through the moving split-window procedure described above, species abundances were the relativized frequencies of occurrence within each group, and environmental data were the group median elevations and soil depths. Species which occurred in fewer than three quadrats, or fewer than two groups, were not included in Analysis 1 or 2, respectively. In both analyses, an unrestricted random permutation procedure (99 permutations) was used to test the effect of elevation and soil depth on the ordination (ter Braak 1987).

Finally, we compared the species mixtures associated with old pits, old mounds, and non- tipup background substrates graphically, by examining DCA site scores for quadrats categorized into these three groups. To complete this categorization, we extrapolated from our observations of morphological development in Hurricane Andrew tipup landforms, in conjunction with interpretation of other bedrock and soil topographic features. The following criteria were used to distinguish topographic features resulting from past uprooting events from those formed by karst processes: 1) karst features are usually deeper than 50 cm at PI and 30 cm at LP, 2) active karst (doline) features are usually vertically walled and relatively narrow, 3) tipup features are frequently characterized by the presence of rock clasts on the surface or buried in shallow sediment adjacent to a bedrock depression, 4) tipups at our sites generally created a bedrock depression which ranged from 10 to 40 cm in depth, and from 30 to 300 cm in its horizontal dimensions, and 5) tipup features may be accompanied by localized surface mounding of soil or a soil-rock mixture.

RESULTS

Uprooting and mortality resulting from Hurricane Andrew. The pre-hurricane stands at Pine Island and Lostman's Pines differed dramatically in structure. The symmetrical unimodal distribution at PI was peaked in the 22 and 27 cm classes ([Figure 4A](#)). In contrast, the strongly left-skewed diameter distribution at LP decreased from maxima in the 7 and 12 cm size classes ([Figure 4B](#)).

Though both sites were within the path of Hurricane Andrew, the storm's eye passed north of Pine Island and south of Lostman's Pines. As a result, the strongest winds came from different directions at the two sites, and this was reflected in the predominant orientation of treefalls (PI, median=75° , range 13°-143°; LP, median=222° , range=173°-321°). There was no relationship between tree diameter and direction of fall ([Figure 5](#)).

On a density basis, total hurricane-related mortality was considerably higher at PI (61%) than LP (20%). The low initial representation of small trees at PI may have been a factor in the higher mortality observed at that site, because mortality generally increased with diameter in both study areas ([Figure 4](#)). The two stands also differed in the character of the mortality they suffered. At Pine Island, almost two-thirds of tree deaths were the result of bole breakage, and this percentage was even higher in size classes above 30 cm DBH. In contrast, uprooted and standing dead trees accounted for more than half of all hurricane-induced mortality at Lostman's Pines. In the >30 cm size classes at LP, where mortality was concentrated, uprooting was the most common cause of death. Uprooted trees were consistently among the tallest individuals in their diameter class, while the shortest pine trees in each diameter class were usually those which died as a result of bole breakage ([Figure 6](#)).

Tip-up extent, morphology, and development. The one-hectare plots at Pine Island and Lostman's Pines included 39 and 31 newly uprooted trees, respectively. LP pits were shallower and wider, but about the same length as those at PI ([Table 1](#)). Average pit area was therefore about 30% greater at LP (2.19 m²) than at PI (1.63 m²). In total, Hurricane Andrew-initiated pits scarred 0.64% of the rockland

surface at PI, and 0.68% at LP. Assuming a current mound:pit area ratio of one-third to one-half (based on our intensive tipup profiles), slightly less than one percent of the surface at each site was impacted by uprooting.

Table 1: Mean dimensions of tipup pits at Pine Island (39 pits) and Lostman's Pines (31 pits), in cm, May 1994. Standard deviations are in parentheses.

Pit Dimension	SITE	
	Lostman's Pine	Pine Island
depth	10.9 (5.8)	27.3 (7.6)
width	113.9 (57.2)	89.7 (37.0)
length	223.8 (121.4)	215.9 (80.5)

Bole diameter was positively associated with all three dimensions of pit size at both sites, though correlations with pit depth were not as strong as those with the two horizontal dimensions ([Figure 7](#)). Relationships between diameter and pit length and width were similar at PI and LP, but Pine Island trees created deeper tipup pits than LP trees of identical girth.

Pit and mound development over the 1994-96 period ranged from negligible to the complete release of all root-bound material after consumption of the tree root and bole in the prescribed fire ([Figure 8](#)). Depending on orientation of the root ball, any released rock and/or soil material either fell back into the pit or contributed to a growing mound of colluvium adjacent to the "hinge" of the tree (Beatty and Stone 1985). At Lostman's Pines, where most of the root-bound materials were mineral sediments, both infilling and mound-building were usually substantial, and were often nearly completed during the course of the study ([Table 2](#), [Figure 8](#)). In many cases, unfilled pit volume was largely a function of lost root biomass. At Pine Island, where the root mass frequently bore an attached load of medium-to-large rocks, infilling of the pit sometimes created positive relief, but was usually incomplete and uneven ([Table 2](#), [Figure 8](#)). Because of the coarse nature of the colluvial material, PI mounds were also uneven, with locally abrupt relief. Infilling at PI is limited by the lack of sediment and a effective mechanism to transport it (i.e., water movement).

Table 2: Mean change in depth (cm) for three substrate types in two tiup environments at Pine Island (PI) and Lostman's Pine (LP), May 1994-January 1997.

Site	Mineral Soil	PIT			MOUND	
		Litter	Rock	Mineral Soil	Litter	Rock
LP	2.4	0	0	5.0	0	0
PI	0.8	0.3	14	-0.2	-3.0	8.4

Plant species colonization of tipup microhabitats. Individual species frequencies in Pit, Mound, and Control plots at the two study areas in 1996 are listed in Appendices 1 and 2. A DCA ordination of a

joint data set indicated little overlap in species composition between the two study areas ([Figure 9](#)). PI and LP plots were entirely segregated from one another along Axis 1, which explained 12.8% of the observed variation in the species-site matrix. Of the 170 taxa sampled, 75 were exclusive to PI, 55 were found only in the LP plots, and 40 were common to both data sets. Because of the lack of overlap in plant community composition between sites, we ordinated plots within each study area separately ([Figures 10](#) and [11](#)). While no habitat type was entirely segregated in either ordination, Pit plots in the Pine Island ordination occupied the upper one-half of the diagram, and Control and Mound plots were intermixed in the lower half ([Figure 10](#)). At Lostman's Pines, Pit and Mound plots occupied opposite sides of the DCA diagram, and Control plots occupied an intermediate position in ordination space ([Figure 11](#)).

Table 3: Mean species richness, and mean proportion of occurrences among six growth forms in Control, Mound, and Pit plots at Pine Island (26 plots of each type) and Lostman's Pines (17 plots each). Shaded Pit or Mound categories differed significantly in number of species occurrences from associated Controls at $\alpha=0.05$.

Site/Microhabitat	Mean Species Richness	Fern	Frob	Graminoid	Shrub	Tree	Vine
Pine Island							
Control	23.46	4.75	38.36	21.48	15.57	7.05	12.79
Mound	12.54	10.12	31.9	14.11	15.03	12.27	16.56
Pit	25.73	11.06	36.02	18.98	15.1	7.32	11.51
Lostman's Pines							
Control	16.12	0.73	48.18	43.43	1.09	2.55	4.01
Mound	19.76	0.89	52.38	33.63	1.79	5.06	6.25
Pit	11.94	0.00	41.87	50.74	0.49	4.43	2.46

The June 1996 distribution of species among growth forms and microhabitats ([Table 3](#)) suggested several differences between the two study areas. For instance, mean species richness of Mound plots at Pine Island (12.54 species/plot) was about half that of Control and Pit plots at the same site (23.46 and 25.73 species, respectively), while LP Mounds had higher species richness (19.76 species/plot) than Control (16.12 species) or Pit environments (11.94 species). The between-site contrast in the relative suitabilities of Mound and Pit habitats for post-fire plant establishment was at least in part a result of hydrologic conditions in the fall and winter of 1995-96. During the very wet months which followed the May 1995 fire and continued through the following winter, tipup mounds at LP were frequently the only locations above water, while nearly all Pits were inundated by several inches of water. At Pine Island, standing water was rarely observed in any of the Pit locations during the period following the July 1995 fire, and Mound substrates were exposed and dry to the touch. The two study areas also differed in the background importance of ferns and woody or semi-woody growth forms. Depending on habitat, ferns, shrubs, trees, and vines together accounted for 40-54% of all species occurrences at Pine Island. At Lostman's Pines, forbs and graminoids were the dominant growth forms, and ferns and woody plants accounted for only 7-14% of total occurrences. G-statistics based on the proportions listed in [Table 3](#) indicated that site effects on growth form distribution were statistically significant ($p<0.01$, $df=5$) for all three microhabitats (Control, $G_{\text{adjusted}}=52.43$; Pit, $G_{\text{adjusted}}=64.54$; and Mound, $G_{\text{adjusted}}=60.43$; $G_{\text{crit}}=20.55$).

The analyses of variance indicate a statistically significant interaction of microhabitat and growth form at both sites (PI, $F_{10,250}=12.04$; LP, $F_{10,160}=6.09$). At Pine Island, all growth forms except trees exhibited significant habitat effects. Compared to Control plots, Mounds at PI supported significantly fewer occurrences of forb, graminoid, and shrub species, and Pit environments supported more ferns (Table 3). At Lostman's Pines, significant effects of habitat were only observed for forbs, trees, and vines. Individual contrasts at LP indicated that, in comparison to Control environments, Mounds were favorable locations for forbs and vines, and Pits were unfavorable for forbs (Table 3).

The microhabitat associations of individual species were examined by frequency analysis. Tables 4 and 5 list the significant ($p<0.01$) species associations. Because these lists were drawn from many individual comparisons, a few spurious relationships are very likely included.

At Pine Island, 14 species were positively associated with Pit habitats, and five were negatively associated with them (Table 4). Whereas only one of the Pit-associated species (*Tetrazygia bicolor*) was also included in the large (23 species) Mound-averse group, two Pit-associated taxa (*Pteris bahamense* and *Schinus terebinthifolius*) were among the three species which demonstrated a preference for Mounds over Control environments. Of the three most common species in PI pits (frequency > 75%), two (*Thelypteris kunthii* and *Pteris bahamense*) were ferns with frequencies of less than 5% in Control areas. Another Pit-associated species was *Pinus elliotii* var *densa*, the dominant tree in the rockland forests. No South Florida endemics were positively associated with Pit or Mound habitats at Pine Island, but two endemics (*Heterotheca graminifolia* and *Phyllanthus pentaphyllus*) were negatively associated with these disturbed environments.

In contrast to the many Mound-averse species identified at Pine Island, Lostman's Pines had none (Table 5). Instead, eight LP species were classified as Pit-averse, i.e., more than any other category. This list included one endemic plant (*Dyschoriste oblongifolia*). Mounds at LP provided a favorable environment for seven herbaceous species, including two South Florida endemics (*Evolvulus sericeus* and *Chamaesyce porteriana*). Despite the wet conditions described earlier for LP Pits, five Pit-associated species were identified, including four graminoids and one wetland tree (*Annona glabra*).

Spatial variation in substrate and vegetation along transects. Soil depth averaged 20-23 cm along the Lostman's Pines transects, and only 5-6 cm at Pine Island (Table 6). Compared to PI, variability in soil depth at LP was lower on the basis of coefficient of variation, higher on the basis of standard deviation. We consider c.v. to be the more appropriate metric in this case. However, the coefficient of variation was not the proper measure of variability in surface elevation, because benchmarks at the two sites were assigned arbitrary data. Based on standard deviations, PI exhibited about twice the variation in surface elevation as LP (Table 6).

Table 6: Soil depth and relative surface elevation along three transects at Pine Island and Lostman's Pines (refer to Figure 3 for locations). Elevations are relative to a single benchmark with arbitrarily assigned elevation at each site. Values are means of 91-153 measurements at 0.3 m intervals. Standard deviations are in parentheses.

Site	Transect	Soil Depth (cm)	Relative Surface Elevation (m)
Lostman's Pine	L-31	20.6 (15.0)	0.440 (0.034)
	L-100	23.0 (11.8)	0.360 (0.030)

	L-150	21.2 (12.5)	0.431 (0.037)
	P-25	6.7 (5.6)	0.969 (0.056)
Pine Island	P-105	5.3 (6.2)	0.819 (0.085)
	P-185	5.9 (6.2)	0.688 (0.070)

CCA analyses of the PI and LP transect data, with Elevation and Soil Depth as environmental variables, are illustrated in Figures [12A](#) and [12B](#). While the two canonical axes explained a very small proportion of the total variation in plant species presence/absence in 0.3 X 0.3 m quadrats (3.2% and 1.2% at PI and LP, respectively), permutation tests for both data sets indicated significant relationships between plant species composition and the measured environmental variables. Of the two, Elevation had the stronger effect at both sites (note vector lengths in Figs. 12A and 12B). However, species' positions within these ordinations exhibited little or no relationship to those which might be expected on the basis of the habitat affinities identified in Tables [4](#) and [5](#). For instance, if observed positive association with Pits or negative association with Mounds resulted from topographically-related factors, species which exhibited such habitat preferences ought to have clustered in the low-elevation half of the CCA species-environment biplots. Instead, the large groups of species with these characteristics at Pine Island formed a loose swarm centered on the origin of [Figure 12A](#). Other species groups also clustered around the origin of their site's ordination diagram (Figs. [12A](#) and [12B](#)), indicating an absence of consistent within-group preferences with respect to Elevation or Soil Depth.

Elevation indices for the major species at Pine Island ([Table 7](#)) and Lostman's Pines ([Table 8](#)) were also derived from the transect data. Each species' index was its score on Axis 1 of the CCA, when Elevation was included in the analysis as the single environmental variable, and Soil Depth was a covariate. At Pine Island, species preferences ranged from *Verbena maritima* at high elevations to *Panicum virgatum* at low; at Lostman's Pines, the high and low poles were represented by *Vernonia blodgettii* and *Asclepias lancifolia*, respectively. *Cladium jamaicense*'s association with high elevations at LP was probably a result of post-fire flooding and consequent mortality at low elevations. In general, a wide range of elevation preferences was observed within most of the PI and LP growth forms. For instance, among the tree species occurring in three or more Pine Island quadrats, *Quercus virginiana* was associated with high elevations, *P. elliotii* var *densa* with medium elevations, and *Schinus terebinthifolius* with low elevations. Only two tree species were sufficiently frequent to be indexed at Lostman's Pines, and both *P. elliotii* var *densa* and *Ilex casseine* were associated with moderately high elevations.

Consideration of spatial variation in plant species composition along individual transects lead to the conclusion that all six exhibited a *transitional* spatial structure (Isaaks and Srivastava 1989), i.e., point-to-point variation increased with increasing distance until a demonstrable plateau was reached. Thus, the variograms were generally well-fit by the exponential model (R^2 values ranging from 85- 91%), which approached an asymptote within the 60-unit separation distance. However, the distance within which this asymptote, or sill, was reached (the *practical range*) varied broadly. For example, the variogram of Transect L-150 ([Figure 13B](#)) had a relatively steep initial slope, reaching a sill of 0.31 within only 15 units ([Table 9](#)). In contrast, Transect P-105 ([Figure 13A](#)) approached its sill of 0.42 more gradually, and this was reflected in a longer range of 32 units ([Table 9](#)). In flat curves like the latter, the dissimilarity predicted by the exponential model at lag 1 (the *nugget*) sometimes exceeded the observed value by a considerable margin. Both steep and flat variograms were observed at either site; practical ranges at PI varied from 12 to 41 units, and at LP from 15 to 40 units. However, PI variograms had higher sills than

those of their LP counterparts, and were also characterized by slightly wider differences between nugget and sill dissimilarity ([Table 9](#)). Finally, several variograms at each site, including the two illustrated in [Figure 13](#), exhibited secondary patterning around the exponential line, suggestive of periodic repetition of compositional units along the transect.

Table 9: Parameters of variograms based on species composition in contiguous 0.3 x 0.3 m quadrats on six transects. The **nugget** is defined as the dissimilarity predicted by the best-fit-exponential model at a lag distance of 1 unit, the **sill** as the model value at lag 60, and the **practical range** as the lag distance at which the model dissimilarity equals the nugget plus 95% of the difference between nugget and sill. See Figures [13A](#) and [13B](#) for examples.

Site	Transect	Nugget	Sill	Practical Range
Pine Island	P-25	0.249	0.345	11.65
	P-105	0.313	0.421	32.25
	P-185	0.326	0.404	40.52
Lostman's Pines	L-31	0.264	0.329	39.79
	L-100	0.238	0.314	25.54
	L-150	0.248	0.313	14.53

Distinct compositional structuring within transects at both sites was revealed via the moving split-window procedure ([Figures 14A-F](#)). Four, five, and four major peaks were recognized in Pine Island Transects P-25, P-105, and P-185, and three, five, and five peaks in Lostman's Pines Transects L-31, L-100, and L-150. Interpeak distances at Pine Island and Lostman's Pines were similar [Pine Island: mean=23.9 quadrats, s.d.=11.0, n=11; Lostman's Pines: mean=25.1 quadrats, s.d.=8.9, n=11]. It should be recognized, however, that the mean size of the compositional units bounded by these peaks (*ca* 7-8 meters) is strongly scale-dependent, decreasing at smaller window sizes and becoming larger as window size is increased.

CCA analyses based on 15 and 16 such units (including end units comprised of three quadrats or more) are illustrated for Pine Island and Lostman's Pines in [Figures 15A and 15B](#). Total variance in the Species x Site matrix at PI was about twice that of LP, and the percentage explained by the two canonical ordination axes was also slightly higher (28% v. 22%). In both cases, this percentage was more than eight times that explained by the canonical axes for the CCA analyses based on individual quadrats (i.e., [Figures 12A and 12B](#)).

At Pine Island ([Figure 15A](#)), the three transects were for the most part separated from one another along Axis 1, which was closely associated with Elevation. In contrast, within-transect variation at Pine Island ran perpendicular to the Elevation vector and parallel to the Soil Depth vector. Transects P-25 and P-185 generally tracked from a shallow-soil to a deep-soil-associated end, but Transect P-105 exhibited little soil-related variation. The permutation test indicated that both Elevation and Soil Depth were significantly ($p=0.01$) related to the composition of the 15 Pine Island vegetation units.

As at Pine Island, Elevation was closely associated with Axis 1 of the Lostman's Pines CCA ordination ([Figure 15B](#)). Again, most among-transect variation was arranged along Axis 1, with Transect L-100 at its low-elevation end and Transects LN and LS together at the high- elevation end. As

before, within-transect variation at Lostman's Pines was largely perpendicular to the Elevation vector and parallel to the vector for Soil Depth. Unlike Pine Island, where the permutation test confirmed the association of both environmental variables with plant species composition, only Elevation exhibited a significant relationship at Lostman's Pines ($p=0.01$), while Soil Depth did not ($p=0.18$).

Much of the variation in elevation and soil depth in our two study areas appeared to be associated with old tipups. Their distribution and extent are summarized in [Table 10](#) and Appendix 3 ([A](#), [B](#), [C](#), [D](#), [E](#), & [F](#)). Nearly 75% of the area along the three Pine Island transects exhibited a substrate morphology indicative of origin in the past uprooting of a tree. At Lostman's Pines, the percentage similarly affected (57%) was also substantial. In contrast, karst processes were evident along only 15% and <1% of the length of the PI and LP transects, respectively. These percentages appear to contradict expectations regarding the relative importance of bioturbation and karstification as erosional processes in limestone settings (Brooks 1967).

Table 10: Occurrence of geomorphic features along transects at Pine Island (PI) and Lostman's Pines (LP). Individual transects profiles are illustrated in Appendix 3 ([A](#), [B](#), [C](#), [D](#), [E](#), & [F](#))

Site	Transect		Current Tipups		Relict Tipups		Karst Features		Undisturbed Bedrock
	ID	Length	Number	Length	Number	Length	Number	Length	Length
LP	L-31	50 m	0	0 m	15	27.1 m	13	8.9 m	14 m
	L-100	50 m	0	0 m	22	32.9 m	9	7.0 m	10 m
	L-150	50 m	0	0 m	14	25.0 m	11	7.2 m	17.8 m
	P-25	40 m	1	1.9 m	17	20.7 m	0	0.0 m	7.4 m
PI	P-105	40 m	0	0 m	18	29.7 m	3	0.6 m	9.7 m
	P-185	40 m	0	0 m	16	29.1 m	0	0.0 m	10.9 m

We applied DCA analysis to sites categorized as old pits, old mounds, or background substrates which bore no evidence of past uprooting. The data were species presence/absence in the 400+ individual quadrats arrayed along the transects at each site. Unlike the habitat segregation demonstrated in the analysis of fresh substrates (Figures [10](#) and [11](#)), the ordination pictured in [Figure 16](#) indicates a virtually complete compositional overlap among the three paleoenvironments at both sites.

DISCUSSION

In forested settings, disturbance-related canopy mortality creates light gaps of variable size, thereby permitting the establishment of a range of tree species, and sometimes enhancing species diversity (Denslow 1980; Runkle 1984). A second element of environmental heterogeneity is added when these mortality events also include the wholesale dislodging of the root mass of large trees. In such cases, the microtopography and mineral soil exposure at the base of the fallen stems may comprise ecologically significant edaphic niches for specially-adapted plant species (Hutnik 1952; Thompson 1980; Beatty 1984). When the disturbance event is a major windstorm, these sites may be widespread and areally important; in our study areas, for instance, pits and mounds created by Hurricane Andrew accounted for about 1% of the ground surface of the two study plots. Their dynamic nature was also evident, as root

masses slumped measurably, creating colluvial mounds, and pits partially infilled over the two-year period between our initial and final surveys. Though they remained recognizable features responsible for much of the variation in surface elevation and soil depth in the rockland, our surveys indicated that pits and mounds continued to moderate over longer time periods. Interactions between plant species and pit/mound habitats followed a parallel course. While a number of species were strongly associated with one or the other of these environments during the immediate post-hurricane years, old pits and mounds did not maintain distinct assemblages with the passage of time. Moreover, spatial analyses suggested that the most important scale of variation in species composition was somewhat coarser than the 1-3 meter scale represented by the tipup features. Apparently, while tree uprooting plays a dominant role in creating the rockland landscape, the consequences of individual tipups on species distributions are more ephemeral, and in time become difficult to detect against background variation. Nevertheless, the strength of these transitory associations suggests their potential to influence the abundance or even survival of local plant populations. Below we discuss these issues in more detail.

Plant assemblages on tipup substrates following Hurricane Andrew

Species richness. Post-hurricane plant community development in newly-created pit and mound environments followed opposite trajectories in the two study areas. At Pine Island, mean species richness was higher in pits (and control sites) than on mounds, while at Lostman's Pines, mounds were the most speciose habitat and pits the least (Table 3). While these patterns are to some extent specific to the hydrologic conditions and fire management activities which took place during the study period, they are probably fairly representative of the relative responses of the two communities during wet years, which occur periodically under the current water management system, and were certainly more frequent during the pre-drainage era (Fennema et al. 1994). The high water condition during the winter of 1995-96, which made deep pools of pits at LP, while barely (and rarely) inundating PI pits, was a physical factor that may have had a role in these responses, by allowing mesic plants which survived the fire or germinated soon thereafter to persist in PI pits, but not in LP pits. Another factor was the finer-textured sediment of the LP mounds, which may have provided more moisture for plant germination and establishment than the rock, rubble, and root which made up the typical PI tipup mound. As much as anything, the contrasting responses we observed at PI and LP illustrate the wide functional variation encompassed under the category 'South Florida pine forests'. Variants range from wet, sandy, herb-dominated communities like LP, through mixed-form assemblages such as we studied at PI, to xeric Florida Keys pine rocklands in which the forest understory is dominated by woody species. Our current research suggests that pit and mound features have different ecological meaning depending on a community's position within this hydrologic and edaphic spectrum.

Most studies of regeneration in tipup environments have been carried out in temperate forests, where mounds are generally favorable and pits unfavorable microsites (Goodlett 1954, Denny and Goodlett 1956, Goder 1961, Lyford and MacLean 1966, Collins and Pickett 1982). Tipup mounds in temperate forests frequently provide a relatively warm, well-aerated seedbed for freshly-exposed seed from a long-lived seedbank, while pits are cold and wet locations which develop thick litter layers that smother small-seeded germinants. As in our subtropical pine forests, however, the suitability of the two seedbeds in temperate environments varies with edaphic context and the ecology of individual plant species. For instance, pits in northern hardwood forests may provide superior moisture conditions in rocky or excessively-drained soils (Cook 1971), and the rapid accumulation of litter in these depressions favors the establishment of large-seeded species of maple or beech under some conditions (Hutnik 1952, Henry and Swan 1974, but see Webb 1988).

Species composition. In our study, pits were occupied by distinct plant species assemblages during the immediate post-hurricane years, especially at Pine Island (Figures 10 and 11). PI pits were characterized by a mixed assemblage of all growth forms, but ferns, especially *Thelypteris kunthii* and

Pteris bahamense, were most prominent (Tables 4 and 5, Appendix 1). *T. kunthii* was most abundant in the relatively cool, shaded zone at the base of the upturned PI root slabs, less prevalent in more exposed positions within the pits, and rarely found on either the xeric mounds or in the control environment. *P. bahamense* was less specific with respect to position within the pits, and was also more common on mounds than in undisturbed locations. While ferns are known to respond rapidly to disturbance types which expose mineral or rock substrates, they vary widely in their moisture requirements (Lellinger 1985). Koop (1981) singled out *Thelypteris phlegopteris* and *T. dryopteris* as species characteristic of tipup mounds in beech-hornbeam forests in Germany.

By virtue of their elevated topographic position, mounds at Lostman's Pines provided a refuge for a number of mesic plants during the prolonged high water conditions of 1995-96 (Table 5, Appendix 2). As a group, however, the species composition characteristic of LP mounds was not clearly distinguishable from that found outside the areas directly affected by uprooting (Figure 11). In most of the other studies cited in the previous section, the plant species which exhibited an affinity for tipup mounds were trees or shrubs. In contrast, the only woody plant at LP to demonstrate a microhabitat preference for either pits or mounds was *Annona glabra*, a swamp forest species whose frequency was highest in pits. One possible explanation for this difference is that many of the earlier studies assessed microhabitat preferences on the basis of the distribution of adult trees many years after the initiating disturbance, and therefore reflect not only initial establishment but long term survival. These are not necessarily correlated with one another, however. In wetland or transitional upland settings exemplified by the pine forests we studied, microsites which provide favorable conditions under very wet conditions may be unfavorable during drought years, and vice versa. Based on climatic records, both extremes of hydrology are likely to occur at least a few times during the lifetime of a canopy tree. *P. elliottii* var *densa*, the lone canopy dominant in the sites examined, demonstrated an early affinity for pits at PI; in contrast, pine seedlings were most frequent on LP mounds during the wet years after Hurricane Andrew, but the effect was non-significant (Appendices 1 and 2). Only time will tell whether the patterns observed over the period of our study will hold up over the longterm. Most of the adult pine trees at both sites were rooted at the apex of a conspicuously raised surface, which appeared in most cases to be elevated as a result of the displacement of rock by the developing tap root. These raised surfaces may represent significant edaphic microsites in their own right when tree mortality is not accompanied by uprooting, but post-hurricane colonization of such locations was not addressed in this study.

Our results demonstrate a strong connection between biological diversity and heterogeneity in the physical environment of South Florida pine rocklands. The separation of tipup pits (and to a lesser extent, tipup mounds) from control sites in Figures 10 and 11 suggests that in the first few years after disturbance, a group of species which are uncommon elsewhere in the pine forest are able to thrive in these fresh substrates. Though none of the associations are obligate, their net result is to increase overall plant community diversity. Among the species which demonstrated a strong association with tipup features, none are currently listed as endangered or threatened, but several are endemic to South Florida pine rocklands (Tables 4 and 5). As a group, they are disturbance specialists in a community of disturbance-adapted plants. Restoration efforts whose aim is to reestablish the full complement of rockland species will need to consider the type of microsite variation which sustain such plants at the scale demonstrated in this study.

Background variation in pine forest plant species composition

The scale of compositional variation within stands. We used two methods to examine spatial structuring in plant species composition in our study areas. One method was to construct a variogram, based on compositional variation among pairs of small plots separated by fixed distances along long transects. This approach has not been used extensively with plant community data, though variogram model-fitting has recently become a popular tool in assessing pattern in environmental or biological

variables, usually considered one at a time (Robertson 1987, Jackson and Caldwell 1993a, Schlesinger et al. 1996, Robertson et al 1997). Jackson and Caldwell (1993b) developed a singular variogram model for a multivariate data set by combining the effects of four soil variables into a single index. For our multivariate, presence-absence data sets, we found it most appropriate to substitute mean dissimilarity (PD) for the semivariance on which standard variograms of univariate metrics are based. Our second method of describing spatial structure was more direct. We used a moving split window algorithm to identify sharp breaks in species composition along the transects, then examined the distribution of sizes among the composite "natural" units between breaks. While there was considerable variation among sites and transects within a site, both approaches identified substantial spatial patterning at a scale larger than the individual 0.09 m^2 quadrat, but smaller than the transects as a whole.

Our variograms indicated that all six transects exhibited a transitional structure, i.e., compositional variation among plots increased with distance, but ultimately reached a plateau (Figures [13A](#) and [13B](#)). The distance effect was substantial along our transects, with among-plot dissimilarity at plateau distance or beyond generally 120%-140% of variation at 30 cm distance, the smallest distance considered ([Table 9](#)). The practical range, or distance at which the plateau was reached, varied between 4 and 14 meters ([Table 9](#)). We interpret the practical range to be an indication of the dominant scale of patchiness within the pine forest understory community. What process or forcing factor might be responsible for variation at this scale? One possibility that may be invoked on scale considerations alone is structure within the slash pine canopy itself. These very open forests sometimes include sections which have thinned to a density of 80 large trees per hectare or less (Ross unpublished data). Assuming the site was still fully occupied at this late stage of development, the average tree would have a zone of influence of 125 m^2 , which equates to a diameter of 12.6 meters. Oldeman (1990; p. 155) defined an eco-unit as "...the unit of vegetation which started its development at the same moment and on the same surface." By Oldeman's view, eco-units are initiated following the death of a dominant canopy tree, and continue to develop through regeneration, juvenile, mature, and senescent phases. While an eco-unit may fragment or coalesce with an adjacent unit, all portions tend to share a common history and environment, affected profoundly by the developing canopy. Perhaps the dominant scale of variation evident in our variograms of understory species composition was in part a reflection of the eco-unit structure of the two study areas.

The moving split window analyses ([Figures 14A-F](#)) broadened the results of the variogram models regarding scale in an important way: they demonstrated that the spatial structure along the transects was not continuous, but was in fact arranged in discrete compositional units separated by distinct borders. These units averaged 7-8 meters in size (which is consistent with the variogram results), but varied widely, from about 3 meters ([Figure 14B](#)) to nearly 15 meters ([Figure 14E](#)). The variogram models average out this patch size variation in searching for broad trends, while the split window procedure focuses directly on it. We are probably safe in suggesting that there are a number of disturbance types, environmental conditions, or biological interactions in South Florida pine forests which can and do combine to produce patches of relatively uniform vegetation in our study areas. While these combinations may lead to a range of patch sizes, we think the frequency of patches in the 5-15 meter range suggest the operation some underlying organizing principle, perhaps the eco-unit concept discussed above.

Effects of measured environmental variables. Our data indicated that rockland species composition was affected by both elevation and soil depth. However, the relative effects of the two variables on species composition appeared to be scale-specific. Elevation was the better overall predictor of plant species composition in either individual or composite plots. However, canonical correspondence analysis based on the composite units ([Figures 15A and 15B](#)) indicated that elevation was most strongly associated with coarser-scale effects, i.e., differences among transects, while soil depth was a more

important source of variation within individual transects.

The percentage of total compositional variation explained by the two variables ranged widely, depending on the site and the scale considered. The latter was again a particularly important consideration. At Pine Island, the percentage of total variance explained by the two environmental variables was 9X higher when the data were species frequencies in composite "natural" units defined by the moving split-window technique *cf* species presence/absence data in individual 0.09 m² plots. The pattern was similar at Lostman's Pines, where the percent of compositional variation explained was nearly 20 times higher at the coarser scale. Perhaps spatial structuring of rockland plant populations into smaller subpopulations overrides and obscures physical effects at the finest scale considered in this study. We are not aware of other studies which have addressed scale effects on the environmental correlates of plant species composition. It does appear to us that compositional patterning within pine rocklands or elsewhere is the result of a tension between physical conditions and biological relationships, the former becoming more evident and the latter weakening with distance.

Residual effects of pits and mounds. Pit and mound features remained recognizable for many years after their formation. From a plant's eye view, these weathered surfaces were not equivalent to the fresh substrates which provided uncommon microhabitats for a subset of the rockland flora, however. Our data showed conclusively that the species assemblages rooted in old pits and mounds were no longer distinct from the vegetation around them ([Figure 16](#)). Considering that most of these features had been undergoing physical and chemical weathering, as well as biological succession, for decades or longer, this is not a surprising result. As discussed earlier, species successful at colonizing fresh pits or mounds may be adapted to special conditions of nutrient or moisture availability, seedbed nature, and/or intensity of competition which are characteristic of the recently disturbed tipup environments. As time passes, these disturbed conditions moderate or approach the norm found in undisturbed areas. As indicated in our tipup profiles ([Figure 8](#)), return toward an equilibrial condition probably occurs rapidly at first. However, the equilibrium these features approach is one to which the uprooting process has contributed over many centuries. Relicts of past uprooting events in fact composed the majority of the background rockland surface; more than half the length of our six transect lines were identifiable as old pits or mounds ([Table 10](#)). While these features no longer supported distinct plant assemblages, the uprooting process which created them was responsible for a substantial proportion of the observed variation in elevation and soil depth, i.e., environmental factors along which plant species appeared to arrange themselves, at coarser and finer scales, respectively ([Figures 15A and 15B](#)). Thus, if the direct effects of individual pit and mound features become more diffuse with time, the longterm effects of tree uprooting are already woven into the fabric of the rockland vegetation, through the creation of ecologically significant edaphic heterogeneity, and through the establishment of beachheads from which new plant subpopulations may spread.

CONCLUSION

Depending on their location, South Florida pine forests are more or less susceptible to a range of climatically-induced disturbances, including drought, flood, fire, freeze, storm tide, and hurricane winds. Of these, fire has rightfully received the most attention as a determinant of stand structure and composition. Fire is of course the constant companion of virtually all pine forests, and the development of fire as a management tool in pine forests has, on balance, been a great success story. Nevertheless, in hurricane-prone South Florida, no ecosystem description is complete without consideration of the impacts of hurricanes, and pine rocklands are no exception.

Among the disturbances listed above, hurricanes have the greatest capacity to produce changes in the rockland surface, through the uprooting process we have described. The soil and topographic variability

created and maintained through many generations of high-wind events become a template which modifies the effects of floods, droughts, fires, even freezes. A fall tropical storm pools water in Depression A, barely saturates the soil profile in adjacent Mound B. The effects of a subsequent dry year are moderated in A, exacerbated in B. A fire which reaches incinerating temperatures on Mound B fails to burn in Depression A. The results described in this report have identified and described fine-scale variation in rockland understory vegetation. The uprooting of trees during storms like Hurricane Andrew may contribute to this variation through direct and/or indirect pathways.

LITERATURE CITED

Armson, K. A. and R. J. Fessenden. 1973. Forest windthrows and their influence on soil morphology. *Soil Science Society of America* 37: 781-783.

Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65: 1406-1419.

Beatty, S.W. and E.L. Stone. 1985. The variety of soil microsites created by tree falls. *Can. J. For. Res.* 16:539-547.

Brooks, H.K. 1967. Rate of solution of limestone in the karst terrane of Florida. Publ 6. Florida Water Resources Research Center. OWRR Project Number A-004-FLA, 16p.

Collins, B. S. and S. T. A. Pickett. 1982. Vegetation composition and relation to environment in an Allegheny hardwoods forest. *Am. Midl. Nat.* 108: 117-123.

Cook, B. D. 1971. Tree age distributions in a northern hardwood forest M. Sc. Thesis, McGill University, Montreal, Canada.

Denny, C. S. and J. C. Goodlett. 1956. Microrelief resulting from fallen trees. pp. 59-68 In: *Surficial geology and geomorphology of Potter County, Pennsylvania*. USGS Prof. Paper 288. 68 p.

Denslow, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46: 18-21.

Doren, R. F., W. J. Platt, and L. D. Whiteaker. 1993. Density and size structure of slash pine stands in the everglades region of South Florida. *For. Ecol. and Mgt* 59: 295-311.

Duever, M.J., E.J. Carlson, J.F. Meeder, L.C. Duever, L.H. Gunderson, L.A. Riopelle, T.R. Alexander, R.L. Myers, and D.P. Spangler. 1979. *Resource Inventory and Analysis of the Big Cypress National Preserve*. National Audubon Society Monograph Series 4, New York, New York.

Fennema, R. J., C. J. Neidrauer, R. A. Johnson, T. K. MacVicar, and W. A. Perkins. 1994. A computer model to simulate natural Everglades hydrology. pp 249-289 in *Everglades: the ecosystem and its restoration*. S. M. Davis and J. C. Ogden, eds. 826 p. St. Lucie Press, Delray Beach, FL.

Goder, H. A. 1961. Hemlock reproduction and survival on its border in Wisconsin. *Trans. Wisc. Acad. Sci. Arts Lett.* 50: 175-182.

Goodlett, J. C. 1954. Vegetation adjacent to the border of the Wisconsin drift in Potter County,

Pennsylvania. *Harvard For. Bull.* 25: 1-93.

Henry, J. D. and J. M. A. Swan. 1974. Reconstructing forest history from live and dead plant material --- an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55: 772-783.

Hutnik, R. J. 1952. Reproduction on windfalls in a northern hardwood stand. *Journal of Forestry* 50: 693-694.

Isaaks, E. H. and R. M. Srivastava. 1989. An introduction to applied geostatistics. Oxford University Press, New York. 561 p.

Jackson, R. B. and M. M. Caldwell. 1993a. The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. *Ecology* 74: 612-614.

Jackson, R. B. and M. M. Caldwell. 1993b. Geostatistical patterns of soil heterogeneity around individual perennial plants. *Journal of Ecology* 81: 683-692.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren, eds. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK. 299 p.

Koop, H. 1981. Vegetatiestructuur en dynamiek van twee natuurlijke bossen: het Neuenburger en Hasbrucher Urwald. Centrum voor Landbouwpublicaties en Landbouwdocumentatie. (Dutch, with English summary).

Leighty, R. G., M. H. Gallatin, J. L. Malcolm, and F. B. Smith. 1965. Soil associations of Dade County. Florida Inst. Food Agric. Sci. Exp. Sta. Circ. S-77A. University of Florida, Gainesville, FL.

Lellinger, D. B. 1985. A field manual of the ferns and fern-allies of the United States and Canada. Smithsonian Institution Press, Washington, D. C., USA. 389 p.

Ludwig, J. A. and J. M. Cornelius. 1987. Locating discontinuities along ecological gradients. *Ecology* 68: 448-450.

Lutz, H. J. 1940. Disturbance of forest soil resulting from the uprooting of trees. Yale University. School of Forestry Bull. No. 45. 37 p. + figs.

Lyford, W. H. and D. W. Maclean. 1966. Mound and pit micro relief in relation to soil disturbance and tree distribution in New Brunswick, Canada. *Harvard Forest Paper* No. 15.

Oldeman, R. A. A. 1990. Forests: elements of silvology. Springer-Verlag, Berlin. 624 p.

Orians, G. H., W. Dunson, J. Fitzpatrick, D. Generoux, L. Harris, M. Kraus, and R. E. Turner. 1996. Ecological assessment of the 1994-95 highwater levels in the Everglades. Report of an expert panel to the Scientific Sub-group of the South Florida Ecosystem Restoration Working Group. 21 pp. + figs.

Pielou, E. C. 1977. Mathematical ecology. Wiley, New York, NY. 385 p.

Powell, M. D. and S. H. Houston. 1996. Hurricane Andrew's landfall in South Florida. Part II: Surface wind fields and potential real-time applications. *Weather and Forecasting* 11: 329- 349.

- Robertson, W. B. 1955. An analysis of the breeding-bird populations of tropical Florida in relation to the vegetation. Ph.D. Dissertation, University of Illinois. 599 p.
- Robertson, G. P. 1987. Geostatistics in ecology: interpolating with known variance. *Ecology* 68: 744-748.
- Robertson, G. P., K. M. Klingensmith, M. J. Klug, E. A. Paul, J. R. Crum, and B. G. Ellis. 1997. Soil resources, microbial activity, and primary production across an agricultural ecosystem. *Ecological Applications* 7: 158-170.
- Runkle, J. R. Development of woody vegetation in treefall gaps in a beech-sugar maple forest. *Holarctic Ecol.* 7: 157-164.
- Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77: 364-374.
- Shaler, N. S. 1891. The origin and nature of soils. Twelfth Annual Report, U.S. Geological Survey. pp. 213-345.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*. Freeman, San Francisco, USA. 877 p.
- StatSoft, Inc. 1995. *STATISTICA for Windows (Volume III): Statistics II*, 2nd Edition.
- Stephens, E. P. 1956. The uprooting of trees: a forest process. *Soil Science Society of America Proceedings*. pp. 113-116.
- ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.
- Thompson, J. N. 1980. Treefalls and colonization patterns of temperate forest herbs. *Am. Midl. Nat.* 104: 176-184.
- Webb, S. L. Windstorm damage and microsite colonization in two Minnesota forests. *Can. J. For. Res.* 18: 1186-1195.
- Webster, R. 1973. Automatic soil-boundary location from transect data. *Mathematical Geology* 5: 27-37.
- Whitaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279-338.
- Wierenga, P. J., J. M. H. Hendrickx, M. H. Nash, J. Ludwig, and L. A. Daugherty. 1987. Variation of soil and vegetation with distance along a transect in the Chihuahuan Desert. *Journal of Arid Environments* 13: 53-63.