Journal of Tropical Ecology (2004) **20**:173–181. Copyright © 2004 Cambridge University Press
DOI: 10.1017/S026646740300124X Printed in the United Kingdom

Understorey fern responses to post-hurricane fertilization and debris removal in a Puerto Rican rain forest

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(*Accepted 26 March 2003*)

Abstract: Controls over net primary productivity are the subject of a long-term experiment within a lowland subtropical wet forest in the Luquillo mountains of Puerto Rico. Responses of the fern community to fertilization and debris-removal treatments and to monitoring activities were assessed 6 y after the experiment began in October 1989, just after the passage of Hurricane Hugo. Negative fern responses to fertilization included a qualitative change in species composition and a 13-fold reduction in density compared with controls. Plants were smaller and spore production rates were lower. Debris removal reduced the number of species and increased the proportion of terrestrial species. Density of *Nephrolepis rivularis* individuals in debris-removal plots was only 5% that of control levels while abundance of *Thelypteris deltoidea* nearly doubled. Buffer-zone fern density was 36% greater than and per cent of leaves damaged was half that of the monitored zones. The magnitude of the responses of ferns to experimental treatments and to monitoring effects suggest that they may be good early indicators of change in a tropical forest.

Key Words: diversity, ferns, herbaceous layer, litter, productivity, pteridophytes, Puerto Rico, tropical forest

INTRODUCTION

Long-term ecosystem studies provide an opportunity to explore the implications of unexpected and often intriguing preliminary results. Such a long-term study to examine controls on above-ground primary productivity in a lowland subtropical wet forest was begun in Puerto Rico just after the passage of Hurricane Hugo in 1989. These experiments are ongoing, however several results for the first 4 y of the study were summarized by Walker *et al.* (1996). Post-hurricane fertilization treatments resulted in greater biomass accumulation in standing litter and slightly higher increases in tree diameters as compared to controls. However, another interesting observation was that the live biomass of ferns in the herbaceous understorey of fertilized plots was much lower than in the controls. Though debris-removal treatments also resulted in higher biomass totals, tree diameters increased at a lower rate compared with controls and fern biomass totals were much higher than controls (Walker *et al.* 1996). In addition, during the first 4 y of monitoring, % fern cover showed a gradual decline in plots receiving regular fertilization treatments (Walker *et al.* 1996).

These general observations of low fern biomass and declining fern cover in the fertilized plots (Walker *et al.* 1996) led us to conduct a more detailed examination of the fern community 6 y after the initiation of these experiments. A much earlier survey of the general ridgetop area of El Verde near the location of these experiments had identified 35 species of fern exhibiting a variety of habitat requirements and size parameters (Smith 1970). Therefore, several responses to the experimental treatments within the fern community could have resulted in the negative biomass and reduced cover results observed in the fertilized plots. Fern abundance could have decreased while the species mix stayed the same. Alternatively, abundance may have remained the same with a change in fern species composition such that species with smaller individuals had replaced species with larger individuals. Smaller plant sizes may have resulted from limitations on individual plant growth or replacement of older plants with younger

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individuals. The increases in fern biomass and cover observed for the debris-removal treatment (Walker *et al.* 1996) could also have resulted from changes in abundance, species mix or plant sizes. Changes in the environment caused by experimental treatments may also be inferred from more detailed observations of the fern community.

Monitoring of these long-term experiments was frequent and limited to the central area of experimental plots (Walker *et al.* 1996). Ferns occupy the lowest level of the forest, therefore trampling by researchers and data collectors could have a significant negative effect on the fern community unless access to the herbaceous layer is restricted. Therefore, we felt it would also be important to compare the fern community in the intensely monitored central zone with the surrounding buffer zone of the plots.

Ferns do occur in the understorey of rain forests in numbers that could provide the basis for quantitative evaluation of a variety of experimental treatments. Whitmore *et al.* (1985) found that ferns constitute 56% of the species and 90% of the terrestrial herb component of a lowland Costa Rican rain forest; at Barro Colorado, ferns accounted for 39% of the species of understorey herbs (Croat 1978). In a study in Ecuador, 26% of the terrestrial species were ferns (Poulsen & Balslev 1991) while in the Luquillo forest of Puerto Rico, ferns can constitute 34% of the species rooted in the herbaceous layer (Chinea 1999). Other studies have found that ferns may be sensitive indicators of microhabitat differences. Siccama *et al.* (1970) found that the understorey vegetation at Hubbard Brook, including specific ferns, played an important role in understanding edaphic gradients. Several recent studies in the Amazonian tropics have detected a role for ferns as indicator species for soil types (Ruokolainen *et al.* 1997, Tuomisto & Poulsen 1996, 2000; Tuomisto & Ruokolainen 1994, Tuomisto *et al.* 1995, 1998; Van der Werff 1992), however these studies have not linked ferns to productivity.

The objectives of this research were to: (1) compare the effects of experimental treatments on fern species composition and abundance; (2) examine how selected plant and leaf size characteristics of specific ferns contributed to general fern cover and biomass differences previously observed; (3) relate fern responses to observable differences in habitat characteristics for each treatment; (4) evaluate the effects of the experimental monitoring process on the fern community.

METHODS

Study area and experimental design

This study was conducted in a tropical wet forest at the El Verde Field Station (18°19′N, 65°49′W) in the Luquillo Experimental Forest of Puerto Rico (Reagan & Waide 1996). El Verde is a field station with a 70-ha research forest that is 350–500 m asl. The tabonuco tree, *Dacryodes excelsa* Vahl (Burseraceae) and sierra palm, *Prestoea montana* (R. Grah.) Nichols (Arecaceae) dominate the forest canopy. Mean annual precipitation is 3500 mm and mean temperature is 22.1 °C (Brown *et al.* 1983). Soils of the area are a complex of upland ultisols and oxisols and are mostly well-drained clays and silty clay loams (Soil Survey Staff 1995).

Puerto Rican ecosystems are influenced by periodic passages of hurricanes. In September of 1989, Hurricane Hugo passed over north-eastern Puerto Rico where the El Verde Field Station is located. It had maximum wind speeds up to 193 km h^{-1} (Scatena & Larsen 1991) and deposited large loads of leaves and both fine and coarse woody debris on the forest floor (Lodge *et al.* 1991). Our fern survey was conducted in 1995 on field plots that had been laid out in 1989 within 4 wk after the passage of Hurricane Hugo using a randomized block design (see Walker *et al.* 1996 for details). There were four blocks for each of three treatments: control (C), fertilization (F) and debris removal (DR). The blocks were located along ridges throughout the research forest. Within blocks, treatment plots were generally less than 100 m apart. This sampling design was sufficient to detect significant differences in forest net primary productivity within 2 y after Hurricane Hugo (Walker *et al.* 1996, Zimmerman *et al.* 1995). All fallen leaves and woody debris were left on the forest floor in C and F plots, while for the DR treatment, all plant debris was removed from the forest floor by researchers during the 3 wk following Hurricane Hugo (Walker *et al.* 1996). No additional debris was removed from the DR plots prior to our survey of the fern community. For F plots, inorganic fertilizers were added to the entire plot every 3 mo at the following rate: 30 g N, 10 g P, 10 g K, 1.9 g Mg, 2.5 g Mn, 2.6 g Zn, 1.5 g Cu, 0.2 g Fe and 0.8 g B m^{-2} y^{-1} (Walker *et al.* 1996). Nitrogen application rates were approximately three times the quantity in annual litterfall (Zimmerman *et al.* 1995) while P and K application rates were about 30 and two times annual inputs from fine litterfall (Lodge *et al.* 1991). From the beginning of the project in September 1989, all data relating to the productivity experiments were collected in the central 10-m × 10-m zones of the 20-m × 20-m experimental plots at intervals varying from every 2 wk for litter samples to every 6 mo for most vegetation measurements (Walker *et al.* 1996).

Fern observations and measurements

In October and November 1995 we conducted a fern survey on these previously established and continuously monitored experimental plots. Prior to our 1995 survey, at 6-mo intervals only generalized cover and biomass data for ferns had been collected (Walker *et al.* 1996). In order to assess trampling effects of repetitive monitoring, all of our observations and measurements of ferns were recorded in both the intensely monitored central area and the outer buffer-zone area of the experimental plots. Fern data were collected in four F plots and four C plots. However, for our observations, fern data were collected in only three of the DR plots. We excluded the fourth DR plot because it included a large charcoal pit and was totally unlike any other treatment plot. Thus ferns were measured in eleven 20-m × 20-m plots totalling 0.44 ha in area.

In order to evaluate treatment effects on fern species richness, diversity and abundance, each individual fern plant rooted within 2 m of the ground was identified and counted. For species with a compact vining habit, each contiguous patch of leaves was counted as an individual plant. Simpson's index of diversity (1/D) gives weight to the abundance as well as number of species (Magurran 1988) in evaluating diversity. For each treatment, D was calculated by summing $(n(n-1))/(N(N-1))$ where n is the number of individuals for a species and N is the total number of individuals observed for that treatment (Magurran 1988). Although counts for some species were very low, to facilitate comparison with other fern studies and to permit comparison of the abundance in the smaller area surveyed for the DR treatments, abundance is presented as plant density ha^{-1}.

Several fern characteristics were measured in order to identify which elements of plant or leaf size may have contributed to changes in the productivity results for biomass and cover observed by Walker *et al.* (1996). Leaves on each plant were counted to determine treatment differences within species. Because leaves of tropical ferns are usually produced sequentially over time, it was assumed that the longest mature leaf on each individual had emerged most recently and that its size would therefore reflect the current productivity level of the plant. Petiole length, lamina length and lamina width of the selected leaf were measured separately to allow a general assessment of the leaf area. In *T. deltoidea* the lower section of the lamina has constricted leaflets along the rachis and this section was included in the petiole measurement.

To determine effects of treatments on spore production, each measured leaf was classified as fertile (sporophyll) or sterile, as not all leaves of adult fern plants have sporangia present (Sharpe & Jernstedt 1990). Phenology studies have shown seasonal production of relatively short-lived fertile leaves, with highest numbers emerging in the summer (Sharpe 1997), therefore this fall survey of sporophylls may slightly overestimate fertility of the leaves sampled. Chronological development in pinnate ferns generally results in increasing numbers of pairs of leaflets as the plant ages (Sato 1990). Leaflet pairs were therefore counted in order to determine if a treatment effect could be detected in relative ages of plants. When any of the elements of leaf size or development were incomplete due to leaf damage, they were not measured and were not included in the sample for that particular leaf characteristic.

Environmental characteristics noted include substrate, height above ground and evidence of leaf damage. Type of substrate was classified as terrestrial (rooted in soil) or non-terrestrial (rooted on wood or rock). If a plant was non-terrestrial, the height of the base of the plant above the ground was recorded. The number of damaged leaves that were broken or had holes in the laminar tissue was noted for each plant.

Fern nomenclature follows Proctor (1989) with the exception of *Polypodium chnoodes* and *P. dissimile* which follow Proctor (1977). Because this study was done at the Luquillo Long-term Ecological Research (LTER) site, data and metadata have been deposited with, and are available from, the data manager for the site (P.O. Box 23341, San Juan, Puerto Rico 00931-3341, USA).

Statistical analysis

Bartlett's tests of equal variances indicated that non-parametric statistical tests were appropriate for this data set and are reported herein. Although the basic experiment is a randomized block design, the non-parametric Friedman two-way analysis of variance requires that data be available for all blocks. Our data set was missing information for one debris-removal treatment block, therefore Kruskall–Wallis one-way analysis of variance by ranks was used for treatment comparisons. Block means of fern density were used for comparison of overall fern density, however, patchy distribution of ferns resulted in additional blocks with no data when analyzing other variables for different species. Therefore, data for dependent variables including leaf count per plant, petiole length, lamina length, lamina width, leaflet pairs, per cent leaves damaged and height above substrate, were pooled for Kruskall–Wallis one-way analysis of variance testing of treatment effects. To contrast the intensely monitored zones of the plots with the outer buffer zones in assessing monitoring effects, plot densities and leaf damage means were subjected to a two-way Friedman analysis of variance appropriate for the nested design. Chi-square tests were used where appropriate and the Mann–Whitney U test was used to compare specific experimental treatments with controls. Significance level was set at alpha equals 0.05. Means ± standard error (SE) are reported throughout. Statistix (Analytical Software 1994) was used for all statistical analyses.

Table 1. Density of individuals of species of ferns in each treatment of a productivity experiment in the tabonuco forest of El Verde, Luquillo Experimental Forest, Puerto Rico. Sampled areas for control and fertilization treatments were 0.16 ha and 0.12 ha for the debris-removal treatment. Species are listed in descending order of abundance ha^{-1} within substrate preference category.

	Treatment				
Species	Control	Fertilization	Debris removal	Overall mean	n
Terrestrial					
Thelypteris deltoidea	1706	88	3283	1548	682
Blechnum occidentale	900	25	83	359	158
Cyathea borinquena	250	88	358	220	97
Lindsaea lancea	156	0	0	57	25
Cyathea arborea	19	0	0	7	3
Thelypteris normalis	13	0	0	5	2
Lindsaea quadrangularis subsp. *antillensis*	0	6	0	2	1
Thelypteris dentata	6	0	0	2	1
Non-terrestrial/terrestrial					
Nephrolepis rivularis	2500	81	133	975	429
Non-terrestrial					
Elaphoglossum rigidum	225	38	42	107	48
Polypodium lycopodioides	81	38	8	45	20
Polypodium chnoodes	94	0	25	41	18
Asplenium serratum	88	13	0	36	16
Asplenium cuneatum	0	44	0	16	7
Polypodium dissimile	0	25	0	9	4
Polypodium latum	6	0	0	2	1
Polypodium piloselloides	6	0	0	2	1
All species	6062	459	3942	3439	1513

RESULTS

Species richness and diversity

Of the total of 1518 individual fern plants rooted below 2 m above the ground, all but five had sufficient plant material available to allow identification (Table 1). Although 17 species were present, nine were represented by fewer than eight individuals. Six species were found in all three treatments while nine species occurred in only one treatment, most in very low numbers (Table 1). C plots had a greater number of species (14) than were observed in F plots (10); however F plots included three species not found in C plots, while C plots had seven species not found in F plots. When species abundance was taken into account, Simpson's diversity index for F plots (7.56) was higher than that for both C plots (3.62) and DR plots (1.42). Though the area surveyed in C plots was only one-third greater than in DR plots, there were twice as many fern species represented in C plots compared to DR plots ($n = 7$) with all DR plot species also found in C plots (Table 1).

Plant abundance

Mean densities of fern individuals in the C, F and DR plots (Table 1) were significantly different ($P = 0.0410$) with ferns significantly less abundant in F plots than in C plots ($P = 0.0143$). The most common fern species was *Thelypteris deltoidea*, while the second most common fern species, *Nephrolepis rivularis*, had only about two-thirds as many individuals ha^{-1} (Table 1). The majority of *T. deltoidea* plants occurred on DR plots, while the majority of *N. rivularis* plants occurred on C plots. Both were uncommon in F plots (Table 1). Though overall fertility levels were low (8.4%) for all species, only one sporophyll was produced in F plots while the percentage of measured leaves that were sporophylls in DR plots (10.2%) was higher than in C plots (7.8%).

Plant and leaf characteristics

Of the six species common to all treatments, growth and size variables of *T. deltoidea* exhibited the largest number of significant responses to experimental treatments (Table 2). Although density was relatively low for *C. borinquena* compared with other species (Table 1), its leaf dimensions are nearly four times as large as those of the more common *T. deltoidea* (Table 2). Leaflet pair counts were significantly lower for F plots only for *T. deltoidea* and significantly lower for DR plots for both *T. deltoidea* and *C. borinquena*. The per cent of leaves damaged was higher in F plots than in C plots for all species except *Blechnum occidentale* and *Polypodium lycopodioides* (Table 2).

Table 2. Plant and leaf characteristics for the six fern species common to all treatments. Data are means ± SE. Species are listed in descending order of abundance ha^{-1}. Significance indications are based on Kruskall–Wallis one-way analysis of variance of the data pooled for each treatment.

Species/character	Control	Fertilization	Debris removal	P
Terrestrial				
Thelypteris deltoidea				
Number of plants	273	15	394	
Sporophyll count	53	0	46	
Leaf count per plant	4.4 ± 0.13	4.3 ± 0.32	3.7 ± 0.09	< 0.001
Petiole length (cm)	15.5 ± 0.44	12.7 ± 1.21	12.3 ± 0.28	< 0.001
Lamina length (cm)	19.3 ± 0.44	16.4 ± 1.02	15.8 ± 0.31	< 0.001
Lamina width (cm)	14.5 ± 0.40	9.7 ± 0.77	13.3 ± 2.36	< 0.001
Leaflet pairs	8.5 ± 0.17	6.2 ± 0.46	7.6 ± 0.09	< 0.001
Leaves damaged (%)	50.0 ± 2.02	70.4 ± 6.48	64.3 ± 0.08	< 0.001
Blechnum occidentale				
Number of plants	144	4	10	
Sporophyll count	4	0	0	
Leaf count per plant	3.9 ± 0.16	2.5 ± 0.29	4.1 ± 0.32	0.155
Petiole length (cm)	7.6 ± 0.33	6.1 ± 1.78	10.0 ± 0.88	0.040
Lamina length (cm)	10.3 ± 0.33	8.6 ± 0.80	15.2 ± 0.95	< 0.001
Lamina width (cm)	4.4 ± 0.17	3.2 ± 0.38	6.3 ± 0.57	0.003
Leaflet pairs	8.3 ± 0.20	8.3 ± 0.63	8.0 ± 0.33	0.960
Leaves damaged (%)	4.7 ± 0.92	0.0 ± 0.00	5.3 ± 3.69	0.636
Cyathea borinquena				
Number of plants	40	14	43	
Sporophyll count	10	0	1	
Leaf count per plant	4.6 ± 0.49	3.3 ± 0.41	2.7 ± 0.18	0.001
Petiole length (cm)	58.3 ± 4.64	25.1 ± 2.80	41.2 ± 3.25	< 0.001
Lamina length (cm)	73.7 ± 5.59	40.7 ± 5.00	54.4 ± 3.86	0.003
Lamina width (cm)	53.4 ± 4.51	28.1 ± 4.12	38.1 ± 3.26	0.004
Leaflet pairs	12.9 ± 0.51	12.2 ± 0.48	11.6 ± 0.30	0.031
Leaves damaged (%)	58.9 ± 5.46	70.0 ± 6.06	43.7 ± 5.75	0.036
Non-terrestrial/terrestrial				
Nephrolepis rivularis				
Number of plants	400	13	16	
Sporophyll count	1	0	1	
Leaf count per plant	3.7 ± 0.09	4.6 ± 0.45	3.8 ± 0.46	0.120
Petiole length (cm)	6.1 ± 0.17	6.5 ± 0.65	7.7 ± 0.92	0.070
Lamina length (cm)	28.2 ± 0.63	34.7 ± 3.81	26.9 ± 3.88	0.057
Lamina width (cm)	4.6 ± 0.07	5.9 ± 0.35	5.1 ± 0.24	< 0.001
Leaflet pairs	36.4 ± 0.61	35.0 ± 2.76	31.0 ± 3.32	0.107
Leaves damaged (%)	0.9 ± 0.46	3.0 ± 2.13	4.2 ± 3.23	< 0.001
Ht. above substrate (cm)	62.5 ± 6.36	75.2 ± 11.90	21.7 ± 11.67	0.080
Non-terrestrial				
Elaphoglossum rigidum				
Number of plants	36	6	6	
Sporophyll count	1	0	1	
Leaf count per plant	9.1 ± 0.95	5.8 ± 1.01	10.5 ± 1.29	0.080
Lamina length (cm)	23.6 ± 1.47	15.9 ± 2.64	20.8 ± 2.49	0.093
Lamina width (cm)	3.4 ± 0.15	2.7 ± 0.38	3.3 ± 0.36	0.204
Leaves damaged (%)	6.3 ± 0.17	12.5 ± 8.54	15.0 ± 7.05	0.421
Ht. above substrate (cm)	53.5 ± 3.96	94.0 ± 18.26	77.7 ± 6.88	0.007
Polypodium lycopodioides				
Number of plants	13	6	1	
Sporophyll count	2	1	0	
Patch size	25.6 ± 8.65	58.0 ± 14.34	14.0 ± –	0.091
Lamina length (cm)	9.3 ± 0.83	12.3 ± 0.80	9.5 ± –	0.203
Lamina width (cm)	1.7 ± 0.12	2.1 ± 0.13	2.0 ± –	0.098
Leaves damaged (%)	12.2 ± 7.98	10.1 ± 3.60	7.1 ± –	0.054
Ht. above substrate (cm)	38.3 ± 10.46	130.0 ± 15.17	30.0 ± –	0.016

Table 3. Comparison of density and mean per cent leaves damaged for individual ferns within monitored and buffer zone areas of plots within four experimental blocks. Significance indications for zone comparisons are based on Friedman two-way analysis of variance for a nested design of monitored and buffer zone areas (df = 1) within blocks (df = 3): *, $P < 0.05$. Block differences were not significant for either of the variables ($P > 0.05$).

	Density ha^{-1}		% leaves damaged	
Block	Monitored zone	Buffer zone	Monitored zone	Buffer zone
1	1367	1978	58.7 ± 5.66	31.9 ± 2.78
2	4600	6917	31.0 ± 6.71	9.4 ± 1.23
3	4000	4367	67.7 ± 2.89	58.7 ± 1.85
4	1533	2589	23.3 ± 3.98	17.0 ± 1.90
Total	1418	2272	54.17 ± 2.42	20.12 ± 1.10
P	0.0455*		0.0455*	

Environment

Of all ferns identified (Table 1), 74% were rooted in soil while 19% occurred on live or dead downed wood (epiphytes) and 7% inhabited rock surfaces (lithophytes). Individuals of *B. occidentale, C. borinquena, Cyathea arborea, Lindsaea lancea, Lindsaea montana*, *T. deltoidea* and *Thelypteris dentata* were found to be almost exclusively terrestrial (> 97%). *Nephrolepis rivularis* occurred as an epiphyte (47%), as a lithophyte (18%) and was also terrestrial (35%). The remaining nine species were non-terrestrial epiphytes and/or lithophytes.

There were twice as many non-terrestrial individuals observed in F plots compared with C plots ($\chi^2 = 183$, $P < 0.0001$). The percentage of fern individuals in C plots ($n = 968$) that were terrestrial was 66%, while only 43% of those in F plots ($n = 72$) were terrestrial. For the facultative non-terrestrial species *N. rivularis*, only 8% of the individuals in F plots ($n = 13$) were terrestrial compared with 37% in C plots. The four non-terrestrial individuals of *B. occidentale* were found on rocks in F plots while all other plants of this species were terrestrial. In contrast, nearly 95% of the fern individuals in DR plots ($n = 473$) were located on soil substrate, possibly reflecting removal of decaying wood that formed the more common type of substrate for non-terrestrial individuals in the other treatment plots. Non-terrestrial individuals of species found in all treatment types were located significantly ($P = 0.0066$) further above the ground in F plots (91.4 ± 7.90 cm; $n = 25$) than in C plots (58.1 ± 4.22 cm; $n = 92$) or DR plots (56.1 ± 10.15 cm; $n = 10$).

Monitoring effects

Significant differences between the intensely monitored 10 m × 10-m central zone of the 20 m × 20-m treatment plots were found (Table 3). Density of individual ferns in the buffer zones was 36% higher than that of the monitored zones, while leaf damage in the monitored zone was more than double that of the buffer zones (Table 3). For C plots, density was 64% higher in the buffer zone than in the monitored zones, while leaf damage was less than half of that seen in the central monitored zone. Density for terrestrial individuals (rooted in the soil) was also significantly lower and leaf damage significantly higher than in the monitored zones ($P < 0.05$), while there were no significant differences for non-terrestrial individuals.

DISCUSSION

Approximately half of the fern species known to occur in the general area (Smith 1970) were found in one or more of the treatment plots, representing both terrestrial and non-terrestrial species. The density of the most common fern species, *T. deltoidea*, in the C plots (1706 individuals ha^{-1}) was comparable to that (1642 individuals ha^{-1}) found in an earlier study of the same general area of the El Verde forest (Smith 1970).

Fertilization effects

Fertilization treatment effects on ferns included lower species richness but higher species diversity, low sporophyll production, greatly reduced abundance, and shorter leaf lamina and widths for most species than were observed in control areas. Furthermore, leaf damage was observed more often in F plots. There were proportionately fewer terrestrial plants in F plots where non-terrestrial plants were located higher above the ground than in control areas.

Though Simpson's diversity index for F treatments was double that of C plots, the reduction in fern species richness compared with controls is similar to the reduction found in the herb layer in a similar temperate forest study (Thomas *et al.* 1999). Greatly reduced abundance for all species in F plots (8% of that found in C plots) and lower values for plant size parameters (lamina length and width) for the majority of fern individuals can further account for the decrease in cover over time and lower fern biomass values reported by Walker *et al.* (1996). In contrast to large changes in size parameters for ferns in the F plots, tree diameter means did not show significant change in 4 y (Walker *et al.* 1996), although increased LAI (Zimmerman *et al.* 1995) did reduce light levels on the forest floor. Low sporophyll production in response to fertilization treatments could have resulted from reduced availability of nutrients necessary for sporophyll initiation (White 1971) or the presence of immature plants as indicated by counts of lower leaflet pairs. Significantly higher levels of leaf damage in F plots than in C plots (Table 2) provide additional evidence of stress.

Terrestrial species had fewer negative responses than those rooted on other substrates (Table 2). Compared to C plots, terrestrial ferns in F plots occurred in significantly lower numbers than non-terrestrial plants, while non-terrestrial plants were rooted higher above the ground in F plots. Therefore, causes for negative responses most likely occur at the level of the herbaceous layer itself, suggesting the following three hypotheses for testing in future studies: (1) presence of competing plants; (2) toxicity of fertilizers to plants rooted in soil; and (3) changes in soil chemistry.

Competition from graminoids may have caused a reduction in numbers of ferns in early stages of the experiment. Walker *et al.* (1996) observed that there had been a sudden large increase in cover of the grass *Ichnanthus pallens* in the F plots during the first 6 mo, although 4 y later biomass of graminoids had dropped to only 11% of C plot values (Walker *et al.* 1996). Vine biomass in the F plots had increased after 4 y (Walker *et al.* 1996) and competition from this life form may also have had a negative effect on plant growth.

It is also possible that ferns on soil substrate are more sensitive to toxic effects of fertilizer application directed toward the ground (Thomas *et al.* 1999). Fertilizer application levels were high at three, 30 and two times mean annual inputs of N, P and K, respectively from fine litterfall (Lodge *et al.* 1991). This effect could explain the higher densities and higher position above the substrate of non-terrestrial individuals in the F plots.

Change in soil conditions in the F plots is a third possible explanation for the greatly decreased numbers and smaller sizes of ferns in F plots compared to both C and DR plots. Tuomisto & Poulsen (1996, 2000) have found that soil characteristics are a key factor in explaining the distribution of ferns in the Amazonian rain forest. The only soil characteristics of these experimental plots for which specific information is available are three organic characteristics measured by Li (1998): soil bulk density, soil moisture and pH. There were no significant differences among the three treatments in soil bulk density or soil moisture, however, Li (1998) found significant differences among treatments in soil pH. Soil pH of the F plots was much more acidic (3.39) than the C plots (4.23) or the DR plots (4.18). Some rain-forest ferns in the Amazon do tolerate soils with pH values of 3.5–3.6 (Young & Leon 1989), which could account for the qualitative change in species composition of the F plots.

Effects of debris removal

Fern responses to the debris-removal treatment included reduced species richness, higher abundance of *T. deltoidea*, lower numbers of non-terrestrial plants and, for *T. deltoidea*, plants with fewer and smaller leaves and fewer leaflet pairs than those observed in control areas. Lower leaflet pair counts for *T. deltoidea* in DR plots compared with C plots suggest that relatively younger plants occur in DR plots. Removal of all leaf litter and woody debris right after Hurricane Hugo would have exposed the mineral soil surface necessary for fern spore germination (Proctor 1989) and subsequent growth of new individuals could explain the lower leaflet pair count classes. That debris removal could have enhanced recruitment of ferns is further supported by the significantly lower plant size parameters. A similar increase in woody seedling density had earlier been observed in the DR plots by Walker *et al.* (1996). Lack of downed woody debris providing fewer non-terrestrial microhabitats for ferns below 2 m may account for the lower number of non-terrestrial species (3) compared with C plots (6).

Monitoring effects

After 6 y of monitoring and measurements done in the central monitoring zones, negative effects on abundance and increased leaf damage for the fern community were significant when contrasted with data for the buffer zones. We found a 64% higher density of fern individuals in the buffer zone compared with the central monitoring area of the C plots; biomass samples taken earlier from the central area of the plots in 1993 (Walker *et al.* 1996) should account for only 4% of this difference. It would therefore appear that the higher intensity of researcher activity within the central area of the plot may have considerable effect on fern populations and possibly other herbaceous-layer plants as well. Therefore, fern cover declines and low values for fern biomass reported in Walker *et al.* (1996) as well as negative responses seen in the F plots in this study, while of interest in relative terms in evaluating treatment effects, may possibly be overestimates of actual treatment effects for ferns. Herbaceous-layer ferns may actually respond more rapidly and in a more meaningful way to experimental treatments than trees and are more accessible to researchers (Tuomisto & Poulsen 2000). However, our results indicate that special precautions should be observed during the monitoring process to ensure that the herbaceous layer remains as undisturbed as possible (Witham *et al.* 1993). Since ferns have been found to affect tree seedling establishment (George & Bazzaz 1999*a*, *b*; Horsley 1993, Horsley & Marquis 1983), for evaluation of tree responses it would also be important to protect the integrity of the herbaceous layer throughout a long-term experiment.

In this study we have examined in detail the responses of individual fern species to fertilization (F) and debris-removal (DR) treatments following the passage of a large hurricane. Small sample sizes and the short time frame available for observation limit our ability to generalize from these results. However, the magnitude of response indicates that ferns are sensitive indicators of change. Since the specific causes of the negative effects of the fertilization treatments on ferns have not been investigated, we have suggested three hypotheses (competition, toxicity and soil changes) for future research. Future studies should reflect changes over time rather than relying on a one-time comparison of control data with treatment data. Not all ferns responded in the same way to the treatments, therefore more needs to be known about the growth and nutrient requirements of individual fern species. The shift in species composition, decreased abundance, lower percentages of sporophylls, increased leaf damage and the loss of net primary productivity for ferns have important implications for biodiversity and ecosystem function.

ACKNOWLEDGEMENTS

We thank the staff, researchers and students at the El Verde Field Station for their support. Jill Thompson and Jess Zimmerman provided invaluable guidance and encouragement throughout the data collection phase of the project. We also thank Janet Pearce Foster, Lawrence Walker, Darrell Herbert and anonymous reviewers for very helpful comments on the manuscript. This study was funded primarily by NSF grant RII-8802961 to the Minority Research Centre of Excellence at the University of Puerto Rico. Additional support was provided by NSF grants RIMI-8903827 to the University of Puerto Rico and BSR-8891902 to the Institute for Tropical Ecosystems Studies, University of Puerto Rico, and the International Institute of Tropical Forestry as part of the Long-term Ecological Research Program in the Luquillo Experimental Forest.

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