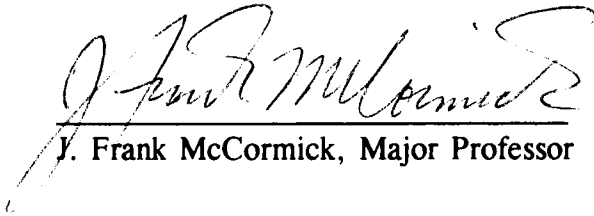
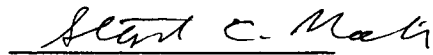


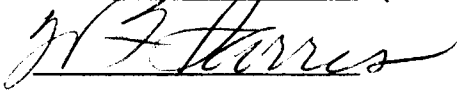
To the Graduate Council:

I am submitting herewith a thesis written by Amy E. Arnold entitled "Influence of Microenvironment on Growth and Nutrient Dynamics of Three Herbaceous Species in the Bisley Experimental Watersheds of Luquillo Experimental Forest, Puerto Rico." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements of the degree of Master of Science, with a major in Ecology.


J. Frank McCormick, Major Professor

We have read this thesis
and recommend its acceptance:





Accepted of the Council:


Associate Vice Chancellor and
Dean of The Graduate School

INFLUENCE OF MICROENVIRONMENT ON GROWTH AND NUTRIENT
DYNAMICS OF THREE HERBACEOUS SPECIES IN THE
BISLEY EXPERIMENTAL WATERSHEDS OF LUQUILLO EXPERIMENTAL
FOREST, PUERTO RICO

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Amy E. Arnold

December 1996

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ABSTRACT

Three tropical herbaceous species, *Dieffenbachia seguine*, *Ichnanthus pallens*, and *Pilea inaequalis*, were investigated in the Bisley Experimental Watersheds of Luquillo Experimental Forest, Puerto Rico. Objectives were:

1. To characterize microenvironments of the three species in terms of light and soil physical and chemical properties.
2. To examine relationships between microenvironment and plant growth and other estimators of plant performance.
3. To describe the ecological life cycles of the three species in terms of recruitment, mortality, growth, and clonal behavior and their role in forest recovery following canopy disturbance.
4. To determine nutrient contents and rates of decomposition of the three species in order to understand their role in nutrient dynamics.

Results supported the following conclusions:

1. Study species habitats were related to microenvironmental differences in soil moisture and nutrients. Soil moisture varied significantly with topographic position, and soil moisture was subsequently correlated with number of soil chemical properties. Light environments were highly variable.
2. Growth of all three species was related to soil properties and/or light differences.

3. Biomass and several measures of plant size were significantly related to soil properties and/or light.
4. Biomass of these herbs was accurately estimated using nondestructive measurements of plant size.
5. All three study species were determined to be r-strategists; however, *Dieffenbachia* exhibited a more conservative life history strategy. Clonal reproduction by means of rhizome fragmentation (*Dieffenbachia*) or rooting at nodes with subsequent fragmentation (*Ichnanthus*, *Pilea*) appeared to be extensively used by study species.
6. *Dieffenbachia*, *Ichnanthus*, and *Pilea* were well-adapted to canopy disturbance, specifically to hurricane disturbance.
7. *Dieffenbachia*, *Ichnanthus*, and *Pilea* concentrated nutrients above substrate levels, and all three species exhibited rapid decomposition rates.

Based on several lines of evidence, *Dieffenbachia*, *Ichnanthus*, and especially *Pilea* populations were found to play an important role in nutrient dynamics, and thereby ecosystem resiliency, following canopy disturbance in the Bisley Experimental Watersheds.

TABLE OF CONTENTS

CHAPTER	PAGE
I. BACKGROUND	1
A. Introduction	1
Studies of plant population dynamics	2
B. Site Description	5
Vegetation and climate	5
Soils	8
Disturbance	13
C. Study Species	14
<i>Dieffenbachia</i> studies	21
<i>Ichnanthus</i> studies	22
<i>Pilea</i> studies	22
D. Purpose and Objectives	23
II. METHODS	25
A. Microenvironment	25
Soil properties	26
Light	28
B. Plant Growth	29
Growth	29
Population demography	30
Clonal characteristics	31
Gas exchange	31
C. Biomass and Nutrient Content	32
Biomass	32
Nutrient content	34
D. Decomposition	34
E. Data Analysis	35
III. RESULTS	37
A. Microenvironment	37
Soil properties	37
Light	48
B. Plant Growth	54
Growth	54
Microenvironment and growth	56
Population demography	56
Clonal characteristics	62
Gas exchange	64
C. Biomass and Nutrient Content	66
Biomass	66
Microenvironment and biomass	67

	Nutrient content	68
D.	Decomposition	72
IV.	DISCUSSION	78
A.	Microenvironment	79
	Soil properties	80
	Soil habitat differences	81
	Light	81
B.	Growth	82
	Species responses to soils	82
	Species responses to light	84
	Life history strategies	85
C.	Biomass and Nutrient Content	88
	Biomass	88
	Nutrient content	90
D.	Decomposition	92
	Species differences	93
	Decay and microenvironment	94
V.	SUMMARY AND CONCLUSIONS	98
	LITERATURE CITED	104
	APPENDICES	113
	VITA	134

LIST OF TABLES

TABLE	PAGE
3-1. Matrix of Spearman Rho correlation coefficients for soil properties in species growth plots, Bisley Experimental Watersheds, Puerto Rico	40
3-2. Mean exchangeable cations, exchangeable acidity, and pH by dominant herbaceous species and topographic position in the Bisley Experimental Watersheds, Puerto Rico	45
3-3. Mean exchangeable cations, extractable P, total N, organic matter, and C/N ratio by dominant herbaceous species and topographic position in the Bisley Experimental Watersheds, Puerto Rico	46
3-4. Mean percent saturation of exchangeable cations in the soil exchange complexes by dominant herbaceous species and topographic position in the Bisley Experimental Watersheds, Puerto Rico	47
3-5. Growth rates for each species across measurement periods (tagged plants only)	55
3-6. Changes in population size of each species in all growth plots for each study period	60
3-7. Changes in mortality of tagged plants over course of study	61
3-8. Clonal behavior in <i>Dieffenbachia</i> , <i>Ichnanthus</i> , and <i>Pilea</i>	63
3-9. Photosynthesis, dark respiration, and P/R ratio for mature <i>Dieffenbachia</i> plants growing under natural high and low light conditions	65
3-10. Comparison of average nutrient concentrations (Avg.), sample size (N), and standard deviation (Std.) of study species	69
3-11. Mean decay constant (k) values for leaf tissues of study species	75
3-12. Mean decay constant (k) values for leaf tissues of study species by topographic position or site	76

LIST OF FIGURES

FIGURE	PAGE
1-1. Map of Luquillo Experimental Forest, Puerto Rico showing location of study area	6
1-2. 1995 daily precipitation values (mm) measured above the forest canopy from an observation tower in the Bisley Experimental Watersheds, Puerto Rico. .	9
1-3. 1995 daily maximum and minimum temperature values (°C) measured above the forest canopy from an observation tower in the Bisley Experimental Watersheds, Puerto Rico.	10
1-4. 1995 daily maximum and minimum relative humidity values (%) measured above the forest canopy from an observation tower in the Bisley Experimental Watersheds, Puerto Rico.	11
1-5. 1995 total daily photosynthetic photon flux density (PPFD, moles day ⁻¹) measured above the forest canopy from an observation tower in the Bisley Experimental Watersheds, Puerto Rico.	12
1-6. Illustration of adult <i>Dieffenbachia seguine</i> Schott. (Araceae).	15
1-7. Illustration of adult <i>Ichnanthus pallens</i> (Sw.) Munro (Gramineae).	17
1-8. Illustration of adult <i>Pilea inaequalis</i> (Juss. ex Poir.) Wedd. (Urticaceae). .	19
3-1. Box plots showing the range of soil moisture and bulk density (g cm ⁻³) across topographic positions for study sites in the Bisley Experimental Watersheds, Puerto Rico.	38
3-2. Box plots showing the range of soil chemical properties across topographic positions for study sites in the Bisley Experimental Watersheds, Puerto Rico	42
3-3. Daily total PPFD (μmol m ⁻² s ⁻¹) in open vs. closed canopy sites in the Bisley Experimental Watersheds, Puerto Rico.	49
3-4. Photosynthetic photon flux density (mmol hr ⁻¹) in open vs. closed canopy sites on sunny day (Julian day 101, 1995) in the Bisley Experimental Watersheds, Puerto Rico.	51

3-5.	Photosynthetic photon flux density (mmol hr^{-1}) in open vs. closed canopy sites on cloudy day (Julian day 84, 1995) in the Bisley Experimental Watersheds, Puerto Rico.	52
3-6.	Functional relationship between average canopy openness and PPFD ($\mu\text{mol m}^{-2}\text{s}^{-1}$) for growth measurement plots	53
3-7.	Flowering incidence vs. average canopy openness and PPFD for <i>Pilea</i> and <i>Ichnanthus</i>	59
3-8.	The concentration of nutrients (mg g^{-1}) within study species as compared with exchangeable soil nutrient concentrations within the upper 10 cm of soil. .	70
3-9.	Percent initial weight remaining vs. time in days for leaf litter in <i>Dieffenbachia</i> , <i>Ichnanthus</i> , and <i>Pilea</i>	73

CHAPTER I

BACKGROUND

A. Introduction

Tropical rain forests are among the most diverse and productive ecosystems on earth. Over two-thirds of the world's species occur here (3 to 30 million), the majority of which are still unknown to science (Raven 1988). Unfortunately, some of these species will disappear before being discovered, due to rapid deforestation and changes in land use. This destruction is taking place because of increased demand for agricultural land, minerals, and fuel by growing human populations (and also natural disturbance). These ecosystems are in many cases, poorly managed, partially due to a lack of understanding of their structure and function (Lugo & Brown 1981; Brown *et al.* 1983). Only through basic scientific research, enlightened land use policies, and improved management strategies can these ecosystems be sustainably managed. An understanding of forest responses to natural disturbance is helpful in understanding forest responses to anthropogenic disturbances. Subsequent management of disturbed forests should be based upon an understanding of the natural resiliency of these ecosystems.

The purpose of this research is to examine the population dynamics, microenvironment, and nutrient dynamics of three species of ground layer herbs in the

Bisley Experimental Watersheds as they recover from the effects of Hurricane Hugo and two subsequent, less-destructive hurricanes. It is hypothesized that herbs are important in forest recovery following canopy disturbance, since they are among the first species to colonize disturbed sites, and apparent rapid turnover rates may provide significant inputs to nutrient cycling. In addition to colonizers, herbs present before canopy disturbance can experience accelerated growth upon exposure to increased solar radiation. By understanding microenvironmental requirements, life history strategies, nutrient contents, and decay rates of component herbaceous species, one can develop better methods for managing agroecosystems as well as disturbed natural ecosystems (Mooney *et al.* 1980).

Studies of plant population dynamics

Most studies of population dynamics of tropical rain forest species have focused upon perennial woody species, *i.e.*, trees and shrubs (Sarukhan 1980; Valerio 1983; Smith 1987; Sharpe 1988; McCormick 1995). This dearth of research on tropical herbs may be due to the fact that species richness of tropical ground herbs is relatively poor when compared to the great diversity of tropical woody species (Richards 1952; Smith 1987). In contrast, most demographic studies in temperate regions have involved herbaceous species (*e.g.*, Vivian 1967; Sharitz & McCormick 1972; Cid-Benevento & Werner 1986; Fielder 1987; Hutchings 1987; Miller & Werner 1987; Fone 1989) and have been restricted to woodland and grassland species (Harper 1977).

Luquillo Experimental Forest (LEF). Autecological studies of plant species in the LEF are numerous but have primarily been confined to arborescent species: the sierra palm, *Prestoea montana* (R. Grah.) Nichols. (= *Euterpe globosa*) (Bannister 1970); the shrub *Palicourea riparia* Benth. (Lebron 1977); and tree species *Inga vera* (Willd.) (Muniz-Melendez 1978); *Buchenavia capitata* (Vahl) Eichl. (Sastre-DeJesus 1979); *Cecropia schreberiana* ex. *C. peltata* L. (Silander 1979); *Didymopanax morototoni* (Aubl.) Decne. & Planch. (Nieves 1979), as well as *Manilkara bidentata* (A.DC.) Cher. (You 1991), to name a few. For a review of the population dynamics of selected tree and shrub species of the LEF, refer to McCormick (1995).

Research on herbaceous vegetation in the LEF has been very limited. Edmisten (1970) studied germination responses of bird-dispersed *Phytolacca icosandra* seeds. *Phytolacca icosandra* seeds subjected to light scarification (from wild bird digestive tracts or weak acids) and warm soil temperatures showed improved germination. Following germination, seedlings subjected to full-sun (as opposed to 50% and 10% full sun) exhibited the highest growth.

Walker (1994) examined the effects of fern thickets on landslide succession in the LEF. Fern thickets were more prevalent in the upper portions of landslide scars, where thin mineral soils were exposed, as opposed to the lower portions of landslide scars, which had soils containing higher organic matter and nutrients (Guariguata 1990; Walker 1994). Fern thickets increased germination of several tree species as compared to adjacent bare soil; however, tree seedlings experienced suppressed

growth in the fern thickets, suggesting that fern thickets delay succession (Walker 1994).

Tropical herbaceous understory. Few comprehensive demographic studies of tropical herbaceous understory plants exist in the literature. By and large, the primary focus of most studies has been on phenology and/or pollination (Stiles 1975; Beach 1982; Valerio 1984; Kiew 1985; Young 1986). However, Sharpe (1988) thoroughly studied the growth and demography of a small terrestrial neotropical fern, *Danaea wendlandii* (Marattiaceae) in La Selva, Costa Rica. Growth rates were determined to be quite slow for this species (only 1.1 to 1.6 leaves per plant per year), and plants were estimated to live a maximum of 25 years.

In a study of another neotropical understory herb, *Calathea ovandensis*, spatio-temporal variation in basic demographic parameters (growth, recruitment, and mortality) and the influence of environment on these parameters were examined in southern Mexico (Horvitz & Schemske 1995). When this species was subjected to different treatments of light, density, and substrate over time, it was found to have a long-lived seed bank, highly variable seedling recruitment, high seedling mortality, low mortality of adult plants, fertility that increased with plant size, and the ability of large plants to shrink, rather than die, in adverse environments. Survival, growth, and reproduction were observed to vary significantly through space and time.

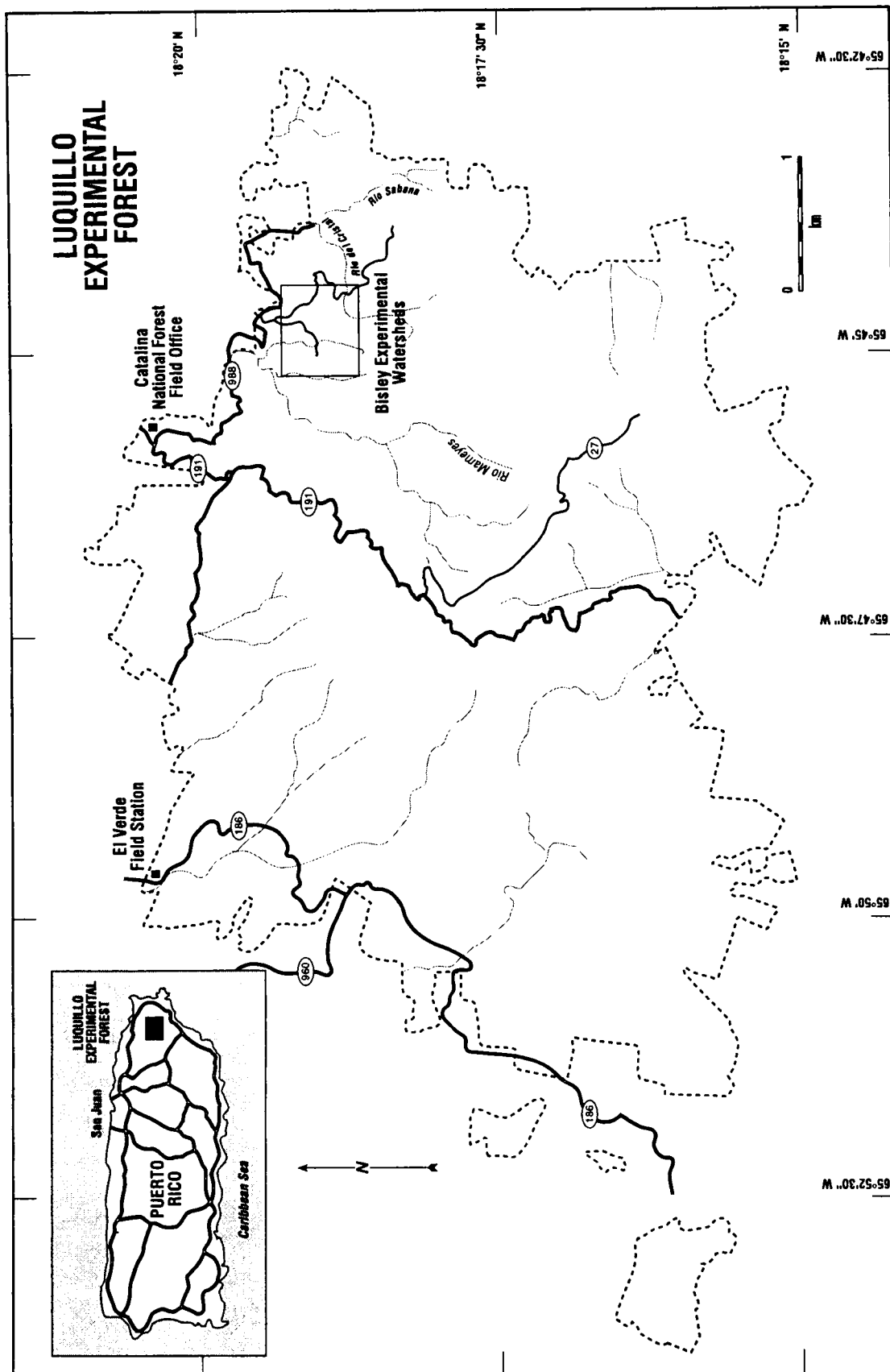
B. Site Description

The Bisley Experimental Watersheds are located in Luquillo Mountains on the island of Puerto Rico, the easternmost and smallest island of the Greater Antilles (Fig. 1-1). The Bisley Watersheds have a complex terrain of highly dissected northeast-and northwest-facing slopes. Slopes are usually convex-concave in shape, with upper slopes becoming convex as they approach long, narrow ridges (Scatena 1989). Middle segments are straight, and lower segments become concave as they enter first-order stream valleys. Elevation in the Bisley area ranges from approximately 260 to 450 m, and the landscape is characterized by steep topography, with over one-half of the drainage area having slopes greater than 45 percent (Scatena 1989).

Vegetation and climate

The predominant physiognomic and climatic type of the Bisley Experimental Watersheds has been classified differently by several authors. Beard (1944) described the area as lower montane rain forest, whereas Ewel and Whitmore (1973) termed it subtropical wet forest. Under Holdridge's (1967) classification system, the Bisley area is known as subtropical moist forest. Wadsworth (1951) described the vegetation as tabonuco forest, which was named after the common name of the dominant tree species, *Dacryodes excelsa*. Other important tree species in the Bisley Experimental Watersheds include *Prestoea montana* and *Sloanea berteriana*.

FIGURE 1-1. Map of Luquillo Experimental Forest, Puerto Rico showing location of study area. Shown are Luquillo Experimental Forest, the Bisley Experimental Watersheds, the El Verde Field Station, and the Catalina Caribbean National Forest Office.



Rainfall in the Bisley area averages about 3500 mm annually and is generally well-distributed throughout the year (Scatena 1989). Air temperature shows little seasonal variation in the El Verde research area of the LEF, varying by approximately 3.5 °C around an annual average of 23.6 °C (Silander 1979). Relative humidity in the LEF is usually high, averaging between 96 and 100 percent in the understory (Brown *et al.* 1983). Refer to Figs. 1-2 through 1-5 for a summary of Bisley climate data for 1995 (Scatena, unpublished data).

Soils

Soils in the Bisley Experimental Watersheds are derived from quartz-poor volcanoclastic sandstone parent materials (Scatena 1989). The primary order to which these soils belong is the Ultisols, which indicates that these soils are clayey, leached, and highly weathered. Soils are classified as part of the Humatus-Zarzal-Cristal complex (Johnston 1992). Zarzal soils occupy upper to mid-slope positions and are typically yellowish-brown clays (Scatena 1989). Cristal soils occupy lower slope positions that are somewhat poorly drained and are pale brown clays with well-developed low chroma and red mottles. Humatus soils are well-drained, ridge-top soils having yellowish-brown clays at the surface, underlain by yellowish-red friable clay. In poorly drained valleys and some lower slopes, Coloso soils predominate. These soils are structureless, and grey to bluish green in color (Johnston 1992).

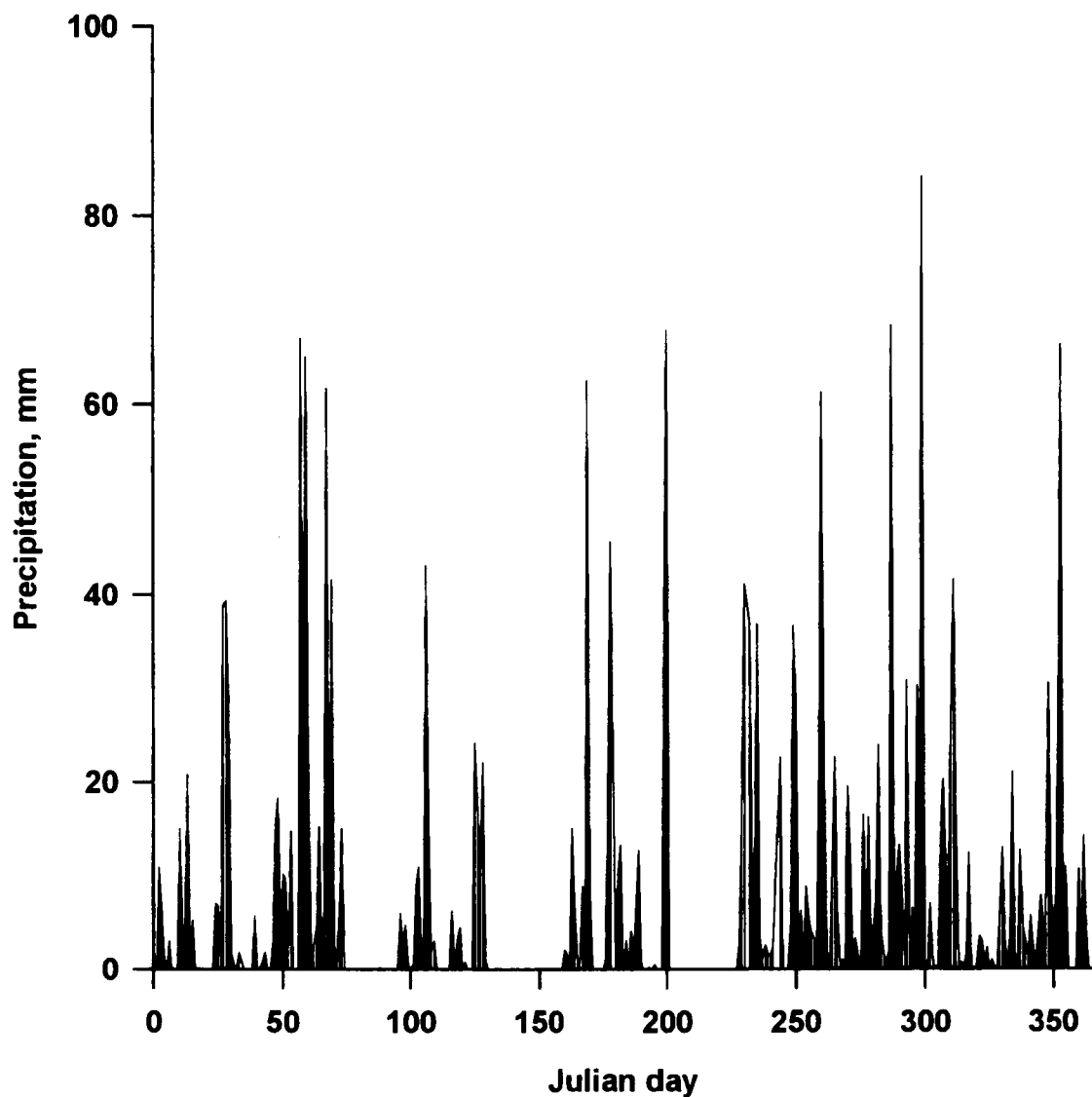


FIGURE 1-2. 1995 daily precipitation values (mm) measured above the forest canopy from an observation tower in the Bisley Experimental Watersheds, Puerto Rico. In Julian days, day 1 = January 1. No data available for days 130-158 and 201-226.

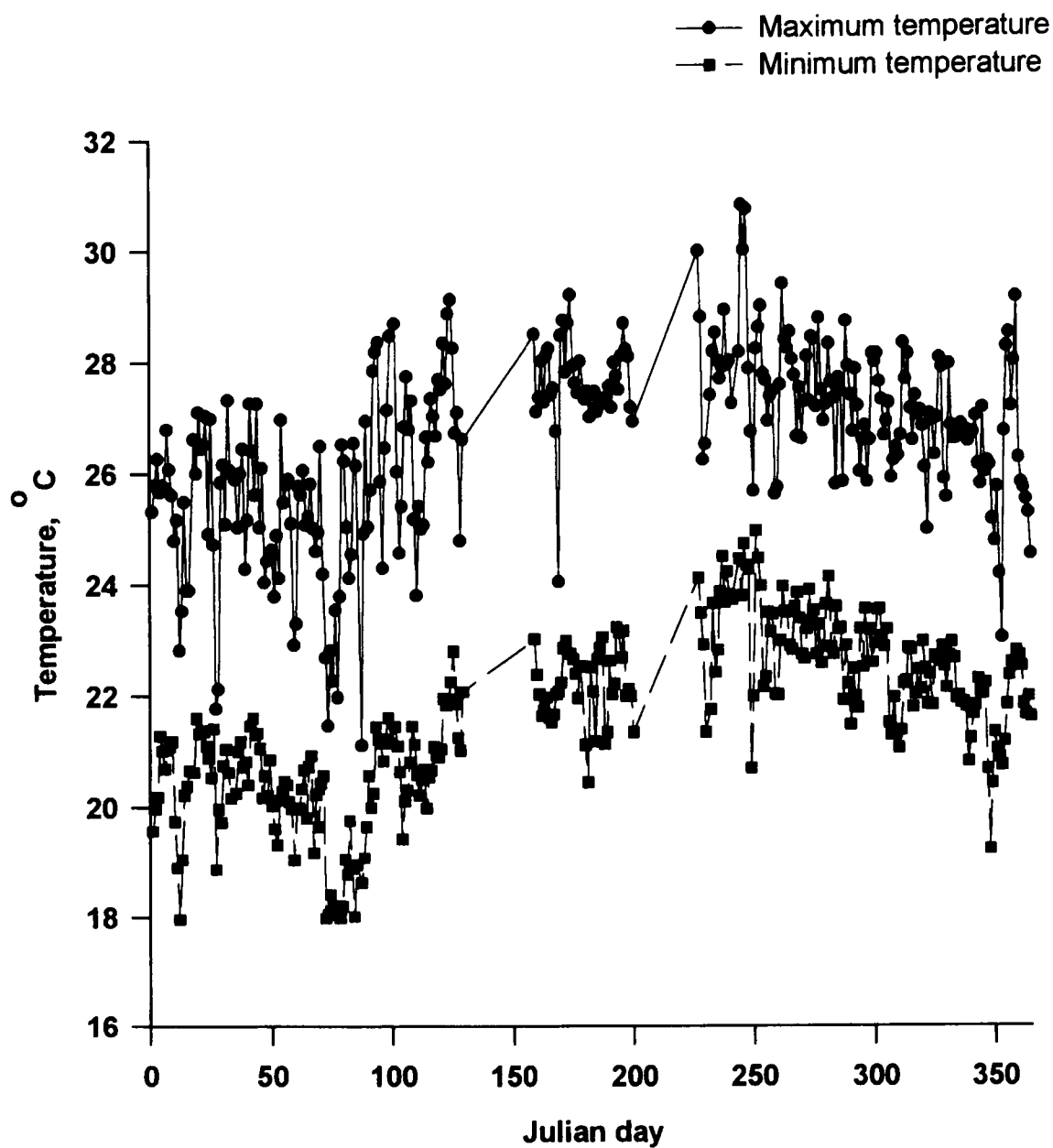


FIGURE 1-3. 1995 daily maximum and minimum temperature values (°C) measured above the forest canopy from an observation tower in the Bisley Experimental Watersheds, Puerto Rico. No data available for days 130-158 and 201-226.

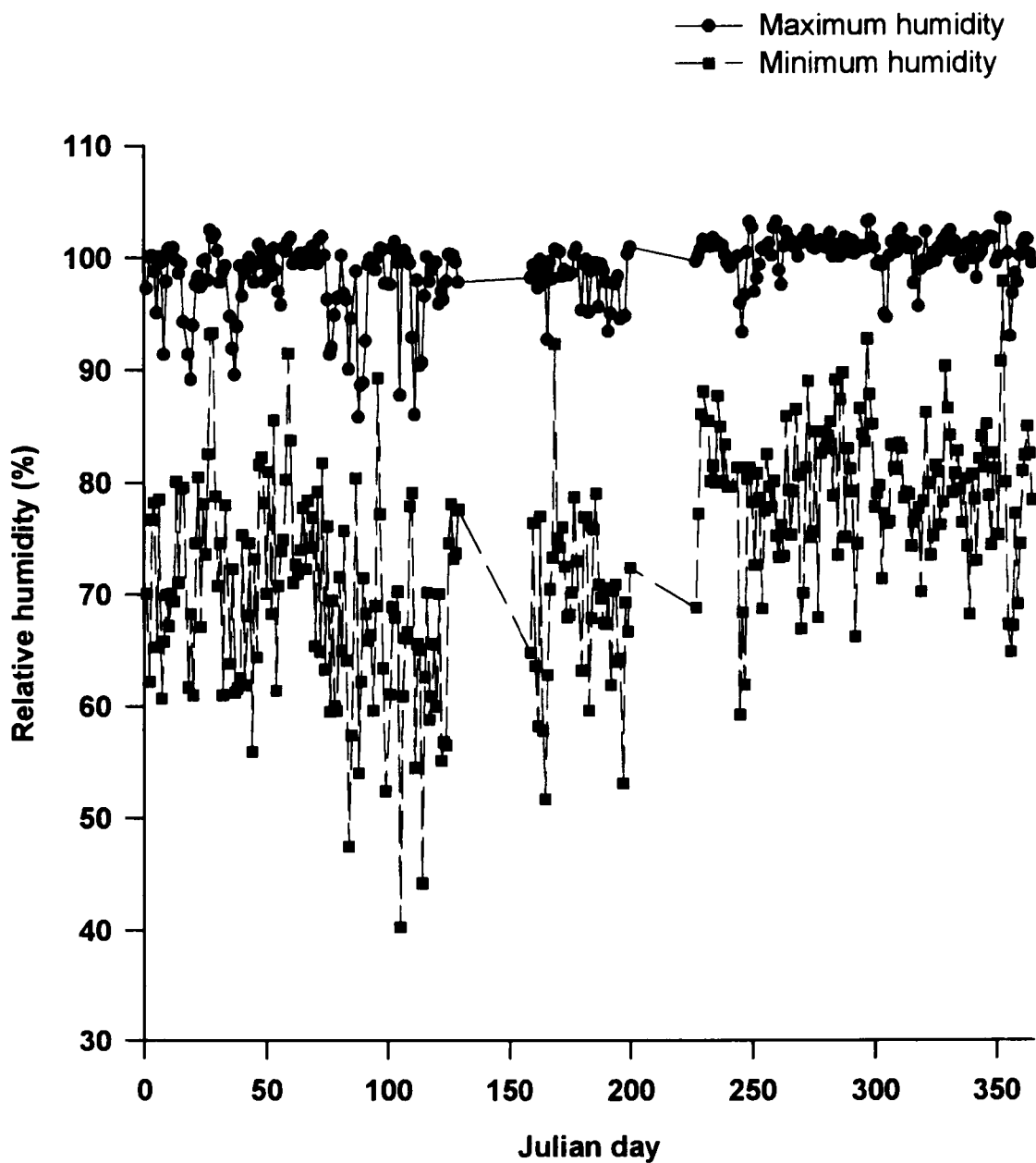


FIGURE 1-4. 1995 daily maximum and minimum relative humidity values (%) measured above the forest canopy from an observation tower in the Bisley Experimental Watersheds, Puerto Rico. No data available for days 130-158 and 201-226.

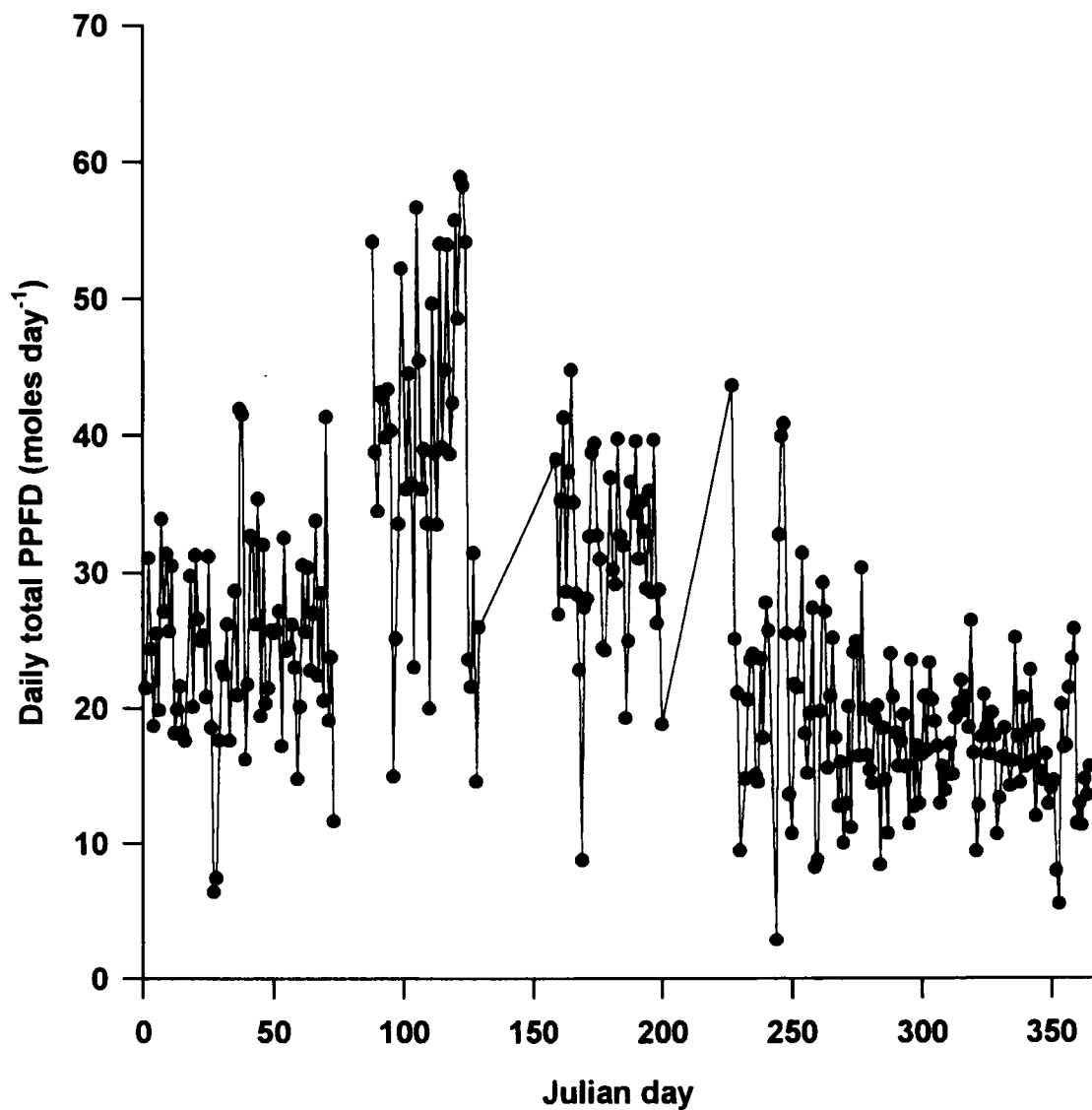


FIGURE 1-5. 1995 total daily photosynthetic photon flux density (PPFD, moles day⁻¹) measured above the forest canopy from an observation tower in the Bisley Experimental Watersheds, Puerto Rico. No data available for days 130-158 and 201-226.

Disturbance

The major types of natural disturbance affecting the Bisley Experimental Watersheds are treefalls, landslides, and hurricanes (Waide & Lugo 1992). The Bisley Experimental Watersheds are rapidly recovering from a catastrophic disturbance (*i.e.*, Hurricane Hugo of 1989) and recently experienced a less-severe disturbance (Hurricanes Luis and Marilyn of 1995). Over the past 300 years, hurricanes of the magnitude of Hugo strike the LEF approximately every 50-60 years, whereas hurricane damage of the magnitude of Luis and Marilyn occurs approximately every 22 years (Scatena 1989).

Hurricane Hugo struck the Bisley Watersheds of the LEF on September 18, 1989 with maximum sustained wind speeds of 166 km hr⁻¹ and maximum storm rainfall of 339 mm (Scatena & Larsen 1991). In the LEF, over 56 percent of the trees were severely defoliated; however, overall mortality was low (7%) (Walker 1991). In the Bisley Watersheds, 50 percent of aboveground biomass had fallen to the ground, and this area had received more damage than most of the LEF (Scatena, *et al.* 1993). Litterfall resulting from Hugo was 1.2-2 times higher than the annual input received by the LEF (Lodge & McDowell 1991). Average maximum canopy height was reduced by as much as 50 percent in some areas, and the effects on forest composition from this storm may last for years (Brokaw & Grear 1991). In a recent review of the population dynamics of several dominant tree species in the LEF (McCormick 1995), it was suggested that hurricanes are not only beneficial, but necessary, if these species are to retain their dominance in the forest.

For additional descriptions of the research area, the reader may refer to Odum and Pigeon (1970), Brown *et al.* (1983), Lugo (1986), and Scatena (1989).

C. Study Species

The herbaceous species selected for this study are *Dieffenbachia seguine* Schott., *Ichnanthus pallens* (Sw.) Munro, and *Pilea inaequalis* (Juss. ex Poir.) Wedd. *Dieffenbachia seguine* (family: Araceae) is a large perennial (mature plants > 0.5 m tall) found to grow primarily in moist areas, sometimes forming dense stands (Croat 1983) (Fig. 1-6). *Ichnanthus pallens* (family: Gramineae) is a low-growing (mature plants 0.4-1.0 m tall) (Zuloaga 1981) abundant perennial grass species that grows under a variety of microhabitat conditions (Fig. 1-7). *Pilea inaequalis* (family: Urticaceae) is a low-growing (mature plants 0.2 m tall) abundant perennial which is found in moist hillsides and forest habitats (Liogier 1985) (Fig. 1-8).

Ichnanthus pallens and *Pilea inaequalis* were selected because they are two of the most common herbs in the Bisley Experimental Watersheds and were prominent in early recovery following Hurricane Hugo (China 1996, personal communication). *Dieffenbachia seguine* was selected as a contrasting species; it has a more restricted habitat distribution (favoring moist, disturbance-prone valleys), and its large size and unusual growth habit make it an interesting species for study. Although few investigations of these particular species exist, there are several examples of studies of species within the same genera.

FIGURE 1-6. Illustration of adult *Dieffenbachia seguine* Schott. (Araceae).



FIGURE 1-7. Illustration of adult *Ichnanthus pallens* (Sw.) Munro (Gramineae).



FIGURE 1-8. Illustration of adult *Pilea inaequalis* (Juss. ex Poir.) Wedd.
(Urticaceae).



***Dieffenbachia* studies**

There are approximately 30 species belonging to the genus *Dieffenbachia* (Howard 1979). *Dieffenbachia seguine* is a terrestrial aroid found throughout Central America and the West Indies. It appears to be closely related to, and in fact may be the same species as *Dieffenbachia longispatha*, which occurs in Costa Rica, Honduras, Panama, and possibly as far south as Venezuela and Columbia (Croat 1978).

Dieffenbachia seguine, also known as "dumb cane," can cause a temporary loss of speech or death if eaten (Velez 1950; Walter & Khanna 1972; Brown 1988). This species is often grown as an ornamental plant and can escape from cultivation in the tropics. Stems of *Dieffenbachia seguine* grow erect, but usually do not exceed 1 m in height before collapsing, apparently under their own weight (Ray 1992). Stem collapse results in some lateral displacement of the shoot apex, which permits this species to be somewhat mobile and possibly encounter a more favorable microhabitat (Ray 1992). *Dieffenbachia* plants generally have very brittle stems, which when broken or cut can lead to the development of new plants (Velez 1950; Croat 1983).

Young (1986) studied the pollination biology of the colonial terrestrial herb *Dieffenbachia longispatha* (Araceae) and found a great deal of variation in flowering from year to year (68% in 1981 versus 9% in 1983) and averaging 27 percent over a four-year period. Abortion of inflorescences in this species was common (52% in 1982 and 47% in 1983).

In a pollination study of *Dieffenbachia oerstedii*, the main pollinator was identified to be a scarab beetle, *Cyclocephala pubescens* (Valerio 1984). Blooming for this species occurred mainly from May through June. Fruit maturation took approximately 11 to 13 months, and only 18.5 percent of the unmanipulated inflorescences monitored actually produced fruit.

***Ichnanthus* studies**

Rogers (1969) reported that there are approximately 122 taxa belonging to the genus *Ichnanthus*. *Ichnanthus pallens* is a highly variable species (Stieber 1975) that has been found in Cuba south to Trinidad, Mexico, Central America, and in South America to Paraguay and southern Brazil (Rogers 1969). The species has been introduced in southeast Asia and in Africa (Zuloaga 1981). *Ichnanthus pallens*, although sometimes considerably weedy, can be an important component in certain types of plant communities (Rogers 1969). In a study of the vegetation structure of the El Verde forest, Puerto Rico, *Ichnanthus pallens* had the highest relative density (32.9%) among the ground layer herbs surveyed (Smith 1970).

***Pilea* studies**

The genus *Pilea*, largest in the Urticaceae, contains approximately 400 species (Skean & Judd 1988), with the majority of those found in tropical America, Asia, and Africa (Liogier 1985). A few species are grown as ornamentals (*e.g.*, "aluminum plant" *Pilea cadierei* and "artillery plant" *Pilea microphylla*) (Skean & Judd 1988).

The distribution of *Pilea inaequalis* includes Puerto Rico, Hispaniola, Jamaica, and the Lesser Antilles (Liogier 1985).

Shreve (1914) measured growth rates of several tropical herbaceous plants and found that *Pilea nigrescens* exhibited a relatively slow growth rate in leaf length (approximately 0.41 mm day^{-1}). This Jamaican species, when compared to the temperate species *Pilea pumila*, was found to grow six to eight times more slowly (Shreve 1914).

Cid-Benevento (1986) examined factors that limit distribution of *Pilea pumila* to woodland habitats, and determined that competition from other herbs did not affect survivorship to reproduction. Rather, physiological tolerances to light and moisture were more important in preventing *Pilea pumila* from reproducing in 1- and 3-year-old successional fields.

References to the study species in future sections of this paper will be by genus only.

D. Purpose and Objectives

The purpose of this study is to describe the influence of microenvironment on growth and nutrient dynamics of three herbaceous species in the Bisley Experimental Watersheds as they recover from the impacts of Hurricane Hugo. The primary hypothesis is: these species contribute to rapid nutrient cycling in the post-hurricane disturbed forest, and thereby contribute to ecosystem resiliency. The following objectives have been developed:

1. To characterize microenvironments of the three species in terms of light and soil physical and chemical properties.
2. To examine relationships between microenvironment and plant growth and other estimators of plant performance.
3. To describe the ecological life cycles of the three species in terms of recruitment, mortality, growth, and clonal behavior and their role in forest recovery following canopy disturbance.
4. To determine nutrient contents and rates of decomposition of the three species in order to understand their role in nutrient dynamics.

CHAPTER II

METHODS

A. Microenvironment

In order to determine how the performance of these herbaceous study species vary under different microenvironmental and site conditions, three plots were located in both high and low light regimes at three distinct topographic positions (3 plots x 2 light regimes x 3 topographic positions = 18 plots) for each species (provided that populations of the study species were found living on a given topographic position/light regime). The topographic positions used in this study were ridges, slopes, and valleys. A ridge was defined as a long, raised structure or landform usually found separating two stream drainages (Art 1993). A slope was defined as an inclined landform, typically with straight middle segments, convex upper segments (near ridges), and concave lower segments (near valleys) (Scatena & Lugo 1995). A valley was defined as a lowland, usually long and narrow, found between mountainous or hilly terrain, with or without permanent streams. Because *Dieffenbachia* was not observed on ridges or high light slopes, and *Pilea* was not found growing on ridges, 18 plots were established for *Ichnanthus*, 12 for *Pilea*, and 9 for *Dieffenbachia*. *Pilea* and *Ichnanthus* plots measured 1 m². Due to its relatively larger size, *Dieffenbachia* plots measured 2 m² (i.e., 1 m x 2 m). Plots were arbitrarily selected to ensure sufficient population densities for measurement. An effort was made to have plots with at least 15 individuals of the species of interest.

Microenvironmental data were collected to quantify differences in soil and light characteristics in each habitat in order to relate these differences to measures of plant performance (*i.e.*, density, biomass, growth, etc.). With microenvironmental data it is also possible to determine the effect of topographic position on differences in soil characteristics, which may aid in explaining variability in productivity for different topographic positions.

Soil properties

Soil moisture. To determine the soil moisture content of the various topographic positions, soil cores were removed from the top 10 cm of soil at each site within 1 m where growth and biomass plots were located. Cores were taken from this depth because this is where the majority of fine roots are concentrated; thus, this depth is the most biologically important in terms of moisture and nutrient availability (Silver & Vogt 1993). Cores were not removed from within individual plots as this would have affected growth and mortality of the plants under study. All sites were sampled for soil moisture on the same day. Three replicates were taken for each site, and sampling was repeated approximately every two weeks from late May until July 1995 for a total of five sampling times. Soil cores were promptly taken to the lab and weighed fresh using an analytical balance. After weighing, cores were dried at 65 °C for 48 hrs. to prevent rotting. Soils were then re-dried at 105 °C for 48 hrs and re-weighed. Soil moisture content was calculated using the following formula from Miller and Donahue (1995):

$$\text{mass water ratio} = \frac{\text{moist soil wt.} - \text{dry soil wt.}}{\text{dry soil wt.}}$$

Bulk density. Bulk density was determined using the cores from which soil moisture content was determined. Bulk density was calculated by dividing the oven-dried soil weight by the inside volume of the corer (Miller & Donahue 1995).

Chemical properties. Samples for soil nutrient analyses were taken from the upper 10 cm of soil within each growth plot, with a minimum of six samples using a 2.0 cm inside diameter corer. After collection, samples were air dried, ground, and passed through a 0.85 mm sieve. Soil nutrient analyses were performed using standard methods (Silver *et al.* 1994) at the International Institute of Tropical Forestry, Rio Piedras, Puerto Rico. Soils were analyzed for exchangeable calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), aluminum (Al), iron (Fe), manganese (Mn) ($\text{cmol}(+)\text{kg}^{-1}$), percent carbon (C), percent nitrogen (N), extractable phosphorous (P) ($\mu\text{g g}^{-1}$), as well as estimated cation exchange capacity (ECEC, $\text{cmol}(+)\text{kg}^{-1}$) and pH (H_2O). Soil samples were removed from growth plots during the period of December 1995-January 1996 and were ground and analyzed during January-March 1996.

Light

Photosynthetic photon flux density (PPFD). To characterize general differences in daily light totals for open and closed canopy environments, photosynthetic photon flux density data were collected using a microclimate station consisting of 6 Li-Cor quantum sensors. Readings were recorded and averaged hourly with a Campbell Scientific 21X datalogger. The datalogger was situated in a valley with open and closed canopy light conditions. Three quantum sensors were situated above 3 growth plots under an open canopy, and 3 were placed above 3 growth plots under a closed canopy. The quantum sensors were leveled and placed approximately 50 cm above the herb layer in the center of each plot.

Light environment was also characterized for all of the growth and biomass plots using a portable Sunfleck Ceptometer. The ceptometer was held in a level horizontal position approximately 50 cm above the study species in each plot. Each recorded measurement consisted of four sample readings averaged for each plot between 10:00 a.m. and 1:00 p.m. Ideally, these measurements should be made under completely cloudy or completely clear conditions, so that changes in light from canopy cover will not be confused with changes in cloud cover. Because of variability in PPFD readings due to differences in cloud cover, these measurements were taken 7 times for growth plots and twice for biomass plots. These measurements were taken during the months of May through August 1995.

Canopy openness. To further characterize the light environment, a concave spherical densiometer was used to measure percent canopy openness above the study

species in all the biomass and growth plots. These measurements were repeated twice during May-July 1995 and repeated a third time in January 1996. With the densiometer held level above the plot, canopy openness was determined by averaging measurements for the north, south, east, and west directions.

B. Plant Growth

Growth measurement plots were located based on topographic position and light regime (see section A above). At each plot, fifteen individuals were tagged and measured for various indicators of growth. Selection of criteria for measurements of growth was based upon the following considerations: (1) are the measurements repeatable?, (2) can the measurements be accurate?, and (3) is the criterion likely to represent total plant growth, i.e., biomass production? Plots were established in December 1994-January 1995 and were measured for growth during January 1995, May 1995, July 1995, and January 1996.

Growth

For each species, the following measurements were made on all tagged individuals in growth plots.

Dieffenbachia. Stem diameter was measured at the point where the plant's rhizome was rooted in the soil and near the top of the plant at the uppermost leaf scar. Plant vertical height was measured to the uppermost leaf scar and also to the highest point on the plant. Number of inflorescences, if present, was counted. In

addition, leaf number and the length and width of the uppermost fully expanded leaf were measured.

Ichnanthus. Stem length from the point where the stem is rooted to the stem's apex was measured and number of leaves as well as inflorescences was counted. Evidence of herbivory was noted, if present.

Pilea. Number of leaves and length and width of the largest leaf were measured. Inflorescences were also counted and evidence of herbivory was noted, if present.

Population demography

For determination of population increase in *Dieffenbachia*, the total number of individual plants (*i.e.*, rooted stems) were counted for each growth plot. Due to the highly clonal nature of *Ichnanthus*, and because of difficulty in counting individual stems in extremely dense populations, percent cover (instead of number of individuals) was determined for each plot. For *Pilea*, total number of individuals (*i.e.*, rooted stems) were counted for each plot.

For determination of plant mortality, missing tagged plants were only considered dead when they were not found during the subsequent censusing period. For the final measurement period, all missing plants were reported as dead.

Clonal characteristics

To assess clonal characteristics of these herbs, 15 mature individual plants of each species growing in groups outside of permanent plots were selected for excavation. An individual plant was defined as a single rooted stem. To prevent selecting individual plants of the same clone, spacing between individuals selected for excavation was ≥ 10 m. *Dieffenbachia* plants were selected behind the Sabana Field Station near the Sabana River (Fig. 1-1). *Ichnanthus* and *Pilea* plants were selected along El Cristal Road in Bisley. For each individual selected, stem length was first measured (see section on growth), and then roots and rhizomes were carefully excavated using a garden trowel. The number of ramets connected to each individual and the distance from each ramet to the selected individual was then recorded.

Gas exchange

Dieffenbachia was the only species on which photosynthesis and dark respiration measurements were made due to equipment problems and time constraints. Photosynthesis and dark respiration of *Dieffenbachia* were measured using a portable photosynthesis system (LI-6200) by Li-Cor Inc. (Li-Cor 1989). Photosynthesis was measured for adult plants under *in situ* light conditions. A minimum of four plants for each species/site condition were measured. On each plant, $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$ were measured on one fully expanded, adult leaf for four consecutive 30 sec. samples.

Following photosynthesis measurements, dark respiration rates were measured by placing a heavy black cloth bag around the leaf for > 10 min., after which the

leaf chamber was placed on the same leaf for four consecutive 30 sec. samples.

Measurement units were $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$.

Photosynthesis and dark respiration measurements were taken during June-July 1995. During all measurements, leaf temperature remained within 3°C of the initial value and relative humidity within 10 percent of the initial value.

C. Biomass and Nutrient Content

Biomass

To determine differences in biomass allocation to different above ground organs, one plot was established for future removal of above ground biomass for each species at each topographic site and light condition in January 1996. These plots were harvested in July 1995. Samples from each plot were subdivided according to plant organ, which consisted of stems, leaves, and inflorescences. After cleaning plant organs of adhering materials, samples were dried at 65°C for 2 weeks and then weighed using an analytical balance.

In order to adequately relate measures of plant size to biomass and also to assess biomass differences by microenvironment, all 39 growth plots were harvested for biomass in January 1996. For each plot harvested, a maximum of ten plants were removed and measured according to species-specific size criteria. Plant density was determined in harvested plots. To minimize differences in moisture loss, fresh weight was measured on the same day that plants were harvested. Following fresh weight measurement, samples were dried and weighed.

Dieffenbachia. Fresh harvested *Dieffenbachia* plants were weighed using spring balances in the field. Due to their relatively large size and substantial moisture content, *Dieffenbachia* plants were dried at 100 °C for a minimum of 120 hrs. Measurement criteria for plants individually harvested and weighed included leaf number, stem length, and diameter at base and at uppermost leaf scar of plant.

Ichnanthus. Plants were weighed fresh using an analytical balance in the laboratory. Measurement criteria for plants individually harvested and weighed included leaf number and stem length.

Pilea. Plants were weighed fresh using an analytical balance in the laboratory. Measurement criteria for plants individually harvested and weighed included leaf number, stem length, and length and width of the largest leaf.

From the above fresh weight and dry weight biomass data for each species, percent water content of each species was determined using the following formula from Chapman (1976):

$$\% \text{ water content} = \frac{\text{fresh wt.} - \text{dry wt.}}{\text{dry wt.}} \times 100$$

Water content was measured to determine if there were differences between species and if water content differences could be related to topographically-influenced soil moisture conditions. Water content was calculated for whole plants only, *i.e.*, not for individual plant organs.

Nutrient content

Individual samples of *Dieffenbachia* were analyzed for N, P, K, Mg, and Ca using standard methods (Scatena *et al.* 1993) by the International Institute of Tropical Forestry analytical laboratory. Nutrient data for *Ichnanthus* and *Pilea* were obtained from Scatena *et al.* (1993), whereas *Dieffenbachia* samples were specifically harvested and analyzed for this study. Nutrient pools of study species and soils were compared.

D. Decomposition

In order to determine short-term decomposition rates of the three study species under different microenvironmental conditions, foliar decomposition rates were measured using mesh litterbags. This experiment was initiated in May 1995 and continued through July 1995. Fresh foliage was used due to the difficulty in obtaining uniformly senescent leaves in sufficient numbers. It is common to see leaves of these herbs decaying while still attached to the live plant.

A total of 288 litterbags were used. Bags were made of weather-resistant nylon mesh with an average mesh size of 2 mm. Bags were sewn on three sides with nylon thread, labeled with aluminum tags, and weighed empty. Fresh, healthy leaves were collected from the field from live plants and stored overnight prior to placement inside litterbags. For *Dieffenbachia*, a mature fresh leaf blade was placed inside a litterbag measuring 50 x 25 cm. For *Ichnanthus* and *Pilea*, 5-8 g of fresh leaves were placed inside each 25 x 25 cm litterbag. Litterbags were weighed again after fresh leaves were placed inside and sewn shut.

Litterbags were placed on the forest floor in plots representative of ridge, slope, or valley topography with high or low light conditions (3 topographic positions x 2 light regimes = 6 plots). These plots were located within 10 m of established growth plots. Litterbags were put out on the same day that bags were filled with fresh foliage and weighed. A subsample of litterbags with leaves were initially placed in the drying oven to obtain a dry weight conversion factor (*i.e.*, dry weight for day 0) for each species.

On retrieval from the field, three bags of each species were randomly selected from each site, cleaned of all outside adhering materials, and placed inside a drying oven at 65°C for 48 hrs.. Litterbags for *Ichnanthus* and *Pilea* were retrieved after 16, 29, 43, and 58 days in the field, whereas *Dieffenbachia* litterbags were retrieved after 16, 22, 29, 36, and 43 days in the field.

E. Data Analysis

To determine if the data were normally distributed, the Shapiro-Wilk test was used. For data that were normally distributed, analysis of variance was used to examine the effects of microenvironment on measures of species performance. Regression techniques and Spearman Rho correlation coefficients were calculated to determine relationships between continuous variables (SAS Institute 1995). In the case where data were not normally distributed, values were either log transformed, or Wilcoxon/Kruskal-Wallis nonparametric tests (instead of ANOVA) were used to determine differences between treatments (SAS Institute 1995). To determine which

treatment levels of an independent variable were significantly different, Student's t and/or Duncan's multiple range tests were used (SAS Institute 1995; Sokal & Rohlf 1981). All statistical tests were performed using the software programs SAS® and/or JMP® (SAS Institute 1995).

CHAPTER III

RESULTS

A. Microenvironment

Soil properties

Soil moisture. Soil moisture content was found to vary significantly between all topographic positions ($p < 0.01$) (Fig. 3-1). Overall, ridges had the driest soils (mean = 49.76%), slopes were intermediate (mean = 57.82%), and valleys had the wettest soils (mean = 62.95%).

When soil moisture levels were compared, significant differences between species habitats were observed ($p < 0.01$). On average, *Pilea* favored moist sites (mean = 64.57%) and differed significantly from *Ichnanthus* (mean = 53.34%), which was found to grow in drier soils. Soil moisture of *Dieffenbachia* habitats was intermediate between soil moisture of habitats of the other two species (mean = 62.47%). When soil moisture levels of species habitats were analyzed separately by topographic position, on slopes, *Pilea* (mean = 65.84%) differed significantly from both *Ichnanthus* (mean = 50.39%) and *Dieffenbachia* (mean = 56.04%) in soil moisture ($p < 0.01$). However, soil moisture differences between species habitats in valleys were not significant.

Growth rates of some study species varied significantly with soil moisture and/or its surrogate variable, topographic position. In *Ichnanthus*, absolute growth rate significantly differed according to differences in soil moisture ($p < 0.05$), and a

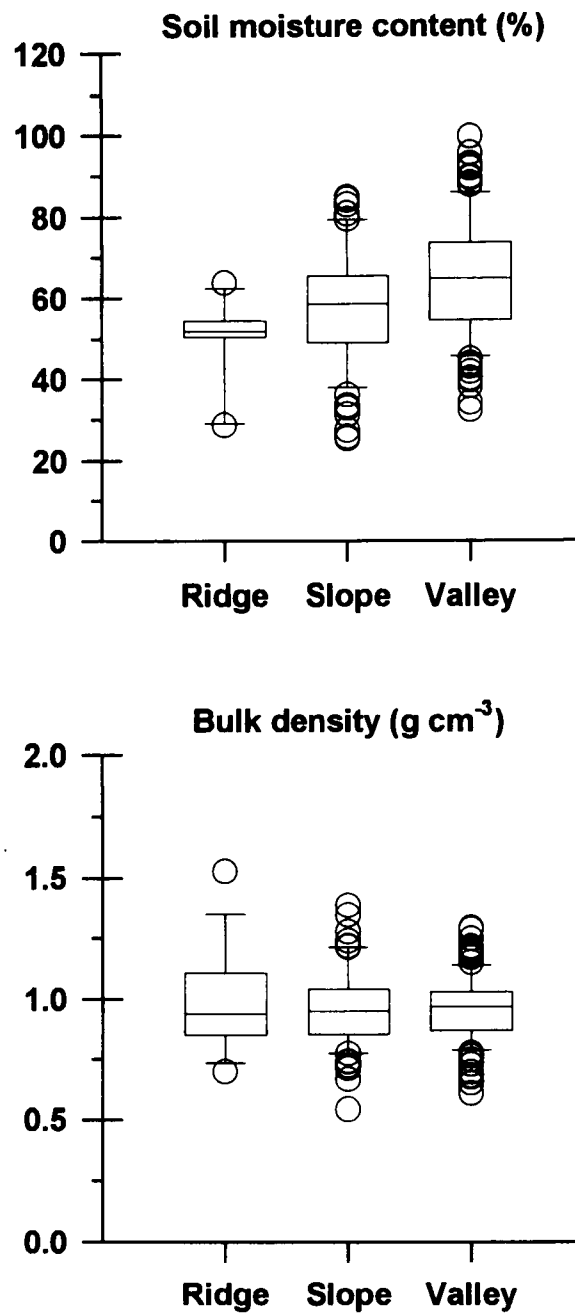


FIGURE 3-1. Box plots showing the range of soil moisture and bulk density (g cm^{-3}) across topographic positions for study sites in the Bisley Experimental Watersheds, Puerto Rico. Horizontal bars dissecting the boxes represent the median, boxes are the interquartile range, and circles represent outliers.

similar pattern was found in *Pilea* ($p < 0.001$). Because soil moisture is largely determined by topographic position, the effect of topographic position on absolute growth rate was also examined. Growth differed significantly with topography only in *Ichnanthus* ($p < 0.01$), with plants living on slopes (mean growth index = 117.07 leaves*stem length (cm) mo^{-1}) growing 13-22 times faster than plants on ridges (mean = 8.87) or in valleys (mean = 5.26).

Soil moisture was significantly correlated with a number of soil chemical and physical properties (Table 3-1). Soil moisture was positively correlated with exchangeable Ca, Mg, K, Mn, ECEC, pH, and exchangeable acidity. Soil moisture was negatively correlated with exchangeable Al and Fe, bulk density, and extractable P. Soil organic matter was positively correlated with total N and extractable P (as found by Silver *et al.* 1994) and also exchangeable Na and Fe. Exchangeable acidity was positively correlated with exchangeable Fe, and both were positively correlated with exchangeable Al and extractable P and negatively correlated with soil moisture, exchangeable Ca, Mg, K, Mn, and pH. Refer to Table 3-1 for complete results.

Bulk density. No statistically significant topographic pattern was observed for bulk density (Fig. 3-1). This agrees with Silver *et al.* (1994). Average bulk densities of soils on ridges, slopes, and valleys differed from the mean bulk density of 0.63 g cm^{-3} for Bisley soils as reported by Silver *et al.* (1994), probably due to differences in sample removal methods and possible soil compaction in this study. However, these values are within the range of those reported by Edmisten (1970) for nearby El Verde soils. Unlike soil moisture, there was no significant relationship between bulk density

TABLE 3-1. *Matrix of Spearman Rho correlation coefficients for soil properties in species growth plots, Bisley Experimental Watersheds, Puerto Rico. Significant correlations are marked with * ($p < 0.05$), ** ($p < 0.01$), and NC (no comparison).*

soil property	soil moisture (%)	bulk density (g cm ⁻³)	Ca ²⁺	Mg	K	Na	Al	ECBC	Organic matter (%)	N (%)	pH	P (μg g ⁻¹)	Fe	Mn	Exchangeable acidity
soil moisture (%)	NC														
bulk density (g cm ⁻³)	-0.37*	NC													
Ca	0.61**	0.00	NC												
Mg	0.67**	-0.13	0.89**	NC											
K	0.44**	-0.25	0.55**	0.65**	NC										
Na	-0.01	-0.23	0.07	0.20	0.37*	NC									
Al	-0.54**	-0.14	-0.94**	-0.84**	-0.45**	0.08	NC								
ECBC	-0.06	0.07	0.10	0.22	0.34*	0.30	0.07	NC							
Organic matter (%)	-0.15	-0.10	0.09	-0.02	0.19	0.56**	0.08	0.25	NC						
N (%)	0.08	-0.31	0.15	0.13	0.39*	0.59**	0.04	0.18	0.86**	NC					
pH	0.63**	0.10	0.90**	0.78**	0.46**	-0.15	-0.90**	-0.05	-0.15	-0.10	NC				
P (μg/g)	-0.47**	-0.10	-0.24	-0.19	0.19	0.55**	0.37*	0.35*	0.67**	0.60**	-0.40*	NC			
Fe	-0.63**	-0.08	-0.83**	-0.82**	-0.33*	0.18	0.87**	0.05	0.32*	0.22	-0.84**	0.55**	NC		
Mn	0.82**	-0.34*	0.75**	0.73**	0.50**	0.01	-0.71**	-0.12	-0.18	0.02	0.74**	-0.48**	-0.67**	NC	
Exchangeable acidity	-0.49**	-0.15	-0.91**	-0.77**	-0.40*	0.06	0.95**	0.14	0.01	-0.04	-0.89**	0.33*	0.82**	-0.68**	NC

¹Measurement units for elements lacking units and estimated cation exchange capacity (ECBC) above are in cmol(+)kg⁻¹.

and study species. However, bulk density was negatively correlated with Mn ($p < 0.05$) (Table 3-1).

Chemical properties. A number of soil chemical properties varied significantly ($p < 0.05$) with topographic position (Fig. 3-2). Concentrations of exchangeable Ca and Mg, and pH values increased from ridges to valleys, whereas exchangeable acidity, Al, and Fe decreased (Tables 3-2 and 3-3). Additionally, ECEC, C/N ratios, and exchangeable K and Mn also differed significantly across topographic positions. For a listing of soil chemistry data, refer to Appendix A.

Exchangeable nutrients were also compared across topographic positions using the relative saturation of the exchange complex by a given element (*i.e.*, exchangeable nutrients $\text{cmol}(+) \text{ kg}^{-1}$ / estimated cation exchange capacity $\text{cmol}(+) \text{ kg}^{-1}$) (Table 3-4). Percent saturation of Ca increased from ridges to valleys, and percent saturation of Al decreased from ridges to valleys. Ridges had significantly more Mg and Na occupying exchange sites. Percent saturation of Mn and K were lowest on ridges, whereas percent saturation of Fe was lowest in valleys.

When differences in soil chemical properties were compared for habitats of each study species, several soil chemical properties varied significantly (Tables 3-2 and 3-3). Exchangeable Ca in soils occupied by *Pilea* was significantly higher than in soils occupied by *Ichnanthus*. Exchangeable Mg, K, and Mn levels were significantly higher in soils of *Pilea* habitats. *Ichnanthus* soils had significantly lower exchangeable acidity and extractable P, lower pH values, and were higher in exchangeable Al, C/N ratios, and Fe.

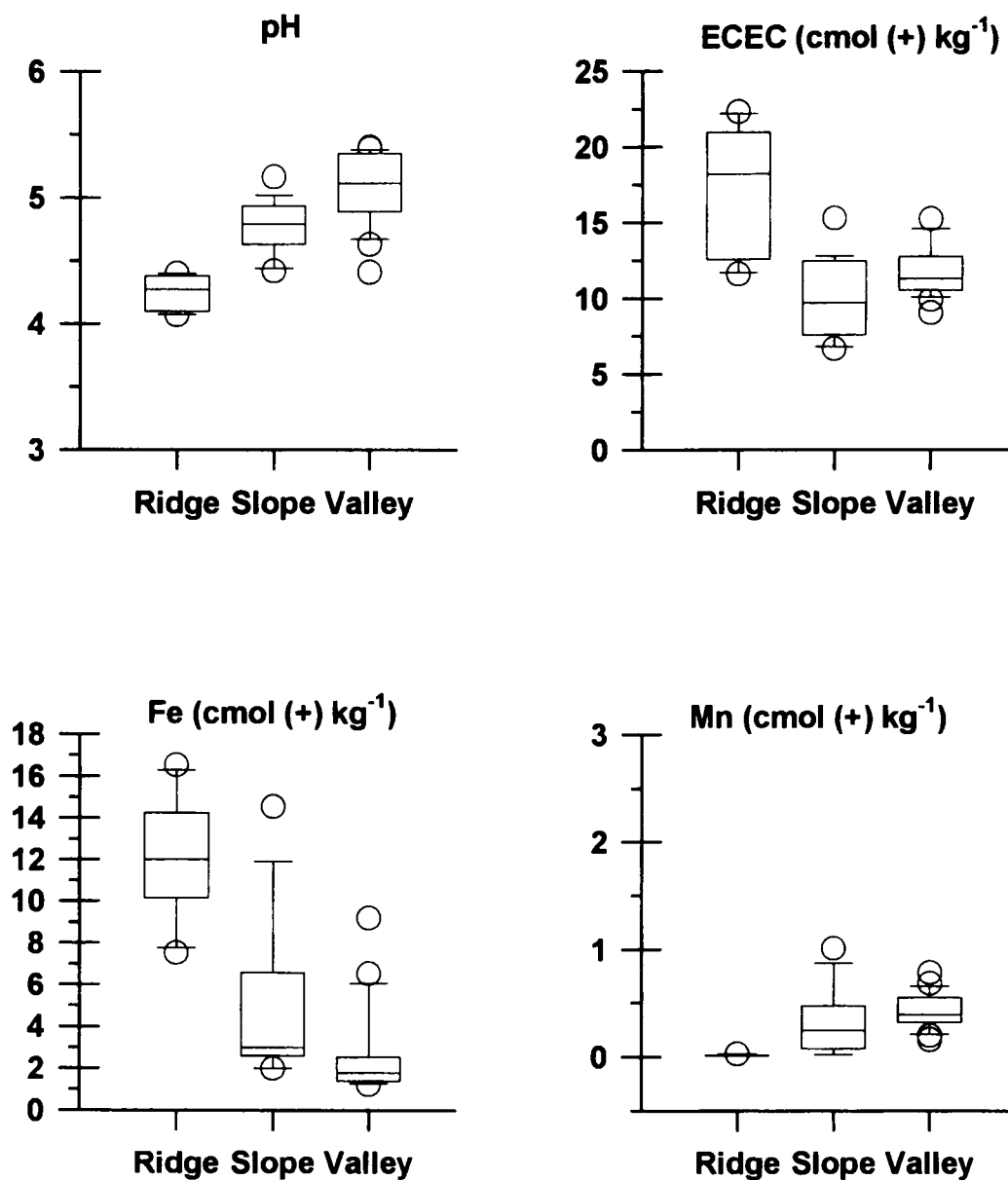


FIGURE 3-2. Box plots showing the range of soil chemical properties across topographic positions for study sites in the Bisley Experimental Watersheds, Puerto Rico.

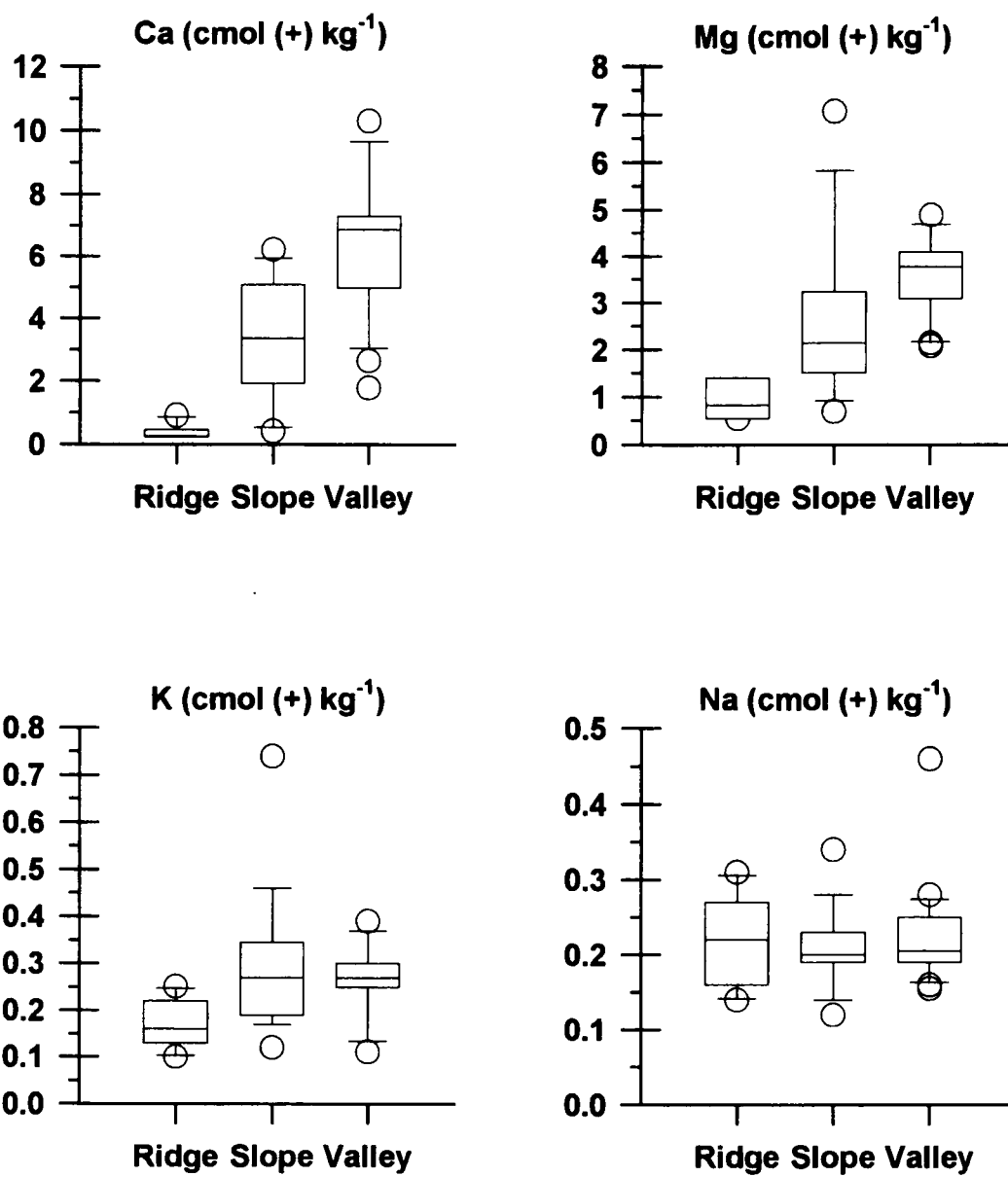


FIGURE 3-2. *Continued.*

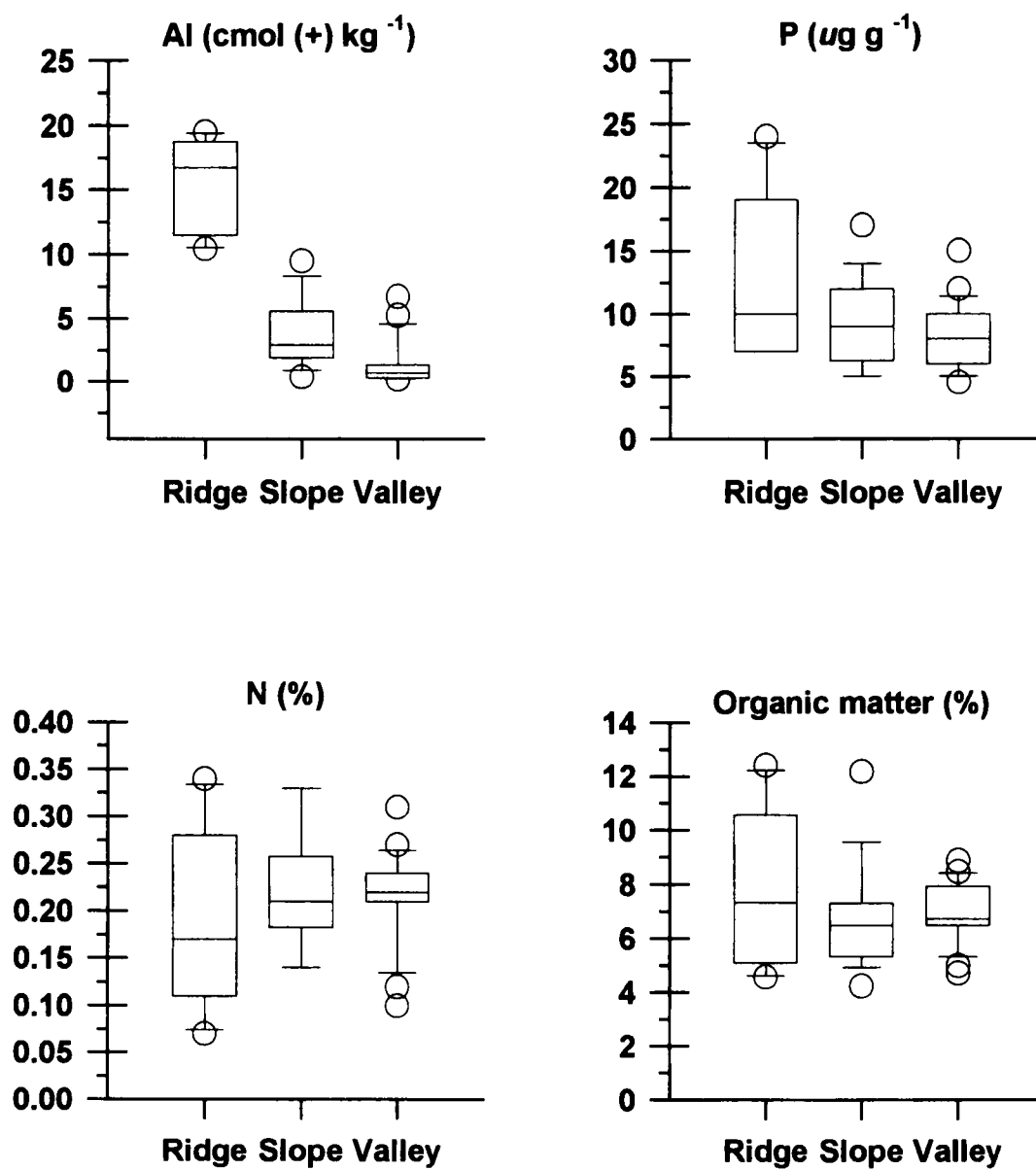


FIGURE 3-2. *Continued.*

TABLE 3-2. Mean exchangeable cations, exchangeable acidity, and pH by dominant herbaceous species and topographic position in the Bisley Experimental Watersheds, Puerto Rico. Standard errors (se) are to right of means. Different letters indicate significant differences ($p < 0.05$) between topographic positions or species.

Species		Exchangeable																					
		n	Ca	se	Mg	se	K	se	Al	se	Na	se	acidity	se	pH (H2O)	se							
<i>Dieffenbachia</i>		9	4.684	0.828	ab	2.726	0.428	a	0.210	0.034	a	2.068	1.587	a	0.214	0.021	a	1.745	1.589	a	4.921	0.107	a
<i>Ichnanthus</i>		18	2.782	-0.586	a	2.029	0.304	a	0.229	0.024	a	7.705	1.122	b	0.228	0.015	a	7.704	1.124	b	4.617	0.076	b
<i>Pilea</i>		12	6.229	0.717	b	3.991	0.371	b	0.348	0.029	b	1.473	1.374	a	0.211	0.018	a	1.473	1.376	a	5.086	0.093	a
Species																							
(slopes only)																							
<i>Dieffenbachia</i>		3	2.697	0.852	ab	1.597	0.771	a	0.187	0.070	a	3.323	1.505	a	0.190	0.026	a	2.353	1.577	a	4.843	0.079	a
<i>Ichnanthus</i>		6	2.292	0.602	a	1.697	0.545	a	0.225	0.049	a	5.237	1.064	a	0.207	0.023	a	5.235	1.115	a	4.565	0.056	b
<i>Pilea</i>		6	4.950	0.602	b	4.122	0.545	b	0.417	0.049	b	2.451	1.064	a	0.225	0.024	a	2.453	1.115	a	4.951	0.056	a
Species																							
(valleys only)																							
<i>Dieffenbachia</i>		6	5.678	0.577	a	3.291	0.288	a	0.222	0.037	a	1.441	0.425	a	0.226	0.018	a	1.441	0.426	a	4.959	0.069	a
<i>Ichnanthus</i>		6	5.661	1.279	a	3.468	0.458	a	0.291	0.027	a	2.269	1.196	a	0.258	0.042	a	2.268	1.196	a	5.037	0.171	a
<i>Pilea</i>		6	7.648	0.623	a	3.860	0.255	a	0.280	0.026	a	0.495	0.094	a	0.197	0.013	a	0.493	0.097	a	5.222	0.089	a
Topographic position																							
Ridge		6	0.393	0.794	a	0.923	0.508	a	0.170	0.045	a	15.608	1.058	a	0.220	0.026	a	15.608	1.086	a	4.250	0.103	a
Slope		15	3.436	0.502	b	2.647	0.322	b	0.294	0.029	b	3.740	0.669	b	0.211	0.016	a	3.546	0.687	b	4.775	0.065	b
Valley		18	6.329	0.458	c	3.540	0.294	c	0.264	0.026	b	1.402	0.611	c	0.227	0.015	a	1.401	0.627	c	5.073	0.059	c

TABLE 3-3. Mean exchangeable cations, extractable P, total N, organic matter, and C/N ratio by dominant herbaceous species and topographic position in the in the Bisley Experimental Watersheds, Puerto Rico. Standard errors (se) to right of means. Different letters indicate significant differences ($p < 0.05$) between topographic positions or species.

Species	n	Mn	se	Fe	se	P (ug/g)	se	Total N (%)	se	Organic		
										matter (%)	se	C/N ratio
<i>Dieffenbachia</i>	9	0.302	0.061	a 2.709	1.196	a 7.500	1.238	a 0.221	0.021	a 6.777	0.625	a 18.222
<i>Ichnanthus</i>	18	0.158	0.158	a 8.070	0.846	b 11.583	0.875	b 0.209	0.015	a 7.517	0.442	a 22.139
<i>Pilea</i>	12	0.586	0.586	b 2.211	1.036	a 7.750	1.072	a 0.219	0.018	a 6.512	0.542	a 17.750
Species												
(slopes only)												
<i>Dieffenbachia</i>	3	0.152	0.101	a 3.323	1.877	a 7.667	1.786	a 0.233	0.035	a 6.777	0.625	a 16.333
<i>Ichnanthus</i>	6	0.112	0.071	a 8.485	1.327	b 12.167	1.263	a 0.230	0.025	a 7.517	0.442	a 20.000
<i>Pilea</i>	6	0.642	0.071	b 2.663	1.327	a 7.667	1.263	a 0.213	0.025	a 6.512	0.542	a 16.333
Species												
(valleys only)												
<i>Dieffenbachia</i>	6	0.377	0.063	a 2.401	0.865	a 7.417	1.059	a 0.214	0.010	a 6.860	0.233	a 19.167
<i>Ichnanthus</i>	6	0.343	0.063	a 3.653	0.865	a 9.750	1.059	a 0.208	0.034	a 6.972	0.723	a 20.417
<i>Pilea</i>	6	0.531	0.063	a 1.759	0.865	a 7.833	1.059	a 0.225	0.009	a 7.242	0.354	a 19.167
Topographic position												
Ridge	6	0.020	0.092	a 12.073	1.309	a 12.833	1.605	a 0.190	0.026	a 7.882	1.316	a 26.000
Slope	15	0.332	0.058	b 5.124	0.828	b 9.467	1.015	a 0.224	0.016	a 6.746	0.515	a 17.800
Valley	18	0.417	0.053	b 2.604	0.756	c 8.333	0.926	a 0.216	0.015	a 6.998	0.266	a 19.583

TABLE 3-4. Mean percent saturation of exchangeable cations in the soil exchange complexes by dominant herbaceous species and topographic position in the Bisley Experimental Watersheds, Puerto Rico. Standard errors (se) to right of means. Different letters indicate significant differences ($p < 0.05$) between topographic positions or species.

Species	n	Ca	se	Mg	se	K	se	Al	se	Na	se	Mn	se	Fe	se
<i>Dieffenbachia</i>	9	47.03	6.53	27.63	3.25	2.22	0.30	25.20	9.19	2.29	0.21	3.04	0.61	30.94	8.77
<i>Ichnanthus</i>	18	24.54	4.61	17.55	2.30	1.93	0.21	54.09	6.50	1.90	0.15	1.46	0.43	62.18	6.20
<i>Pilea</i>	12	51.49	5.65	31.97	2.81	2.84	0.26	11.97	7.96	1.72	0.18	5.00	0.53	18.39	7.60
Species															
(slopes only)															
<i>Dieffenbachia</i>	3	37.61	10.50	22.64	5.39	2.66	0.59	47.52	12.36	2.69	0.29	2.11	1.21	47.43	15.14
<i>Ichnanthus</i>	6	25.55	7.43	18.51	3.81	2.38	0.42	51.37	8.74	2.20	0.21	1.33	0.86	83.74	10.71
<i>Pilea</i>	6	42.00	7.43	32.84	3.81	3.46	0.42	19.83	8.74	1.84	0.21	5.57	0.86	22.38	10.71
Species															
(valleys only)															
<i>Dieffenbachia</i>	6	51.73	5.37	30.13	2.44	2.01	0.20	14.04	6.79	2.08	0.26	3.51	0.63	22.69	8.13
<i>Ichnanthus</i>	6	45.89	5.37	28.97	2.44	2.42	0.20	20.51	6.79	2.21	0.26	2.93	0.63	32.18	8.13
<i>Pilea</i>	6	60.98	5.37	31.10	2.44	2.22	0.20	4.12	6.79	1.59	0.26	4.43	0.63	14.40	8.13
Topographic position															
Ridge	6	2.18	6.13	5.15	3.22	0.99	0.31	90.39	8.00	1.29	0.24	0.12	0.84	70.62	11.22
Slope	15	34.54	3.88	25.07	2.04	2.87	0.19	37.98	5.06	2.16	0.15	3.18	0.53	51.94	7.10
Valley	18	52.87	3.54	30.07	1.86	2.22	0.18	12.89	4.62	1.96	0.14	3.62	0.49	23.09	6.48

Differences in elemental saturation of soil exchange sites were also compared by the dominant herbaceous species present in a given growth plot (Table 3-4). Soils of *Ichnanthus* plots had significantly lower percent saturation of Ca, Mg, Mn, and Fe in comparison to soils of the other study species. Percent saturation of Al was highest in soils of *Ichnanthus* plots and no significant differences were found in percent saturation of K or Na.

Differences in soil chemical properties associated with for each study species were examined further by analyzing differences in soil chemistry for soils of each species by topographic position. No significant differences in soil chemistry were found between soils of the study species in valleys, whereas a number of significant differences were found on slopes (Tables 3-2 and 3-3). On slopes, exchangeable Ca, Mg, Fe, Mn, and K, as well as percent saturation of Al, C/N ratio, and pH values differed significantly ($p < 0.05$).

When comparing differences in elemental saturation of soil exchange complexes for each species in a given topographic position, *Pilea*-occupied plots were found to have significantly higher percent saturation levels of Mn on slopes (Table 3-4). Also on slopes, *Ichnanthus*-dominated plots had significantly higher percent saturation of Fe than *Pilea*-dominated plots.

Light

Datalogger measurements of PPFD significantly differed between open and closed canopy sites ($2.32 \text{ mol day}^{-1}$ versus $0.24 \text{ mol day}^{-1}$) (Fig. 3-3). There was also

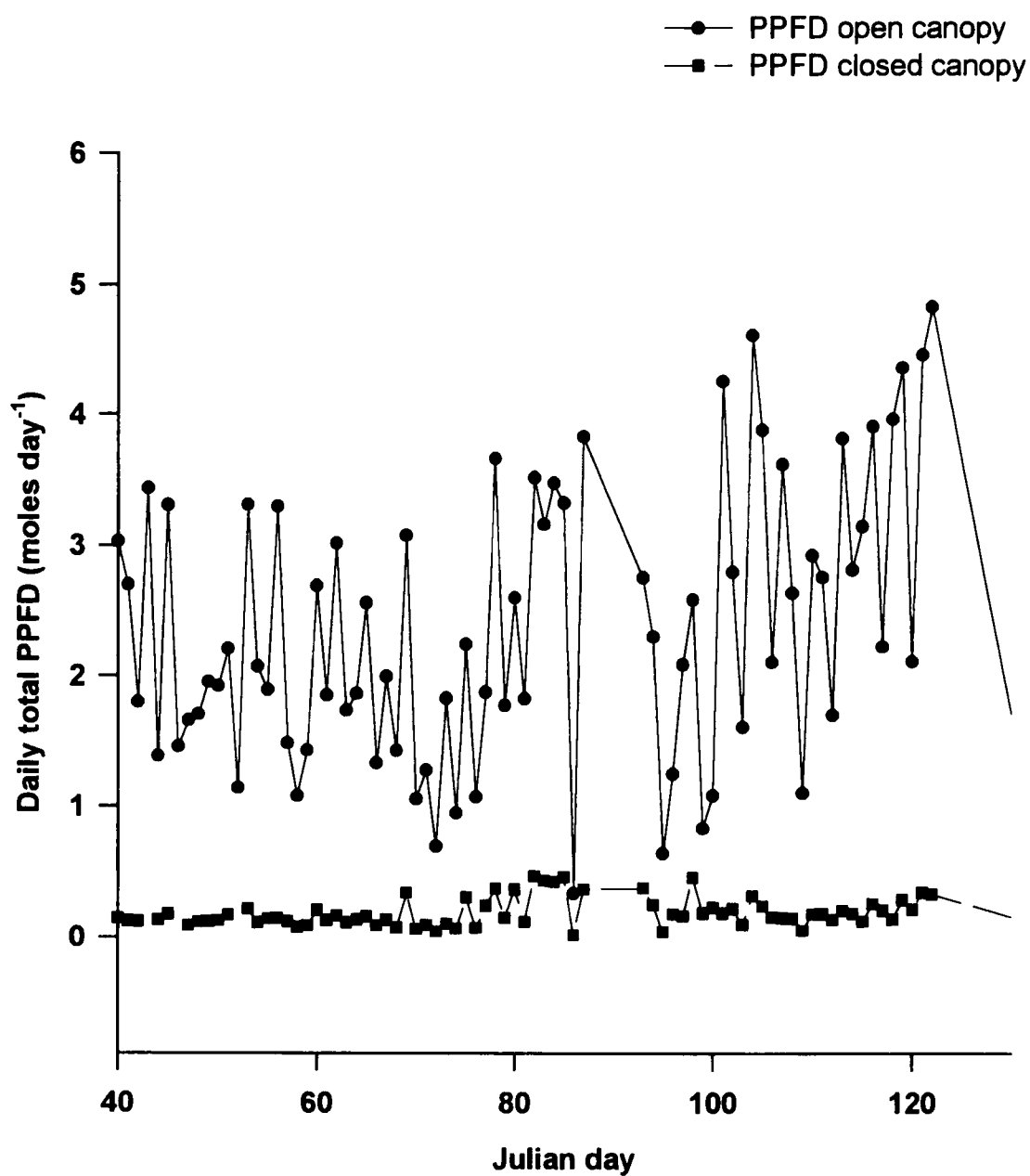


FIGURE 3-3. Daily total PPFD ($\mu\text{mol m}^{-2}\text{s}^{-1}$) in open vs. closed canopy sites in the Bisley Experimental Watersheds, Puerto Rico.

greater variability in PPFD in the open canopy site as compared to the closed canopy site, which was probably due to greater sensitivity of open canopy sensors to changes in cloud cover. In comparing PPFD for a cloudy versus sunny day (Figs. 3-4 and 3-5), the closed canopy site received more light on the cloudy day, probably due in part to the greater abundance of diffuse light.

Canopy openness and PPFD (ceptometer measurements) were found to be significantly correlated ($r_s = 0.77$; $p < 0.01$) (Fig. 3-6). The functional relationship between these variables was determined to be $y = 14.95x - 49.19$, where $y = \text{PPFD}$ and $x = \text{percent average canopy openness}$ ($R^2=0.70$; $p < 0.0001$).

The relationship between PPFD and population size, as well as several other measures of plant performance (e.g., dry weight biomass, total leaf number, etc.) was determined for each species. In *Dieffenbachia*, stem length, leaf number, dry weight biomass, or fresh weight biomass, did not significantly differ according to PPFD, nor did PPFD contribute to plant density or total plant water content. The small number of sample plots ($n = 9$) for *Dieffenbachia* may account for the lack of significance. In *Ichnanthus*, PPFD was again nonsignificant for the above variables. However, the relationship between PPFD and total plants per *Ichnanthus* plot approached significance ($p = 0.063$). *Pilea* was more sensitive to differences in PPFD than the other two species. Total stem length (total = sum for entire plot) varied significantly with changes in PPFD ($p < 0.05$) as did total dry weight biomass ($p < 0.05$), total fresh weight biomass ($p < 0.05$), plant density ($p < 0.01$), and total plant water content ($p < 0.05$).

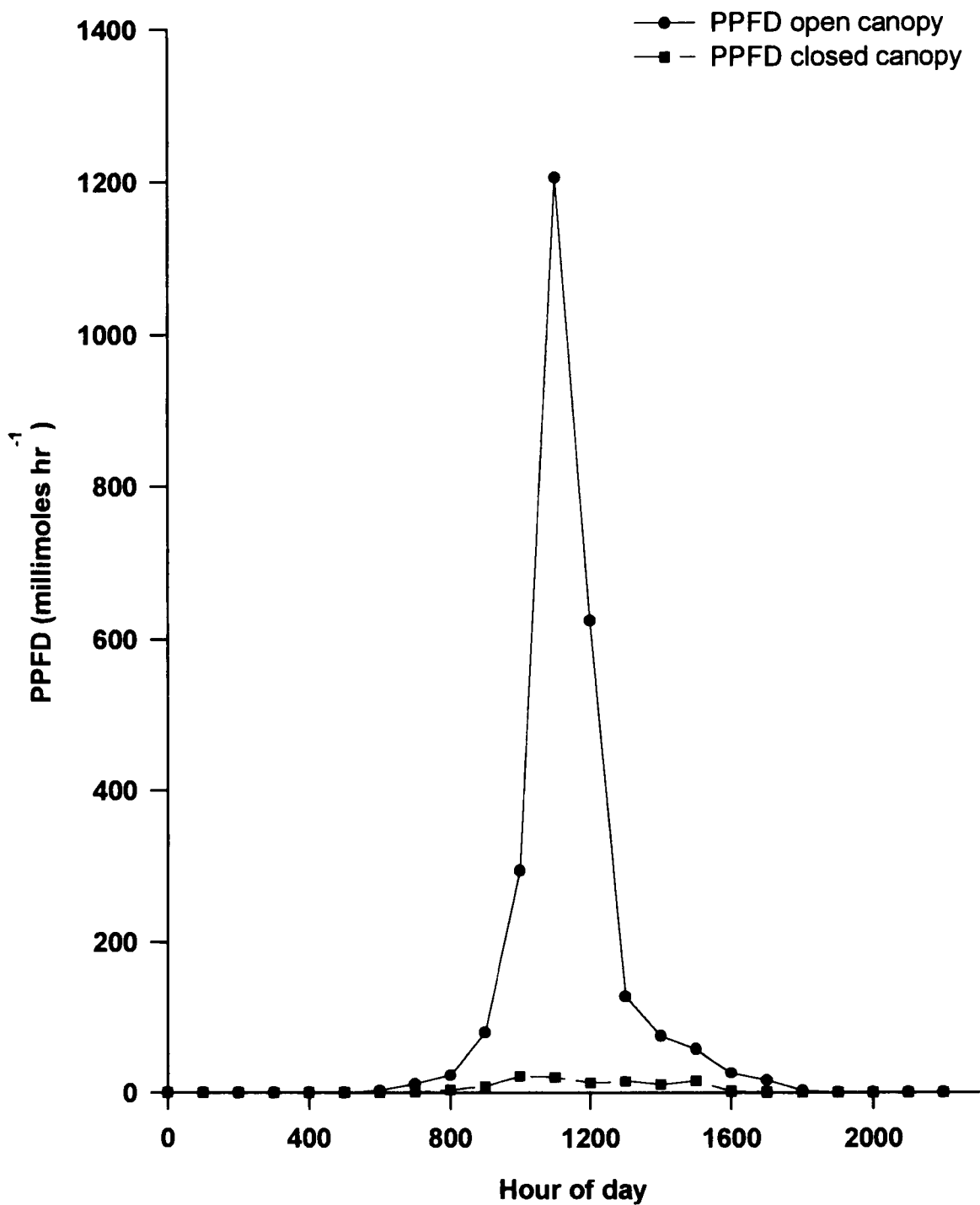


FIGURE 3-4. Photosynthetic photon flux density (mmol hr⁻¹) in open vs. closed canopy sites on sunny day (Julian day 101, 1995) in the Bisley Experimental Watersheds, Puerto Rico.

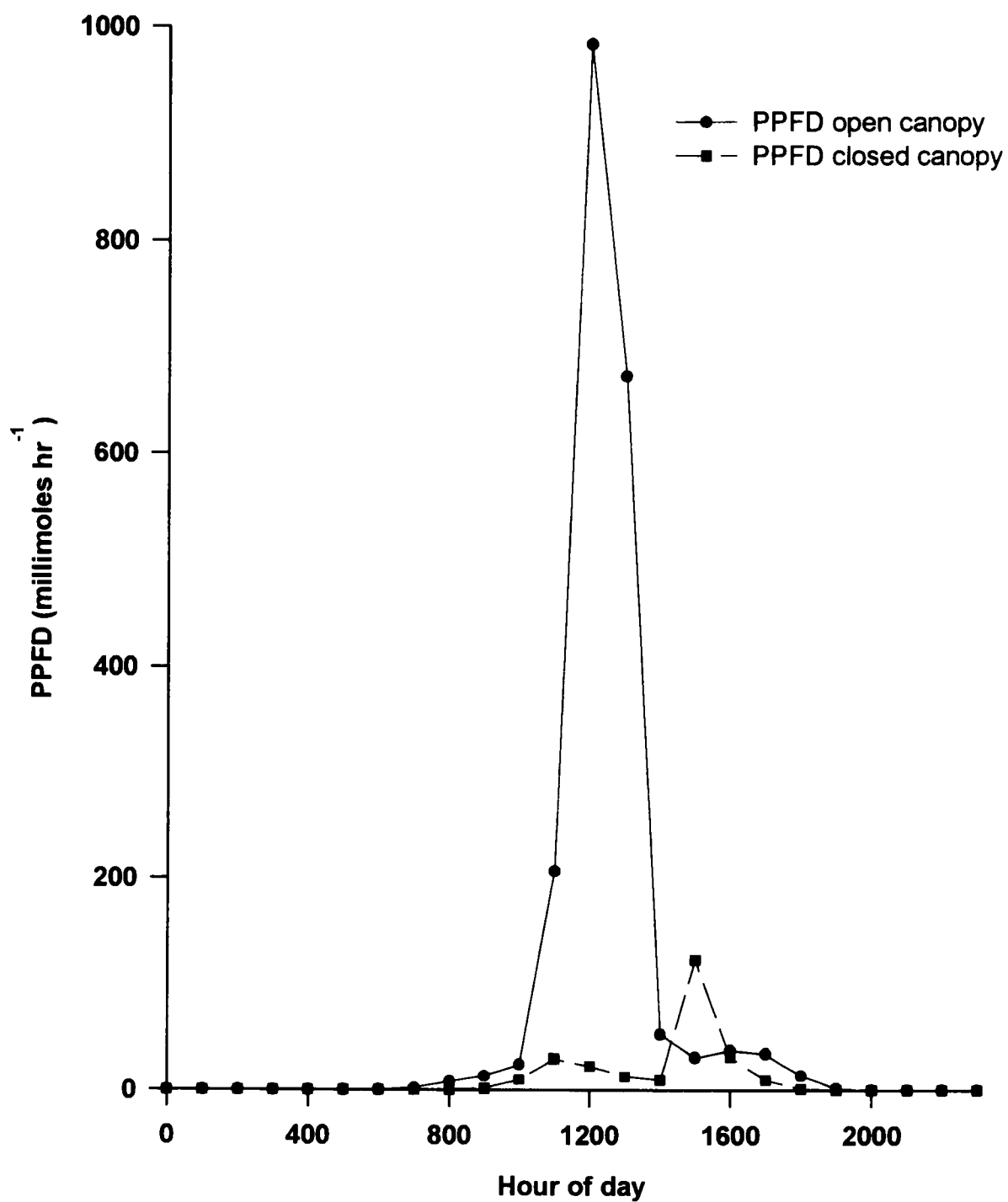


FIGURE 3-5. Photosynthetic photon flux density (mmol hr^{-1}) in open vs. closed canopy sites on cloudy day (Julian day 84, 1995) in the Bisley Experimental Watersheds, Puerto Rico.

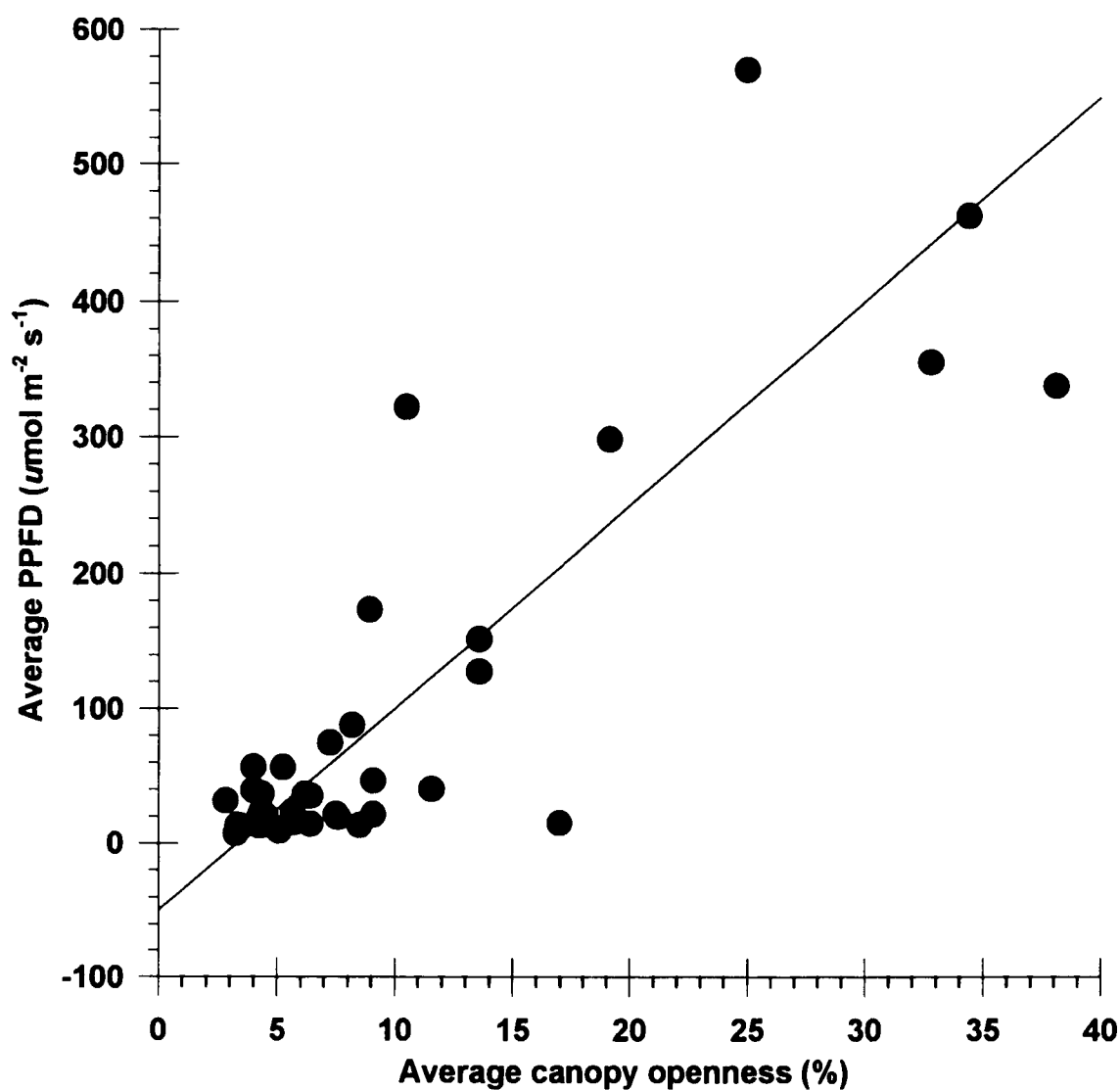


FIGURE 3-6. Functional relationship between average canopy openness and average PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for growth measurement plots (see Methods). ($r_s = 0.77$, $p < 0.01$). Regression equation is $y = 0.047x + 4.98$, $R^2 = 0.71$, $p < 0.0001$.

B. Plant Growth

Growth

Dieffenbachia. Absolute growth rate was calculated for *Dieffenbachia* by using changes in stem volume (cm³) between measurement intervals. Stem volume was the most effective measure of growth, and was also well-correlated to total plant biomass (see section on biomass and nutrient content). By measuring stem length as well as the diameter of each stem beneath the lowermost leaf scar and where the rhizome is rooted in the soil, it was possible to calculate stem volume for

Dieffenbachia:

$$Volume = \frac{(d_1 + d_2)^2}{4} \times \pi \times stem\ length$$

The average absolute growth rate using this measure was determined to be 13.23 cm³ mo⁻¹. Differences in growth rates over measurement intervals were not significant, but the highest growth rate was observed for the period July 1995-January 1996 (28.62 cm³ mo⁻¹) (Table 3-5). Growth rates were negative for the January 1995-May 1995 period, which may have been due to stem dieback. A number of tagged plants had completely lost their leaves in May 1995. For a listing of growth rate plot averages, refer to Appendix B-1.

Ichnanthus. Growth rates were determined for *Ichnanthus* using the product of leaf number and stem length for individual plants over the measurement intervals. This growth index was used because it also correlated to plant biomass and was easy

TABLE 3-5. *Growth rates for each species across measurement periods (tagged plants only).*

Measurement period	Growth rates ¹ of herbaceous species			
	1/95-5/95	5/95-7/95	7/95-1/96	Overall (1/95-1/96)
Species				
<i>Dieffenbachia</i>	-3.13a ²	7.63a	28.62a	13.23
<i>Ichnanthus</i>	-6.81a	21.10a	88.13b	41.35
<i>Pilea</i>	7.52a	-0.91a	27.75a	15.162

¹Measurement units for *Dieffenbachia* are stem volume (cm³ mo⁻¹). Units for *Ichnanthus* are leaf number x stem length (cm mo⁻¹). Units for *Pilea* are leaf number x largest leaf area (cm² mo⁻¹).

²Growth rates with the same letter in a row are not significantly different ($p > 0.05$).

to determine (see section on biomass and nutrient content). Using this index, the average absolute growth rate for the entire study period was 41.35 leaves x cm mo⁻¹. In examining differences in growth rates over the measurement periods, plants grew at a significantly higher rate during the July 1995-January 1996 period ($p < 0.0001$) (Table 3-5). Growth was negative for the January 1995-May 1995 period, which may have been due to dieback of portions of stems. For *Ichnanthus* growth rate plot averages, refer to Appendix B-2.

Pilea. In *Pilea*, absolute growth rate was calculated using an index that was the product of total leaf number times length times width of the largest leaf. This growth index was used because it related well to biomass (see section on biomass and nutrient content). The average absolute growth rate calculated for the study period was 15.16 leaves x cm². Although differences in growth for measurement intervals were non-significant, the July 1995-January 1996 interval had the highest growth rate. Growth was negative for the May 1995-July 1995 period, which was the period of maximum flowering for this species. Growth may have been diminished due to a shifting of resources into sexual reproduction. For *Pilea* growth rate plot averages, refer to Appendix B-3.

Microenvironment and growth

Soil properties. Various soil properties were found to be related to species growth rates, plant size, and flowering. In *Dieffenbachia*, extractable P (x) explained 51 percent of the variation in absolute growth rate (y), averaged over the course of

the study ($p < 0.05$; $y = -6.98x + 66.41$). However, the Spearman Rank correlation coefficient ($r_s = -0.65$) was not significant ($p = 0.06$). In addition, soil P was also correlated with *Dieffenbachia* total stem volume ($r_s = -0.75$; $p < 0.05$). No flowering data were analyzed for *Dieffenbachia* because only two tagged plants were observed flowering in growth plots over the course of the entire study.

In *Ichnanthus*, absolute growth rate varied significantly according to differences in ECEC ($p < 0.05$). Using data from the measurement period of maximum flowering, flowering in *Ichnanthus* was significantly correlated with Ca ($\text{cmol}(+)\text{kg}^{-1}$) ($r_s = 0.59$; $p < 0.01$), Mg ($r_s = 0.61$; $p < 0.01$), K ($r_s = 0.54$; $p < 0.05$), Al ($r_s = -0.67$; $p < 0.01$), exchangeable acidity ($r_s = -0.67$; $p < 0.01$), pH ($r_s = 0.67$; $p < 0.01$), Mn ($r_s = 0.70$; $p < 0.01$), Fe ($r_s = -0.49$; $p < 0.05$), and soil moisture ($r_s = 0.53$; $p < 0.05$).

In *Pilea*, the relative saturation (x) of exchange sites by Al was significantly related to growth (y) ($R^2 = 0.35$; $y = 215.62 - 9.96x$; $p < 0.05$). In addition, total number of leaves in *Pilea* plots was negatively correlated with exchangeable Mg ($r_s = -0.70$; $p < 0.05$) as was sum of leaf area ($r_s = -0.67$; $p < 0.05$). No significant relationships between soil properties and flowering in *Pilea* were observed.

Light. Flowering was positively correlated with canopy openness in *Ichnanthus* ($r_s = 0.47$; $p < 0.05$); however, this relationship merely approached significance in *Pilea* ($r_s = 0.57$; $p = 0.053$) (Fig. 3-7). However, PPFD was significantly correlated with flowering in *Pilea* ($r_s = 0.78$; $p < 0.01$), whereas it was not correlated with flowering in *Ichnanthus*.

Population demography

Population growth between measurement periods was not significant for *Dieffenbachia*, and in fact plant numbers decreased slightly (Table 3-6). In *Pilea*, changes in population density were also nonsignificant. However, *Pilea* experienced its highest population increase during the period of May-July, which coincides with flowering and seed dispersal for this species. In *Ichnanthus*, percent cover increased significantly from the measurement periods of May-July 1995 to July 1995-January 1996 ($p < 0.05$). For *Ichnanthus* only, ECEC was found to be negatively correlated with percent cover ($r_s = -0.49$; $p < 0.05$). Population increase could not be compared between the three species because *Ichnanthus*'s population size was measured as percent cover instead of density.

Average mortality differed significantly between the three study species, with *Dieffenbachia* (mean = 0.11 deaths mo^{-1}) having a significantly lower mortality rate than *Ichnanthus* (mean = 0.88 deaths mo^{-1}) or *Pilea* (mean = 0.67 deaths mo^{-1}) ($p < 0.0001$) (Table 3-7). Over the course of the study period, mortality rate increased for all three species, especially during the period of July 1995-January 1996. Part of this increase in mortality may have been due to increased litterfall resulting from Hurricanes Luis and Marilyn (Scatena, personal communication), which passed near Puerto Rico on September 6 and September 16, 1995, respectively. Due to their comparatively large size, *Dieffenbachia* plants are probably longer-lived than *Ichnanthus* or *Pilea*.

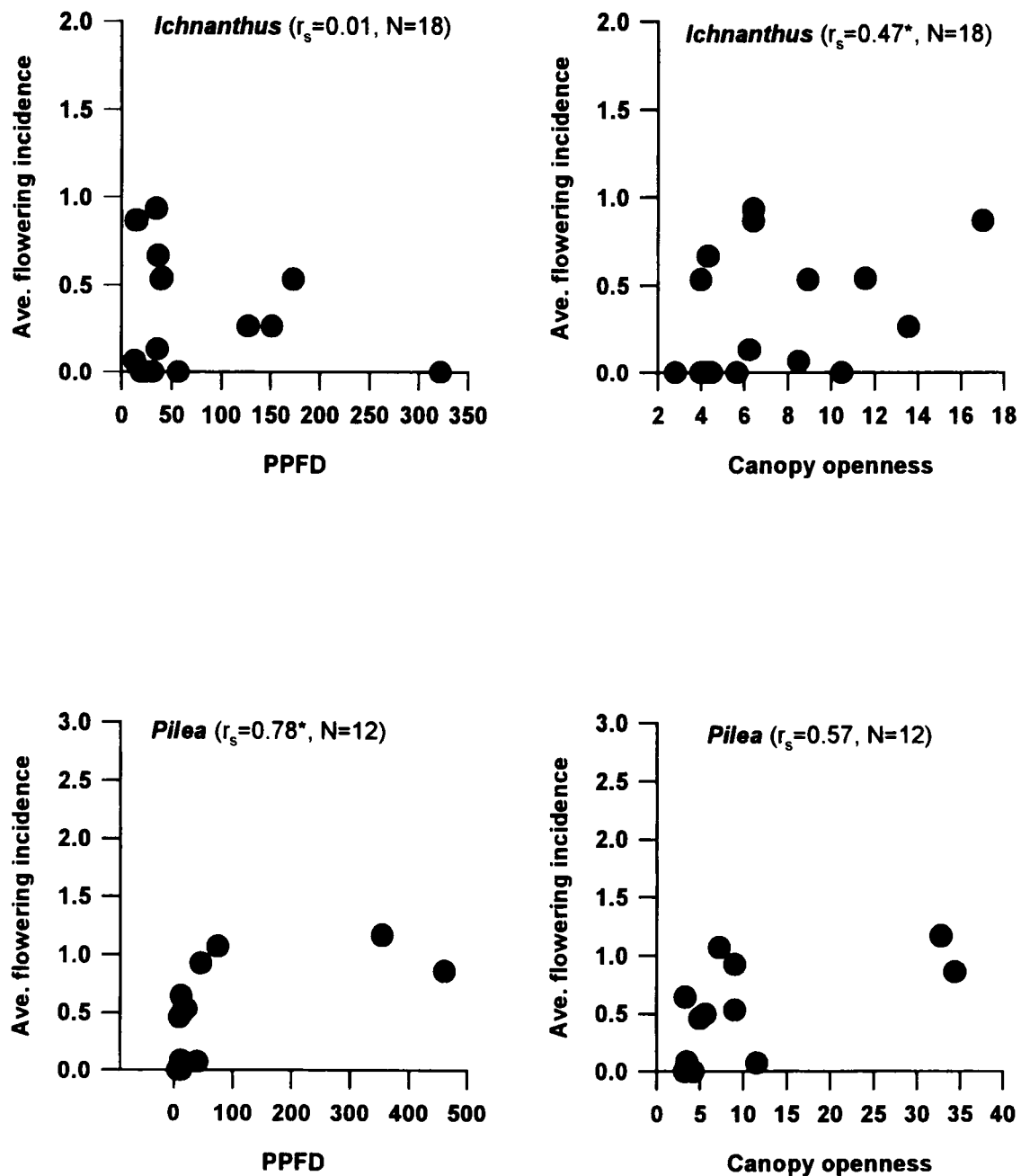


FIGURE 3-7. Flowering incidence vs. average canopy openness and PPFD for *Pilea* and *Ichnanthus*. Flowering data for *Pilea* are from May 1995, whereas *Ichnanthus* data are from January 1995 (periods of highest observed flowering for each species). Flowering incidence is calculated as the average number of inflorescences per tagged plant per plot.

TABLE 3-6. *Changes in population size of each species in all growth plots for each study period.*

Measurement interval	Ave. N	Ave. population increase, plants mo ⁻¹			
		1/95-5/95	5/95-7/95	7/95-1/96	(1/95-1/96)
Species					
<i>Dieffenbachia</i>	15.13	-0.03a ¹	-1.28a	-1.52a	-0.93
<i>Ichnanthus</i> ²	21.63	0.51ab	-0.90a	2.26b	1.05
<i>Pilea</i>	39.91	2.23a	5.54a	2.08a	2.77

¹Means with the same letter are not significantly different by rows.

²Percent cover used instead of plant density.

TABLE 3-7. *Changes in mortality of tagged plants over course of study.*

		Mortality (deaths of tagged stems m ⁻² mo ⁻¹)			
Measurement period		1/95-5/95	5/95-7/95	7/95-1/96	(1/95-1/96)
Species					
<i>Dieffenbachia</i>		0.00 ¹	0.05	0.23	0.11a
<i>Ichnanthus</i>		0.43	1.07	1.18	0.88b
<i>Pilea</i>		0.45	0.54	0.91	0.67b

¹Means with different letters are statistically different by rows at p < 0.05 level of significance.

Clonal characteristics

In comparing clonal characteristics of the three species (Table 3-8), species differed in number of attached ramets, with *Dieffenbachia* having significantly fewer attached ramets than either *Ichnanthus* or *Pilea* ($p < 0.05$). In addition, the distance between ramets was also greater in *Dieffenbachia* (mean = 122.0 cm) than in *Ichnanthus* (mean = 56.5 cm) and *Pilea* (mean = 43.4 cm). This is possibly due to the fact that *Dieffenbachia* plants are usually much larger than the other two study species.

Dieffenbachia. Excavated plants of *Dieffenbachia* were found to have few attached ramets. Of the 15 plants excavated, only two individuals had two attached ramets each. Interestingly, all 15 of the plants excavated exhibited a severed rhizome end. Based on Clegg (1978), the plant model that would be ascribed to *Dieffenbachia* would be that of a "rhizomatous plant, with stems which are storage organs, or organs of perennation as well as a means of clonal growth." And based on the evidence of severed rhizomes on all 15 plants, *Dieffenbachia*'s most common mode of vegetative reproduction is probably by rhizome fragmentation. It was observed in the field that *Dieffenbachia* plants would frequently topple over and were easily broken, probably as a result their small, shallow (~0.5 cm wide x 10-20 cm long) roots. Broken *Dieffenbachia* rhizomes totally devoid of leaves were also observed to re-grow new shoot apices and leaves.

Ichnanthus. Among excavated *Ichnanthus* plants, the average number of attached ramets was 2.73 per plant, and ranged from 7 to 1 ramets. Based on Clegg

TABLE 3-8. *Clonal behavior in Dieffenbachia, Ichnanthus, and Pilea. All distances and heights are in cm (averaged from 15 excavated individuals per species), and se = standard error.*

species	"parent" height ¹	se "parent" height	total "parent" rhizome length ²	se total "parent" rhizome length	# ramets	se # ramets	ramet distance ³	se ramet distance	ramet height	se ramet height
<i>Dieffenbachia</i>	109.37	8.21	122.03	16.02	0.27	0.18	161	29.5	34.75	24.25
<i>Ichnanthus</i>	23.47	2.20	56.47	8.31	2.73	0.49	29.18	4.51	8.90	1.00
<i>Pilea</i>	24.63	2.08	43.35	5.27	4.2	1.32	28.79	3.06	9.70	1.55

¹"Parent" height refers to the vertical stem length of the "parent" plant that was excavated.

²Total "parent" rhizome length refers to the horizontal stem length of the parent plant, which may include several stems connected or not connected to ramets.

³Ramet distance refers to the horizontal stem length required to reach all attached ramets, which may arise from the same stem in series, or from different stems attached to the "parent" plant.

(1978), *Ichnanthus* would be classified as a "decumbent plant which roots at the nodes." It appears that *Ichnanthus* reproduces clonally by "decumbent fragmentation," whereby rooted stems are separated by some means of mechanical disturbance or decay of dead tissue.

Pilea. *Pilea* plants usually had the greatest number of attached ramets of the three species, averaging 4.2 ramets per plant and ranging from 0 to 19 ramets. Like *Ichnanthus*, *Pilea* is probably most appropriately classified as a decumbent plant rooting at the nodes, and decumbent fragmentation is probably the means by which ramets become independent. However, *Pilea* was observed to be capable of sprouting roots at almost any point along its stem, and even detached leaves that had fallen to the ground were observed to sprout roots along leaf veins and petioles.

Gas exchange

Net photosynthesis of *Dieffenbachia* was found to differ significantly with respect to the natural light regimes under which plants were growing ($p < 0.0001$) (Table 3-9). Photosynthesis in the high light plots was much higher ($7.35 \mu\text{mol m}^{-2}\text{s}^{-1}$) than under conditions of deep shade ($1.13 \mu\text{mol m}^{-2}\text{s}^{-1}$). Dark respiration rates were also found to differ in response to natural light conditions ($p < 0.01$). Respiration was much higher in plants growing under conditions of deep shade ($2.71 \mu\text{mol m}^{-2}\text{s}^{-1}$) than those growing under sunny conditions ($0.47 \mu\text{mol m}^{-2}\text{s}^{-1}$).

TABLE 3-9. *Photosynthesis, dark respiration and P/R ratio for mature Dieffenbachia plants growing under natural high and low light conditions.*

Light conditions	Photosynthesis ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	Respiration ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	P/R ratio ¹
High light ²	7.35	0.47	15.66
St. dev. ³	1.91	0.96	
N ⁴	4	4	
Low light ⁵	1.13	2.71	0.42
St. dev.	1.57	2.61	
N	4	4	

¹P/R ratio = Photosynthesis/Respiration ratio.

²Average high light conditions under which measurements were made was $121.90 \mu\text{mol m}^{-2}\text{s}^{-1}$.

³St. dev. = Standard deviation.

⁴Average low light conditions under which measurements were made was $3.83 \mu\text{mol m}^{-2}\text{s}^{-1}$.

⁵N = number of individual plants measured. Each measurement consisted of 4 30-s observations.

C. Biomass and Nutrient Content

Biomass

Dieffenbachia. By using stepwise regression techniques, it was possible to examine the relative importance of the various nondestructive growth measurements of *Dieffenbachia* in predicting dry weight and fresh weight biomass. Stem volume was effective in predicting both dry and fresh weight biomass. The allometric equation ($y_{\text{dry}} = 0.066x - 3.341$; $R^2 = 0.88$; $n = 83$; $p < 0.0001$) gives the structural relationship between stem volume (x) and dry weight biomass (y). Similarly, stem volume (x_1) and leaf number (x_2) were useful in predicting the natural log of fresh weight biomass (y) ($\ln y_{\text{fresh}} = 0.00265x_1 + 0.57780x_2 - 0.00034x_1x_2 + 2.80180$; $R^2 = 0.76$; $n = 83$; $p < 0.0001$). Refer to Appendices C-1 and D for *Dieffenbachia* biomass data.

Ichnanthus. In predicting the natural log of dry biomass (y) for *Ichnanthus* using nondestructive measures of plant size, it was found that leaf number (x_1), followed by stem length (x_2), and the product of the two were the two most important criteria ($\ln y_{\text{dry}} = 0.06486x_1 + 0.01199x_2 - 0.00019x_1x_2 - 2.70634$; $R^2 = 0.54$; $n = 177$; $p < 0.0001$). For the natural log of fresh biomass (y), leaf number (x_1) and stem length (x_2) were again the most important prediction variables ($\ln y_{\text{fresh}} = 0.08181x_1 + 0.01234x_2 - 0.00022x_1x_2 - 1.54194$; $R^2 = 0.57$; $n = 177$; $p < 0.0001$). Refer to Appendices C-2 and D for *Ichnanthus* biomass data.

Pilea. For *Pilea*, the prediction equation for dry weight biomass (y) consisted of a combination of measurement variables. The most important variable was the

product of leaf length*leaf width*leaf number (x_1), and this was followed by stem length (x_2) ($y_{\text{dry}} = 0.00026x_1 + 0.00987x_2 + 0.09912$; $R^2 = 0.91$; $n = 96$; $p < 0.0001$). For fresh weight biomass, the allometric equation consisted of the same terms with the same order of importance ($y_{\text{fresh}} = 0.00338x_1 + 0.07787x_2 + 0.41865$; $R^2 = 0.91$; $n = 96$; $p < 0.0001$). Refer to Appendices C-3 and D for *Pilea* biomass data.

Microenvironment and biomass

Soil properties. For *Dieffenbachia*, Wilcoxon/Kruskal Wallis tests revealed that dry weight biomass did not significantly differ with changes in soil moisture and bulk density. However, fresh weight biomass differed significantly according to differences in soil moisture and bulk density ($p < 0.05$ for both). Among all the soil chemical properties analyzed, only extractable P was found to be negatively correlated with *Dieffenbachia* dry biomass ($r_s = -0.33$; $p < 0.05$) and fresh biomass ($r_s = -0.40$; $p < 0.05$).

In *Ichnanthus*, dry weight biomass was shown to vary significantly according to topography ($p < 0.01$) and soil moisture ($p < 0.01$). Slopes had significantly higher dry weight biomass levels than ridges. Fresh weight biomass was found to vary significantly between topographic position ($p < .01$), soil moisture ($p < 0.01$), and bulk density ($p < 0.05$). Here again, plants growing on slopes had significantly more fresh weight biomass than ridges. Among the soil chemical properties

examined, ECEC was found to be negatively correlated with *Ichnanthus* dry biomass ($r_s = -0.54$; $p < 0.05$) and fresh biomass ($r_s = -0.56$; $p < 0.05$).

Pilea's dry weight biomass varied significantly according to soil moisture ($p < 0.05$) and bulk density ($p < 0.05$). Fresh weight biomass varied significantly according to topographic position ($p < 0.01$), canopy openness ($p < 0.01$), soil moisture ($p < 0.05$), and bulk density ($p < 0.01$). Of all the soil nutrients analyzed, only extractable P was found to be negatively correlated with fresh *Pilea* biomass ($r_s = -0.59$; $p < 0.05$).

Light. For both *Dieffenbachia* and *Ichnanthus*, neither canopy openness nor PPFD were found to vary significantly with fresh or dry biomass. Dry and fresh weight biomass in *Pilea* were found to vary significantly according to canopy openness ($p < 0.05$; $p < 0.01$, respectively).

Nutrient content

A number of important plant nutrients were found to significantly vary by species (Table 3-10). All three species differed significantly in Ca content, with *Pilea* averaging 25.82 mg g⁻¹, *Dieffenbachia* 14.00 mg g⁻¹, and *Ichnanthus* 1.11 mg g⁻¹. Phosphorous and K content in *Ichnanthus* were significantly lower than in the other study species, and Mg was significantly higher in *Pilea*.

Figure 3-8 shows the concentration of nutrients within the three study species in comparison to soil nutrient contents. With the exception of exchangeable Al and Fe, these herbs store more labile Ca, Mg, K, extractable P, Mn, and percent N on a

TABLE 3-10. Comparison of average nutrient concentrations (Avg.), sample size (N), and standard deviation (Std.) of study species.

Species	Nutrients							
	Ca (mg/g)	P (mg/g)	Mg (mg/g)	K (mg/g)	Fe (mg/g)	Al (mg/g)	Mn (mg/g)	N (%)
<i>Dieffenbachia</i>	Avg. = 14.00a ¹	1.64a	4.31a	43.39a	0.14a	0.13a	0.38a	2.96a
N=2	Std. = 0.85	0.06	0.08	1.23	0.02	0.01	0.00	0.06
<i>Ichnanthus</i> ²	Avg. = 1.11b	0.60b	2.38a	24.69b	0.26a	0.23a	0.34a	1.40a
N=5	Std. = 0.76	0.22	0.97	2.21	0.18	0.15	0.17	0.33
<i>Pilea</i> ²	Avg. = 25.82c	1.50a	9.29b	46.85a	2.02a	1.85a	0.18a	1.45a
N=5	Std. = 6.57	0.28	1.81	13.87	1.68	1.60	0.04	0.40

¹Means with different letters are statistically different at p<0.05 level of significance.²Nutrient data for *Ichnanthus* and *Pilea* are taken from Scatena *et al.*, (1993).

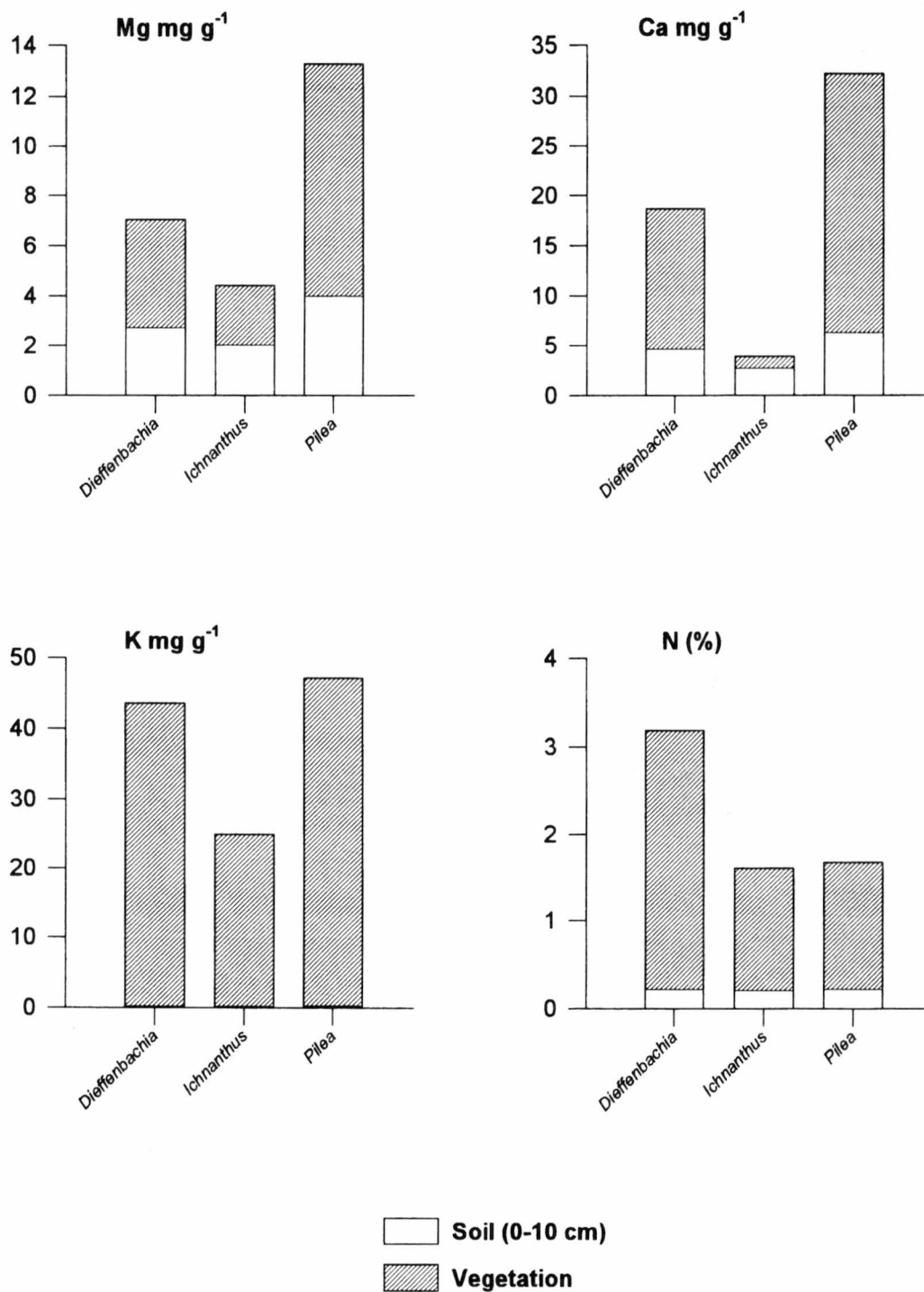


FIGURE 3-8. The concentration of nutrients (mg g⁻¹) within study species as compared with exchangeable soil nutrient concentrations within the upper 10 cm of soil. Nutrients in *Ichnanthus* and *Pilea* are from Scatena *et al.* (1993).

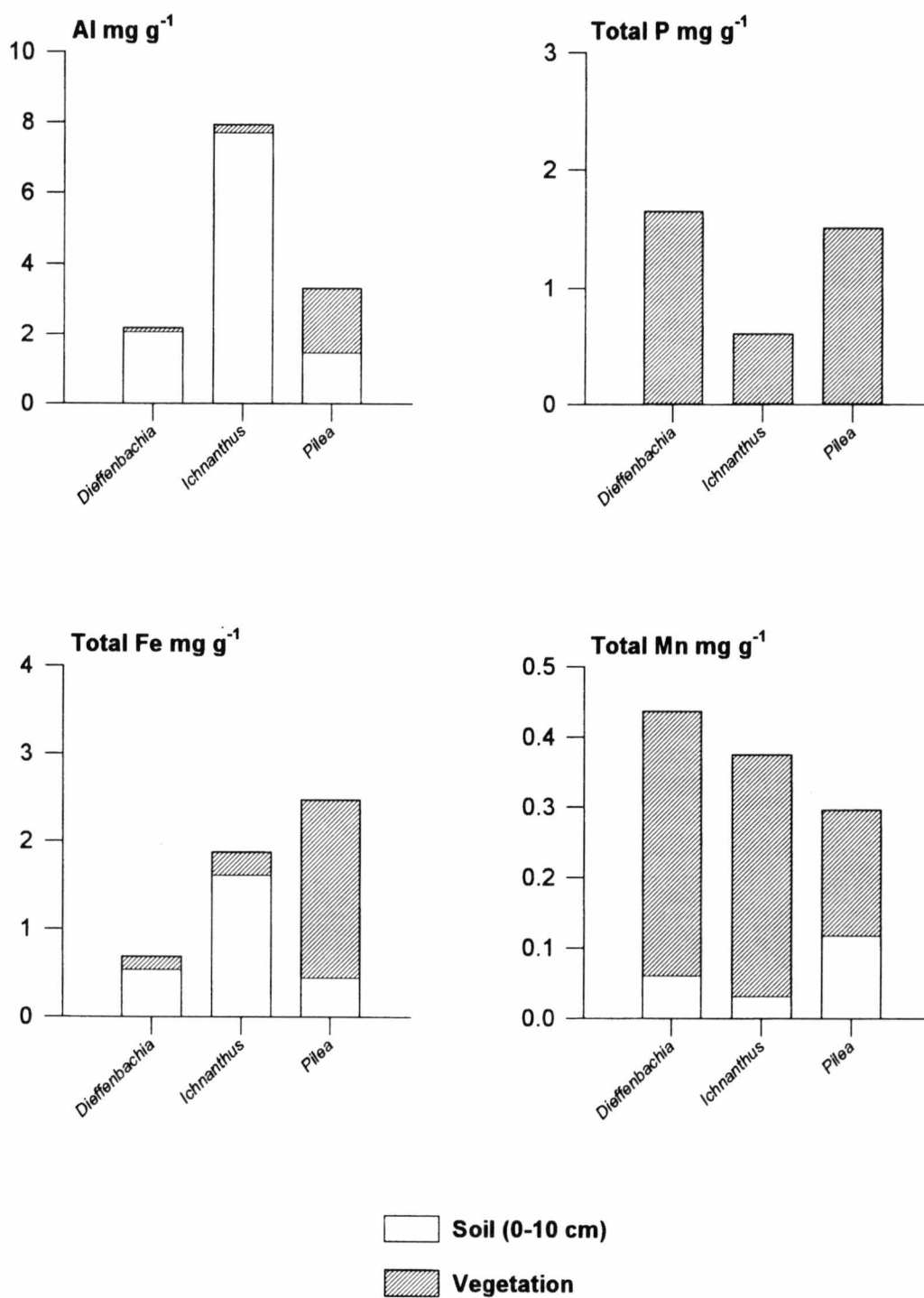


FIGURE 3-8. *Continued.*

mass-weighted basis than that found in the upper 10 cm of soil.

In addition to the above nutrients, percent water content was also determined for each species. Differences between the three species were significant ($p < 0.0001$), with *Dieffenbachia* having the highest water content (mean = 1560.18%), followed by *Pilea* (mean = 831.26%), and *Ichnanthus* (mean = 376.71%). Differences in plant water content according to topographic position were only found for *Ichnanthus* ($p < 0.05$), with plants growing on slopes (mean = 456.71%) containing significantly more moisture than on ridges (mean = 302.42%), and with plants growing in valleys being intermediate in moisture content (mean = 371.01%).

D. Decomposition

Decay constant (k) values were calculated based on the exponential model $\ln(X) = -kt$, where X = weight remaining and t = time in years (Bloomfield *et al.* 1993). For all three species, decay rates were well-modeled using the average natural log of weight remaining versus time, having significant ($p < 0.05$) R^2 values of 0.73, 0.95, and 0.88 for *Dieffenbachia*, *Ichnanthus*, and *Pilea*, respectively (Fig. 3-9). The decay constants calculated for each species also differed significantly ($p < 0.0001$), with *Dieffenbachia* (mean = 13.87) being significantly different from *Ichnanthus* (mean = 8.43) and *Pilea* (mean = 6.27) (Table 3-11).

The effect of topographic position on differences in decay constant values approached statistical significance in *Dieffenbachia* ($p = 0.07$), with slopes averaging 18.74, valleys 13.27, and ridges 9.59 (Table 3-12). Topographic position effects

FIGURE 3-9. Percent initial weight remaining vs. time in days for leaf litter in *Dieffenbachia*, *Ichnanthus*, and *Pilea*.

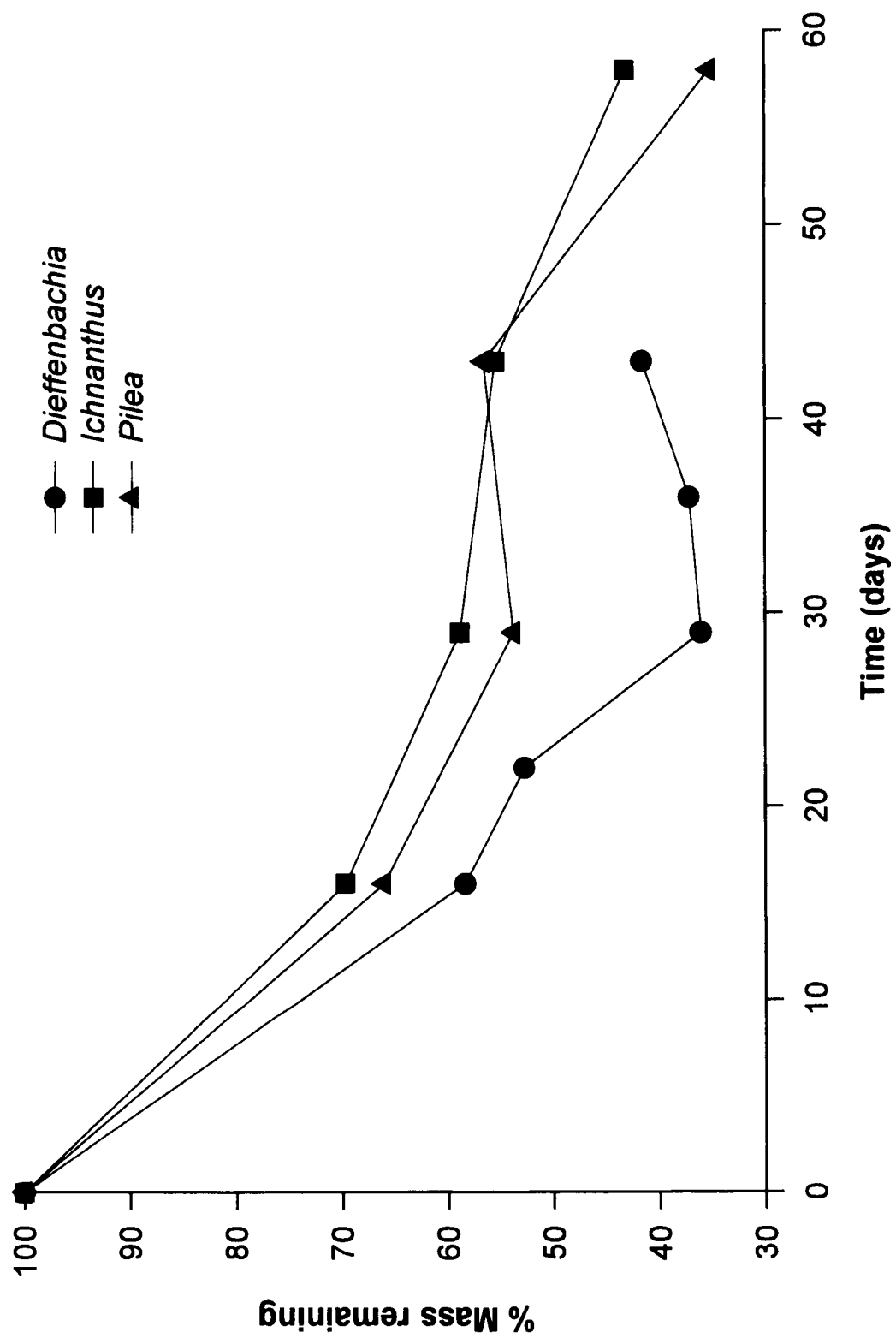


TABLE 3-11. *Mean decay constant (k) values for leaf tissues of study species. Different letters indicate significant differences in species decay rates ($p < 0.05$).*

Species	Decay constant (k)		R ²	n
<i>Dieffenbachia</i>	13.87	a	0.73	108
<i>Ichnanthus</i>	8.43	b	0.95	90
<i>Pilea</i>	6.27	b	0.88	90

TABLE 3-12. *Mean decay constant (k) values for leaf tissues of study species by topographic position or site. Different letters indicate significant differences in decay rates ($p < 0.05$) for a given topographic position or site.*

Topographic position	<i>Dieffenbachia</i>	<i>Ichnanthus</i>	<i>Pilea</i>
Ridges	9.59 a	5.84 a	4.0 a
Slopes	18.74 a	13.27 b	8.0 a
Valleys	13.27 a	5.63 a	6.8 a
Site			
Moist	18.08 a	11.08 a	9.3 a
Dry	9.65 b	5.85 a	3.3 b

were significant for *Ichnanthus* ($p < 0.05$), with slopes (mean = 13.70) differing from ridges (mean = 5.84), and valleys (mean = 5.63). Topographic effects were not significant for *Pilea*.

However, when topographic position was partitioned (based on soil moisture data collected nearby) into the categories of "moist" sites (*i.e.*, moist slopes and valleys) and "dry" sites (*i.e.*, dry slopes and ridges), *Dieffenbachia* exhibited highly significant differences in decomposition rates ($p < 0.001$), with moist sites having decomposition rates nearly twice as fast as dry sites (18.08 versus 9.65, respectively). Decomposition was also faster on moist sites for *Ichnanthus* (11.08 versus 5.85; $p = 0.053$), as it was for *Pilea* (9.25 versus 3.30; $p < 0.0001$).

CHAPTER IV

DISCUSSION

Since this project began 5 to 6 years following Hurricane Hugo, much of the vegetation of the Bisley Watersheds had recovered substantially by the time this study was initiated. Five years following Hurricane Hugo, total aboveground biomass levels of the Bisley Experimental Watersheds had recovered to 86 percent of pre-hurricane values (Scatena *et al.* 1996 in press). This regrowth of tree crowns and tree seedlings into larger size classes led to decreased light availability for growth of ground layer herbs (including study species) and probably slowed their growth rates over time.

On September 6, 1995 and on September 16, 1995, Hurricanes Luis and Marilyn passed near the northeastern coast of Puerto Rico. Disturbance effects from these hurricanes to the Bisley Experimental Watersheds were slight. Although canopy openness over most of the growth plots increased (on average, from 8.41% in May-July 1995 to 10.35% in January 1996) this increase was not statistically significant. Forest stands dominated by *Cecropia schreberiana* were primarily damaged, and litterfall inputs were over eight times higher than average following these hurricanes (Scatena, personal communication). With Hurricane Hugo, damage was significantly greater in valleys than on ridges or slopes (Basnet *et al.* 1992), and probably the same pattern of damage was repeated with Hurricanes Luis and Marilyn.

A. Microenvironment

Soil properties

With regard to the study sites, several soil nutrients and related chemical properties were found to be related to soil moisture (Table 3-1), which itself appears to be largely affected by topographic position (Johnston 1992) (Fig. 3-1). Ridge soils tended to be drier, better-drained, and had higher soil organic matter than valleys, which tended to have frequently saturated soils with more exchangeable bases (Scatena and Lugo 1995). Scatena (1989) observed that soil characteristics within the Bisley Experimental Watersheds appear to be closely associated with local topography and drainage. Jordan (1985) also suggested that soil nutrients may be closely related to soil moisture. Wetter soils (*i.e.*, valleys and moist slopes) in this study were found to have significantly higher levels of exchangeable Ca, Mg, K, Mn, ECEC, and higher pH values. Ridges exhibited significantly higher levels of Fe, Al, exchangeable acidity, and higher C/N ratios. The higher concentrations of bases downslope may be due to migration of fine surface soil particles and plant distribution patterns (Silver 1992). Another possible explanation is that in flooded lower elevation soils, Fe^{3+} is reduced to Fe^{2+} , and since under reducing conditions, Fe^{2+} is easily lost from soil surface coatings, exchange sites are freed up for Ca, Mg, and K (Jenny 1980; Silver *et al.* 1994). Higher pH values downslope is probably due to higher levels of these base cations (Johnston 1992) and less Al^{+3} . The relationship between soil organic matter and N and P (Table 3-1) may indicate that availability of these elements are controlled by biotic processes on slopes and ridges (Silver *et al.* 1994;

Scatena & Lugo 1995). Edwards and Grubb (1977) also reported that N and P tend to be immobilized in more organic soils. Drier, well-drained soils (*i.e.*, ridges and dry slopes) were found to have significantly higher levels of P as well as exchangeable Al and Fe, which is probably due to leaching of base cations. High levels of P in association with Al and Fe (Table 3-1) is probably also due to P fixation by Al and Fe oxides (Sanchez 1976).

Soil habitat differences

All three species' habitats showed marked differences in soil nutrients; however, the degree to which these soil characteristics are linked to topography, microclimate, weathering time, or the plant species/biota was not determined. It is interesting that these relationships exist between nutrient rich plants and nutrient rich soils, which suggests the existence of positive feedbacks between these study species and their soils (Hobbie 1992). Positive feedbacks are further supported based on evidence that species growth rates varied significantly according to differences in several soil properties. The fact that these herbs exist in soils with differing nutrient contents may simply be a result of differences in physiological requirements, or it could be due to other factors not measured (*e.g.*, competition).

When differences in soil chemical properties associated with each study species were examined by partitioning by topographic position, significant differences were found on slopes, but not in valleys. These differences in soil chemical properties of species habitats on slopes may exist as a result of the dominant herbaceous species

present, or may be due to microclimate differences caused by aspect and proximity to ridges and valleys--factors which would likely affect drainage characteristics and soil water evaporation. For these reasons, slopes are probably more heterogeneous than the other two topographic positions. In addition, tree and shrub species may also be influencing local soil differences. The lack of differences between soils of species habitats in valleys may be due to less variability in drainage (*i.e.*, soils with consistently high moisture levels). In valleys, it is not uncommon to see all three study species coexisting in the same area.

The fact that the species generally richest in nutrients, *Pilea*, also tended to grow in soils highest in base cations, indicates that it may play an important role in nutrient cycling. Furthermore, *Pilea* was observed growing (with numerous roots imbedded) on top of recently fallen *Cecropia schreberiana* leaves and on decomposing trees, which suggests the possibility of direct nutrient transfer in this species. Direct nutrient transfer from fallen leaf litter to roots has been documented for P (Herrera *et al.* 1978), and it has been suggested for Mg and Ca (Cuevas & Medina 1988) in areas in the tropics where these nutrients are limiting. Evidence of vesicular-arbuscular mycorrhizal associations are related to nutrient capture in decomposing litter (Herrera *et al.* 1978, Stark and Spratt 1977) and should probably be investigated for *Pilea*.

Light

The total PPFD values between the "open" and "closed" canopy sites monitored by dataloggers approximated values obtained by other workers, although

daily values were generally lower. Values for the "open" canopy site in this study ranged from 0.33 to 4.82 mol day⁻¹ (mean = 2.33 mol day⁻¹). This quantity was approximately 9 percent of full sun exposure. Chazdon and Fetcher (1984) reported that a large gap (>400 m²) received from 3.86 to 13.6 mol m⁻² day⁻¹. Similarly, Denslow *et al.* (1990) found mean PPFD values for 4 gaps greater than 275 m² in Costa Rica ranged from 3 to 11 mol m⁻² day⁻¹. Ashton (1992) reported that for the understory of a Sri Lankan tropical rain forest on a sunny day, light quantities varied between 0.26 and 0.92 mol, which was approximately 1 percent of full sun exposure. For the "closed" canopy site characterized in this study, light values ranged from 0.02 to 1.63 mol m⁻² day⁻¹ (mean = 0.24 mol m⁻² day⁻¹), and this was also approximately 1 percent of full sun exposure.

It is important to remember that microenvironmental data presented in this study apply only to the sites in which the three species were studied in the Bisley Experimental Watersheds, and not to the watersheds at large.

B. Growth

Species responses to soils

Species growth rates were found to significantly differ according to variations in several soil properties. In support of these results, Gentry and Emmons (1987) found that among understory vascular plants, terrestrial herbs were the most sensitive to environmental stress (*i.e.*, decreasing soil fertility). All the understory plants

surveyed by Gentry and Emmons were "extremely sensitive to changes in substrate or rainfall, much more so than the canopy species" (1987).

Dieffenbachia. Growth in *Dieffenbachia* was negatively correlated with increased extractable P. This may be due to increased uptake of P by *Dieffenbachia* from soils where growth was highest. Another possible explanation is that growth in *Dieffenbachia* (whose tissues have high water content) may be reduced in drier soils where P levels are generally also higher (Table 3-1), although no significant relationships between soil moisture and growth were detected.

Ichnanthus. In *Ichnanthus*, absolute growth rate differed significantly according to differences in ECEC ($p < 0.05$). Estimated cation exchange capacity levels were highest on ridges, where growth of *Ichnanthus* was fairly slow. Absolute growth rate was also found to differ significantly according to differences in soil moisture. However, when growth in *Ichnanthus* was analyzed by topographic position, slopes, which were intermediate in soil moisture content, supported the highest growth rates. Growth in valleys was slowest, which was possibly due to flooded soils, accelerated senescence and decay of plant tissues, or increased competition from other species.

Flowering in *Ichnanthus* was significantly correlated with soil moisture, Ca, Mg, K, Al, exchangeable acidity, Mn, Fe, and pH. However, because these soil attributes are closely linked to each other (Table 3-1) the relative importance of these factors is difficult to determine. Nevertheless, soil moisture is probably the most important factor because of its pervasive influence in determining other soil chemical

properties, and it was also shown to significantly affect growth in this species.

Gentry and Emmons (1987) found that flowering and fruit production of tropical understory plants increased in areas with little or no dry season and fertile soils and decreased in forests with a pronounced dry season and poor soils.

Pilea. Growth rates in *Pilea* differed significantly with soil moisture also ($p < 0.001$), but no differences were detected between growth on slopes or in valleys. *Pilea* was found to grow in the wettest soils of the three study species, although *Dieffenbachia* also appeared to be extremely tolerant of saturated soils. Differences in soil chemical properties did not appear to influence growth rate in *Pilea* where it naturally occurs. No significant relationships between soil chemical properties and flowering in *Pilea* were observed.

Species responses to light

Dieffenbachia. Growth rate in *Dieffenbachia* did not differ with respect to differences in PPFD. The lack of significant differences observed in this species was probably due to the small number of growth plots and the variability between them, as well as the spatial and temporal heterogeneity of light conditions inherent to any tropical rain forest.

Ichnanthus. *Ichnanthus* also did not exhibit significant differences in growth with respect to PPFD; however, flowering was positively correlated with canopy openness.

Pilea. Growth in this species was significantly related to PPFD, which may indicate a greater sensitivity to slight changes in light environment not exhibited by the other study species. Flowering was also highly correlated with PPFD levels.

The fact that flowering in *Ichnanthus* and *Pilea* was related to canopy openness and/or PPFD suggests that light is a resource which can affect the reproductive strategy used by these herbs. Gentry and Emmons (1987) in their study of the effects of rainfall and soil fertility on understory species richness and flowering, observed a marked increase in flowering in tree-fall gaps. According to Smith (1987), growth and reproduction of herbs on Barro Colorado Island appear to be tightly linked to light availability in the understory, and as light levels decline, herbs may decrease in size or possibly die unless light levels improve.

Life history strategies

One objective of this study was to describe the life cycles of these species in terms of growth, recruitment, and mortality. All the study species responded positively to the canopy disturbance resulting from the hurricanes, exhibiting increased average growth rates during the July 1995-January 1996 study periods. Growth rates for the study species were highly variable due to differences in microenvironmental conditions, but it appears from growth rate data that canopy disturbance favors these species. Both *Dieffenbachia* and *Pilea* exhibited substantial increases in growth (over three-fold) for the July 1995-January 1996 time interval, but these results were not significant. *Ichnanthus* growth rates showed a significant four-

fold increase during the July 1995-January 1996 measurement interval. Chinea (personal communication) found that one year following Hurricane Hugo, percent cover by herbs and small seedlings was five times higher than pre-hurricane values. Even three years following Hugo, herbs and small seedlings were still at levels three times higher than before the hurricane.

Vegetative reproduction is a highly adaptive life history strategy for tropical rain forest herbs, especially in areas prone to periodic disturbance. Clausen, Keck, and Hiesey (1947) proposed that plants with efficient vegetative reproduction are better equipped to tolerate extreme environmental conditions. Vegetative reproduction is generally faster than seed germination, and allows rapid exploration and exploitation of a heterogeneous habitat with minimal risk (Wiejesinghe 1993). Species with limited periods of seed viability and dispersal may not be able to fully take advantage of gaps, if unable to germinate in time and to compete quickly with established herbs and woody seedlings. Other advantages of clonal reproduction include rapid replication of advantageous genotypes and sometimes extreme longevity (Wiejesinghe 1993).

Dieffenbachia. *Dieffenbachia* populations in growth plots declined during all measurement intervals. For this reason, it is probable that this species had reached maximum densities in most growth plots. The lower mortality rate of this species and its probable longer life-span suggests that *Dieffenbachia* exhibits a more conservative life history strategy with respect to the other herbaceous study species.

Richards (1952) observed that for most tropical herbs, reproduction appeared to be mainly vegetative. Plants such as *Dieffenbachia*, which can multiply from stem/rhizome fragmentation, seem especially well-adapted to disturbance. Furthermore, species such as *Dieffenbachia* can probably persist for long periods under unfavorable conditions, living off stored energy and nutrients in their rhizomes. The ability of this species to "move" by stem displacement from unfavorable habitats is also a distinct advantage (Ray 1992). Due to variable success in sexual reproduction found in other species of this genus (Young 1986), vegetative reproduction gains even more importance.

Ichnanthus. *Ichnanthus* significantly increased in percent cover and exhibited increased mortality during the July 1995-January 1996 measurement interval. The high growth rates and high mortality exhibited by this species indicate that it uses a maximal performance strategy (r-selected). Much of the mortality found in *Ichnanthus* may have been due to litterfall. During growth remeasurement periods, many tagged plants of this species were often found covered by litter. The increased mortality rate for the July 1995-January 1996 measurement period may have been partially due to increased litterfall pulses from the two hurricanes that passed nearby the island.

Ichnanthus, the most common of the three species in the Bisley Experimental Watersheds, also demonstrated clonal growth as part of its life history strategy. The patchy damage resulting from the two hurricanes is probably responsible for the highly variable growth experienced by this species during the July 1995-January 1996

measurement interval. Tagged plants from one growth plot showed an average increase in stem length of 30.5 cm; another plot showed an average decrease of 10.8 cm during the same measurement interval.

Pilea. *Pilea* exhibited high mortality and high growth rates, which indicates that this species uses a maximal performance strategy (r-selected). Much of the mortality in *Pilea* may have been due to litterfall (like *Ichnanthus*) because tagged plants were often found covered by litter. The fact that mortality rates were highest following Hurricanes Luis and Marilyn may have been due to increased litterfall pulses from these disturbances.

Pilea was found to have the highest degree of clonal behavior (average of 4.2 ramets attached to excavated "parent" plants) among the study species. Many broken stems and detached leaves lying on the forest floor were also observed to generate roots. *Pilea* plants also exhibited highly variable growth following the hurricanes. The tagged plants in one growth plot grew an average 24.8 additional leaves, whereas the tagged plants in another plot lost an average 1.3 leaves (accompanied by heavy mortality). These differences illustrate the extreme sensitivity of this species to slight changes in microenvironment.

C. Biomass and Nutrient Content

Biomass

Biomass responses to microenvironment. Biomass varied significantly by topographic position for *Ichnanthus* and *Pilea*, but not *Dieffenbachia*, which may have

been due to the smaller number of plots harvested for this species. Because of the large differences in soil properties (refer to part A, "soil properties," of this section) some of which vary by topographic position, biomass would be expected to vary by topographic position for all three species, with valleys (generally moist, nutrient-rich sites) having higher biomass than ridges and well-drained slopes.

Dieffenbachia's fresh weight biomass was found to significantly differ according to differences in soil moisture and bulk density, but not dry weight biomass. Because this species has such high water content, soil moisture largely determines fresh weight biomass in this species. Differences in average light levels (both PAR and PPFD) were not significantly related to biomass in *Dieffenbachia*, probably because plants in the "closed canopy" environment had attained their size earlier in forest recovery from Hurricane Hugo, and dieback was only beginning. The small number of sample plots probably also contributed to the lack of significance.

In *Ichnanthus*, dry and fresh weight biomass differed significantly according to differences in soil moisture. However, moisture levels as found on slopes were found to be most favorable. No statistically significant relationships between light and biomass were found for *Ichnanthus*, probably due to the highly variable light environment.

Pilea's dry and fresh weight biomass was found to significantly vary according to canopy openness, soil moisture, and bulk density. This relationship between canopy openness and biomass indicates a greater sensitivity to light levels as

compared to the other study species. Limited moisture probably also restricts the habitat of this species to a large degree.

Biomass estimation. Allometric equations developed for estimating biomass related well to nondestructive measurements of plant size. Measurements on live vegetation as opposed to destructive biomass sampling permit continuous monitoring of growth of the same individuals, and this technique facilitates comparisons of growth to microenvironment, which can be difficult to assess due to the spatial and temporal heterogeneity of light and soil conditions within this rain forest.

Nutrient content

These study species clearly store many essential nutrients at concentrations higher than surrounding surface soils (0-10 cm). Their rapid decomposition ensures that these nutrients soon become available to other plants. The greater concentration of biologically important nutrients in these herbs indicate that they may play a significant role in nutrient cycling. According to Scatena *et al.* (1996 in press) aboveground nutrient levels of vegetation following Hurricane Hugo exceeded pre-hurricane values by 102 to 161 percent, with most of these nutrients coming from regenerating vegetation, and with herbaceous dicots having the highest concentrations of nutrients among regenerating vegetation. Silver (1992) found that plant biomass generally stored more K, P, and to a lesser extent, Ca than did soil exchange sites in the Bisley Watersheds.

Dieffenbachia. *Dieffenbachia* had higher concentrations of P, Mn, and N than the other two study species; however, none of the differences in concentrations were statistically significant (Table 3-10). This species resembled *Pilea* more closely in nutrient content, which would be expected since grasses (*i.e.*, *Ichnanthus*) tend to have lower nutrient concentrations than forbs.

Ichnanthus. *Ichnanthus* had the lowest concentrations of Ca, P, Mg, K, and N among the study species. Phosphorous, Ca, and K occurred at significantly lower concentrations in *Ichnanthus* than in the other study species. The fact that *Ichnanthus* exhibits lower nutrient concentrations than the other study species may in part explain its wider distribution and apparent tolerance to a variety of habitat conditions. Relatively speaking, this species would be expected to be of less importance in nutrient cycling because of its lower nutrient content.

Pilea. Of the three study species, *Pilea* had the highest concentrations of Ca, Mg, K, Fe, and Al. Calcium and Mg were stored at concentrations significantly higher than the other study species. *Pilea* is probably more important in nutrient cycling than the other two study species because of its higher nutrient contents; however, Ca and Mg have not been reported as limiting in these watersheds.

Results for the three species in this study show that there is a large amount of variability in nutrient content among them. Of the nutrients examined, Ca varied the most between species (Table 3-10). This was also found by Scatena *et al.* (1993) for vegetation in general in the Bisley Watersheds.

Dieffenbachia, *Ichnanthus*, and *Pilea* were all found to have greater concentrations of P, K, N, Mg, and Mn than that available in the in the soils where they were growing (Fig. 3-8). Furthermore, *Pilea* and *Dieffenbachia* were also found to concentrate a greater proportion of Ca in their biomass than the surrounding soils. Calcium has been implicated as primarily functioning as a structural component in plants (Gosz *et al.* 1973), but the physiological basis for high levels of Ca in *Pilea* and *Dieffenbachia* are unidentified. *Dieffenbachia* is known to contain raphides of calcium oxalate crystals (Walter & Khanna 1972), and Salisbury and Ross (1978, reviewed in Vitousek 1982) reported that most Ca in plants is present as metabolically inactive and immobile calcium pectate and calcium oxalate. Although these herbs comprise an extremely small fraction of aboveground biomass in the Bisley Watersheds, a greater concentration of nutrients (mg g^{-1} per unit dry weight) is stored within them as compared with exchangeable soil nutrient pools (Fig. 3-8). Scatena *et al.* (1993) found that understory vegetation in the Bisley Watersheds in general stored greater concentrations of nutrients per unit dry weight than trees and shrubs. The same pattern was observed in these herbs as well.

D. Decomposition

The purpose of the decomposition study was to determine the rates of decomposition of the three study species in order to better understand their roles in nutrient cycling. A second objective of the decomposition experiment was to determine the influence of topographic position and its subsequent differences in soil

moisture on foliage decay rates. All species in this study experienced a rapid loss of material during the first week of decay, which gradually decreased over time as decomposition-resistant materials remained (Fig. 3-9). The decomposition rates of these herbs appear to be faster than for leaves of woody species in the Bisley Watersheds (LeCaro & Rudd 1985; Bloomfield *et al.* 1993; Sullivan 1993). This indicates that nutrients from these species are returned relatively quickly to the soil.

Species differences

Dieffenbachia. *Dieffenbachia* exhibited the fastest rate of decay among the three species studied. Although there were no significant differences detected in decay rates for ridges, slopes and valleys, *Dieffenbachia* leaves did decay significantly faster on "moist" as compared to "dry" soils.

Ichnanthus. *Ichnanthus* exhibited an intermediate rate of decay, compared to the other species studied. Significant differences in decay by topographic position were observed for *Ichnanthus*, but oddly the fastest decay rates were observed on slopes, which typically would be expected to be intermediate between ridges and valleys. It may be that nutrient rich drainage water runoff from acidic ridge soils hastened decomposition rates here.

Pilea. Leaf litter from *Pilea* was the slowest to decay. However, because fresh leaves were used in the litterbags, some *Pilea* leaves were observed to sprout roots and continue living for some time while in the litterbags, making the decomposition data for *Pilea* questionable. Although there were no significant

differences in decay rates for ridges, slopes, and valleys, *Pilea* leaves did decay significantly faster on "moist" as compared to "dry" soils.

In a study of decay rates of fine roots and foliage of the tropical tree species *Dacryodes excelsa* and *Prestoea montana*, Bloomfield *et al.* (1993) found that one of the best predictors of mass loss was initial Ca. In that study, increased concentrations of Ca were associated with faster decay rates. However, in this study, the species with the highest Ca content was also the slowest in decomposing (*Pilea* 25.823 mg g⁻¹ Ca in aboveground biomass; $k = 6.27$). *Dieffenbachia*, which was by far the fastest-decomposing species, also was high in Ca (13.997 mg g⁻¹ in aboveground biomass), but perhaps more important, this species also contained higher amounts of N (Table 3-10). Litter decay rate in general is positively related to N content (reviewed by Hobbie 1992), although this is not true in the case of plants high in polyphenolics (Palm & Sanchez 1990).

Decay and microenvironment

Both *Dieffenbachia* and *Pilea* leaf litter were observed to decay faster on "moist" as opposed to "dry" soils. Moist soils probably support more active heterotroph populations (*i.e.*, bacteria, fungi, protozoa) and litter is subjected to more leaching in moist sites. Edwards (1982) measured the rate of litter disappearance on contrasting topographic sites in New Guinea and found little difference in decay constants; however, the slowest decay occurred on a ridge gap ($k = 1.03$) and the fastest decay occurred in a valley site ($k = 1.55$), where Ca and Mg turnover was

also higher. Sullivan (1993) also observed slower decomposition rates on Puerto Rican upland sites as compared to riparian sites, although differences were not statistically significant. Dwyer and Merriam (1981) examined decay rates of several litter mixtures by topographic site in Ontario and found that local topography was a more significant factor than litter mixture. They found that bacterial populations were higher in "low" sites and that the interaction of "low" sites and litter type increased decay rates. Although environmental conditions imposed by topographic position are important factors influencing decomposition, species litter differences in terms of nutrient content, tissue differences, and palatability to heterotrophs (Gosz *et al.* 1973) appear to be more important factors in this study. Also important are nutrient demand by heterotrophs, nutrients in current falling litter, precipitation, throughfall (Gosz *et al.* 1973), and direct uptake by feeder roots (Cuevas & Medina 1988; Stark & Spratt 1977) in some ecosystems.

Plant species are capable of influencing the cycling of nutrients in several ways, from differences in uptake, loss, litter quality, and microbial associations with microbes to differences in herbivory effects (Hobbie 1992). Herbs are clearly important in nutrient cycling as they generally exhibit high nutrient quality as well as rapid growth and decomposition. The importance of species richness in herbaceous communities for nutrient cycling has also been demonstrated in other studies (e.g., Scatena *et al.* 1996 in press). Chinea (personal communication) found that within five years following Hurricane Hugo, there were dramatic changes in community

composition and many extinctions of herbs at the local 1 x 1 m plot level, but only a 2 percent decline in the Shannon diversity index was observed over the entire watershed during the recovery period.

Several characteristics of these three herbaceous species leads to the conclusion that they play a significant role in nutrient dynamics, and thereby ecosystem resiliency, following canopy disturbance. First, all three species are capable of reproducing asexually from fragmentation of rhizomes, stems, or leaves. This asexual reproduction can add more vegetative units to post-hurricane populations, compensating in part or wholly, for hurricane-induced mortality. Second, all three species exhibited increased growth during the period immediately following disturbance by Hurricanes Luis and Marilyn, the only significant disturbances during the study period. Third, all three species exhibited biomagnification, or significant concentration of nutrients in plant biomass. Fourth, later in forest recovery, mortality brought on by decreasing light levels (Smith 1987) from a closing tree canopy is followed by rapid decomposition of these herbs, providing a rich source of nutrients to growing tree populations. Under post-canopy disturbance conditions, the ability of these species to (1) rapidly increase population size (asexual and sexual reproduction); (2) increase growth rates; (3) concentrate (biomagnify) high levels of nutrients in biomass, and later, (4) rapidly release nutrients to growing tree populations leads to the conclusion that these herbaceous understory species contribute to rapid nutrient cycling and thereby ecosystem resiliency, following canopy disturbance. Forest managers should not disregard herbaceous understory species when planning and

managing for sustainability. Herbs perform a valuable role as temporary nutrient sinks, and therefore provide an important link to succeeding stages of forest recovery.

CHAPTER V

SUMMARY AND CONCLUSIONS

In characterizing the microenvironments of three species of understory ground herbs, soil moisture and a wide variety of soil nutrients were found to significantly vary according to topographic position. In addition, a number of significant correlations were observed between soil chemical and physical properties.

Light environments of the study species were highly variable due to the intrinsic heterogeneity of the rain forest environment. Differences in canopy cover, sunflecks, cloud cover, and differences in light as a result of slope and aspect all contributed to this heterogeneity. Simple designations of light regimes (*e.g.*, "low" versus "high") are not recommended because of this heterogeneity.

When differences in soil chemical properties in growth plots were compared for each study species, several properties were found to significantly vary by species habitat. While part of these soil differences are probably due to the interaction of topography and drainage, the high nutrient concentration of humus and rapid decay also indicate that these herbs may be creating positive feedbacks where they occur.

The increased growth rates observed for all three species following Hurricanes Luis and Marilyn suggests that low-impact storms may be important in maintaining the environmental conditions necessary for these herb populations. Higher short-term mortality rates were observed in *Pilea* and *Ichnanthus* populations, probably as a result of increased litterfall following these hurricanes.

The three study species exhibited differences in growth, which were correlated with soil properties or light. Likewise, biomass and other nondestructive measures of plant size varied with soil properties and light. Soil moisture was an important variable, as differences in growth and biomass in *Ichnanthus* and *Pilea* were found to significantly vary according soil moisture. Soil P was a significant factor in growth in *Dieffenbachia* and with biomass in *Dieffenbachia* and *Pilea*. *Pilea* responded positively by increasing growth with increasing light levels, and both *Pilea* and *Ichnanthus* increased flowering in response to increasing light. *Pilea* appeared to be most sensitive to changing light conditions.

Because soil nutrients and moisture vary with topographic setting (Scatena and Lugo 1995), plant distributions also vary with topography. However, it should be recognized that landforms are not environmental variables themselves but surrogates for an array of environmental factors including soil moisture, nutrients, light, and disturbance history.

Clonal vegetative growth was observed in all three study species. Because of their growth habit, *Dieffenbachia* plants are capable of "moving" to more favorable habitats, and stem/rhizome breakage propagates this species. *Ichnanthus* and *Pilea* were observed to produce extremely large clones probably in response to disturbance from two hurricanes, which increased litterfall and opened up the canopy in some areas. Broken *Pilea* stems and leaves were observed to sprout roots and continue growing, which minimized impacts from disturbance and herbivory in this species.

Clonal vegetative growth appears to be a highly adaptive life history strategy used by these herbs.

Biomass estimation from nondestructive measures of plant size worked well in most cases for the three species. Regression coefficients for biomass versus plant size measurements ranged from 0.54 to 0.92, indicating that simple field measurements for some herbs may be used instead of destructive harvesting.

When nutrient concentrations of these herbs were compared with available soil nutrients, herbs generally stored much higher nutrient concentrations than soils. Nutrient concentrations varied between the three species. *Pilea* generally was the species richest in nutrients, followed by *Dieffenbachia* and *Ichnanthus*. *Pilea* is probably a more important species in nutrient cycling because of its higher nutrient contents, followed by *Dieffenbachia* and then *Ichnanthus*. Foliar decomposition of these herbs was rapid in comparison to studies of woody species in the Bisley Watersheds. *Dieffenbachia* was the fastest species to decompose, followed by *Ichnanthus* and *Pilea*. These relatively high concentrations plus rapid rates of decomposition indicate that herbs play an important role in nutrient retention following canopy disturbance.

The general importance of herbaceous species in nutrient cycling has been indicated in other studies. The species examined in this study may be valuable indicators of soil conditions because of the many significant differences observed in soil chemical and physical properties where these species grow. *Ichnanthus* was observed growing in drier, more acidic and relatively nutrient-poor soils, whereas

Pilea was observed to grow in richer, moist soils high in Ca and Mg. *Dieffenbachia* favored moist soils intermediate in nutrients.

The fact that the three study species have overlapping habitats may be explained in terms of energy equilibria along multiple environmental gradients (Hall *et al.* 1992). According to this idea, there is a spatial and temporal range along which a species may accumulate the energy necessary to persist and reproduce, so it should be expected that these three relatively abundant species have overlapping habitats.

The sensitivity of these herbs to slight changes in microenvironment indicates that they may change reproductive strategies in response to disturbance. All three study species responded favorably to canopy disturbance. There were local, immediate extinctions of these herbs due to burial from litterfall; however, increased light and nutrient inputs from litterfall probably accelerated growth in survivors. Clonal growth of these herbs ensures rapid response to favorable environments without dependence on seeds. For the three herbaceous species studied here, their high nutrient contents, life cycle strategies that permit rapid clonal growth in response to local disturbance, and rapid decomposition rates all interact to increase resilience in the Bisley Experimental Watersheds.

Results of this research support the following conclusions:

1. Study species habitats were related to microenvironmental differences in soil moisture and nutrients. Soil moisture varied significantly with topographic

position, and soil moisture was subsequently correlated with number of soil chemical properties. Light environments were highly variable.

2. Growth of all three species was related to soil properties and/or light differences.
3. Biomass and several measures of plant size were significantly related to soil properties and/or light.
4. Biomass was readily estimated using nondestructive measurements of plant size.
5. All three study species were determined to be r-strategists; however, *Dieffenbachia* exhibited a more conservative life history strategy. Clonal reproduction by means of rhizome fragmentation (*Dieffenbachia*) or rooting at nodes with subsequent fragmentation (*Ichnanthus*, *Pilea*) appeared to be extensively used by study species.
6. *Dieffenbachia*, *Ichnanthus*, and *Pilea* appeared well-suited to disturbance, specifically to hurricane disturbance.
7. *Dieffenbachia*, *Ichnanthus*, and *Pilea* concentrated nutrients above substrate levels, and all three species exhibited rapid decomposition rates.

Based on several lines of evidence, *Dieffenbachia*, *Ichnanthus*, and especially *Pilea* populations were found to play an important role in nutrient dynamics, and thereby ecosystem resiliency, following canopy disturbance in the Bisley Experimental Watersheds.

Managers need to recognize the role of herbs in recovery of disturbed ecosystems in the wet tropics. Nutrient-rich herb species may serve as a temporary reservoir for nutrients easily lost from tropical soils. Their rapid growth following canopy disturbance ensures rapid uptake of nutrients. As woody vegetation becomes reestablished and shades out these herbs, the litter from these dying herbs decomposes rapidly, providing an accessible and rich nutrient source to the succeeding vegetation.

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APPENDICES

APPENDIX A

APPENDIX A. Soil chemistry data for species growth plots. Unless otherwise indicated, nutrient concentrations are in cmol (+) kg.

plot #	Species	Topographic position	Ca	Mg	K	Mn	Fe	P µg/g	Na	Al	ECEC	% C	% N	C/N ratio	Loss on ignition (LOI)	pH (H2O)
1	<i>Dieffenbachia</i>	valley	4.98	3.09	0.11	0.435	2.035	6.0	0.20	2.09	10.47	3.58	0.17	21	18.79	4.93
2	<i>Dieffenbachia</i>	valley	6.19	3.50	0.26	0.550	2.565	5.0	0.22	1.06	11.23	4.24	0.22	20	18.65	4.89
3	<i>Dieffenbachia</i>	valley	4.49	2.92	0.11	0.233	1.418	4.5	0.16	1.36	9.03	3.93	0.25	16	19.04	4.84
4	<i>Dieffenbachia</i>	valley	7.16	3.76	0.25	0.420	1.905	10.0	0.24	0.35	11.75	3.92	0.21	19	17.01	5.20
5	<i>Dieffenbachia</i>	valley	7.30	4.25	0.32	0.200	1.540	10.0	0.26	0.62	12.75	4.57	0.22	21	18.99	5.13
6	<i>Dieffenbachia</i>	valley	3.95	2.23	0.28	0.425	4.945	9.0	0.28	3.17	9.91	3.97	0.22	18	17.67	4.77
7	<i>Dieffenbachia</i>	slope	1.73	1.41	0.12	0.070	2.830	5.0	0.14	3.41	6.81	3.15	0.19	16	14.64	4.82
8	<i>Dieffenbachia</i>	slope	5.02	1.94	0.19	0.295	3.120	10.0	0.23	2.92	7.39	5.63	0.33	17	19.50	4.92
9	<i>Dieffenbachia</i>	slope	1.34	1.44	0.25	0.090	4.020	8.0	0.20	3.64	6.87	2.89	0.18	16	12.31	4.79
1	<i>Ichnanthus</i>	slope	3.84	2.97	0.29	0.245	2.985	13.0	0.25	1.97	9.31	4.48	0.26	17	17.90	4.74
2	<i>Ichnanthus</i>	valley	7.22	4.89	0.30	0.345	1.290	8.0	0.25	0.32	12.97	3.82	0.21	18	16.65	5.33
3	<i>Ichnanthus</i>	valley	5.43	3.80	0.19	0.363	1.703	8.5	0.20	0.84	10.45	2.78	0.12	22.5	15.21	5.10
4	<i>Ichnanthus</i>	valley	6.62	3.80	0.30	0.600	1.230	5.0	0.19	0.19	11.10	2.93	0.10	28	14.44	5.39
5	<i>Ichnanthus</i>	valley	10.29	4.09	0.39	0.320	1.965	10.0	0.19	0.29	15.25	4.67	0.24	19	18.74	5.36
6	<i>Ichnanthus</i>	ridge	0.91	1.40	0.25	0.030	14.235	24.0	0.31	19.47	22.34	7.30	0.34	21	21.59	4.07
7	<i>Ichnanthus</i>	ridge	0.46	1.40	0.22	0.015	16.510	19.0	0.24	18.66	20.98	6.21	0.28	22	19.45	4.10
8	<i>Ichnanthus</i>	ridge	0.27	1.07	0.16	0.020	10.950	11.0	0.27	18.77	20.53	5.24	0.21	25	17.99	4.19
9	<i>Ichnanthus</i>	ridge	0.24	0.58	0.13	0.020	7.515	7.0	0.20	10.46	11.61	2.99	0.11	26	13.97	4.36
10	<i>Ichnanthus</i>	ridge	0.24	0.55	0.10	0.020	13.075	7.0	0.14	14.81	15.85	2.69	0.07	37	12.78	4.40
11	<i>Ichnanthus</i>	ridge	0.24	0.54	0.16	0.015	10.155	9.0	0.16	11.48	12.58	3.39	0.13	25	14.50	4.38
12	<i>Ichnanthus</i>	valley	2.64	2.15	0.26	0.270	6.525	12.0	0.26	5.25	10.56	4.91	0.27	18	21.11	4.63
13	<i>Ichnanthus</i>	valley	1.77	2.08	0.31	0.160	9.205	15.0	0.46	6.73	11.35	5.22	0.31	17	21.71	4.41
14	<i>Ichnanthus</i>	slope	3.37	1.72	0.23	0.150	7.185	12.0	0.21	2.61	8.14	4.33	0.24	18	17.85	4.73
15	<i>Ichnanthus</i>	slope	2.50	1.74	0.17	0.180	2.865	5.0	0.19	2.08	6.68	3.44	0.14	24	16.20	4.60
16	<i>Ichnanthus</i>	slope	3.08	2.14	0.30	0.045	11.910	17.0	0.28	6.94	12.74	7.16	0.33	22	23.36	4.46
17	<i>Ichnanthus</i>	slope	0.41	0.69	0.17	0.025	11.415	12.0	0.12	8.32	9.71	3.82	0.20	19	16.98	4.44
18	<i>Ichnanthus</i>	slope	0.55	0.92	0.19	0.025	14.550	14.0	0.19	9.50	11.35	4.22	0.21	20	17.76	4.42
1	<i>Pilea</i>	valley	5.71	3.79	0.20	0.575	1.515	6.0	0.16	0.79	10.66	3.82	0.19	21	16.12	5.00
2	<i>Pilea</i>	valley	7.34	3.92	0.27	0.680	1.295	7.0	0.20	0.78	12.51	3.82	0.23	17	15.86	4.89
3	<i>Pilea</i>	slope	6.22	2.21	0.27	0.873	1.990	5.0	0.19	0.40	9.29	3.13	0.14	22	14.01	5.17
4	<i>Pilea</i>	valley	7.11	3.09	0.25	0.780	2.785	8.0	0.21	0.34	10.99	4.98	0.25	20	16.09	5.35
5	<i>Pilea</i>	valley	8.22	3.38	0.27	0.485	1.705	8.0	0.17	0.45	12.49	4.45	0.23	20	15.10	5.40
6	<i>Pilea</i>	valley	7.22	4.89	0.30	0.345	1.290	8.0	0.25	0.32	12.97	3.82	0.21	18	16.65	5.33
7	<i>Pilea</i>	valley	10.29	4.09	0.39	0.320	1.965	10.0	0.19	0.29	15.25	4.67	0.24	19	18.74	5.36
8	<i>Pilea</i>	slope	2.97	2.94	0.38	0.480	2.015	6.0	0.18	6.17	12.64	2.49	0.18	14	17.54	4.90
9	<i>Pilea</i>	slope	4.23	3.36	0.36	0.440	2.010	8.0	0.20	3.74	11.89	3.08	0.21	15	19.12	5.02
10	<i>Pilea</i>	slope	5.94	7.06	0.29	0.595	2.690	9.0	0.34	1.67	15.30	3.82	0.24	16	16.60	4.94
11	<i>Pilea</i>	slope	5.09	5.83	0.74	0.455	2.580	11.0	0.23	0.89	12.78	3.90	0.25	16	17.23	4.72
12	<i>Pilea</i>	slope	5.25	3.33	0.46	1.010	4.690	7.0	0.21	1.84	11.10	3.99	0.26	15	19.75	4.96

APPENDIX B

APPENDIX B-1 *Daffnbackia* growth rate data. All length measurements are in cm. Absolute volumetric growth rate calculated as the change in stem volume over the measurement interval. All data are plot averages.

plot number	date measured	number of unfurled leaves	number of unfurled leaves	uppermost unfurled leaf length	uppermost unfurled leaf width	height to top of plant	height to highest leaf scar	circumference at stem base	circumference at stem top	stem volume	number of flowers	total plant density	days in measurement interval	detrital measurements over interval	absolute volumetric growth rate
1	195	4.40	0.60	35.57	13.13	121.07	78.73	12.00	8.87	858.23	0.00	23			
2	195	3.27	0.47	33.40	13.37	110.90	57.90	8.67	10.70	607.00	0.00	24			
3	195	2.60	0.27	24.97	8.67	86.60	55.67	5.63	7.87	424.85	0.00	22			
4	195	2.07	0.00	19.87	6.83	48.23	27.10	7.90	3.63	120.85	0.00	20			
5	195	1.64	0.00	13.68	3.73	33.77	37.59	5.55	2.86	65.53	0.00	11			
6	195	1.00	0.33	15.85	5.39	60.17	45.85	8.93	4.04	215.44	0.00	7			
7	195	1.86	0.00	20.17	7.17	81.79	60.36	8.93	4.71	447.66	0.00	7			
8	195	2.80	0.00	26.30	9.80	87.40	60.80	9.20	5.10	356.05	0.00	5			
9	195	2.89	0.00	24.36	8.79	112.72	87.56	10.94	7.70	573.42	0.00	22			
1	595	2.87	0.07	25.75	9.54	107.93	61.00	10.17	7.70	573.42	0.00	22	130	0	-2.19
2	595	3.86	0.29	33.08	13.33	129.83	63.21	9.64	8.14	553.98	0.00	25	130	0	-0.41
3	595	2.40	0.53	27.82	10.05	120.95	62.63	8.20	6.03	537.24	0.00	22	130	0	0.86
4	595	0.14	0.00	13.75	6.00	23.00	31.53	7.07	3.60	121.98	0.00	21	130	0	0.01
5	595	0.55	0.00	11.80	3.10	30.30	19.64	5.32	2.77	32.23	0.00	11	130	0	-0.26
6	595	0.71	0.29	15.07	6.14	75.71	45.32	9.07	4.18	225.92	0.00	18	130	0	0.08
7	595	0.60	0.40	31.00	12.25	118.00	83.00	10.80	4.70	518.06	0.00	5	130	0	0.54
8	595	0.80	0.00	40.00	16.00	200.00	68.30	10.20	5.20	458.03	0.00	7	130	0	0.78
9	595	0.00	0.00				94.83	11.50	4.50	657.44	0.00	9	130	0	-0.36
1	795	2.47	0.06	28.55	10.27	122.45	71.93	10.20	7.57	706.56	0.00	37	65	0	2.05
2	795	3.75	0.31	33.07	13.50	131.32	62.66	10.03	8.25	619.53	0.13	28	65	0	1.01
3	795	3.47	0.33	22.60	8.53	105.77	66.30	8.33	6.13	578.06	0.00	24	65	0	0.63
4	795	1.13	0.44	12.38	4.00	60.00	34.34	6.91	3.47	112.00	0.00	22	65	0	-0.15
5	795	0.64	0.27	10.70	2.90	24.29	18.86	5.27	2.55	26.82	0.00	11	65	0	-0.08
6	795	2.20	0.27	19.32	6.86	68.57	44.63	8.77	4.07	204.10	0.00	19	65	0	-0.34
7	795	1.29	0.29	21.00	7.63	120.10	78.08	10.58	4.83	506.96	0.00	7	65	1	-0.17
8	795	1.40	0.60	13.88	5.25	89.75	68.70	9.30	5.10	452.26	0.00	7	65	0	-0.09
9	795	1.78	0.56	17.89	6.39	125.50	94.94	11.61	4.28	620.78	0.00	10	65	0	-0.56
1	196	2.76	0.18	33.20	11.93	136.49	80.10	10.79	7.36	796.12	0.00	34	162	2	0.55
2	196	2.69	0.38	34.68	13.13	190.08	114.37	10.97	8.10	1140.27	0.00	31	162	2	3.21
3	196	2.07	0.20	32.46	12.32	145.70	84.15	7.74	5.69	512.87	0.00	24	162	2	-0.40
4	196	2.31	0.00	19.60	6.38	50.50	28.30	7.01	3.68	79.39	0.00	23	162	4	-0.20
5	196	2.91	0.00	16.47	4.83	32.00	18.35	5.54	2.65	30.57	0.00	11	162	0	0.02
6	196	2.73	0.33	24.90	12.45	106.54	72.83	9.95	5.55	479.05	0.00	19	162	0	1.70
7	196	2.86	0.14	27.48	11.37	133.70	96.72	10.33	6.55	859.30	0.00	8	162	1	2.17
8	196	3.60	0.00	29.38	10.66	114.50	73.60	9.28	5.04	446.55	0.00	7	162	0	-0.04
9	196	3.44	0.11	30.38	12.23	165.19	91.89	11.54	6.33	873.67	0.00	10	162	0	1.56

APPENDIX B-2. *Ichmanthus* growth rate data. All length measurements are in cm. Absolute growth rate calculated as the change in leaf number*stem length divided by the number of days in the measurement interval. All data are plot averages.

plot number	date measured	number of leaves	stem length	leaf number * stem length	number of flowers	percent cover	deaths over meas. interval	days in meas. interval	absolute growth rate
1	1/95	6.87	11.37	86.23	0.00	4.5			
2	1/95	8.67	26.17	234.25	0.54	30			
3	1/95	10.40	29.91	320.67	0.87	40			
4	1/95	9.40	28.17	289.29	0.93				
5	1/95	10.33	26.02	278.27	0.87	15			
6	1/95	8.60	18.95	158.96	0.00	6			
7	1/95	9.40	13.87	133.49	0.00	12.5			
8	1/95	9.07	13.71	135.80	0.00	4			
9	1/95	9.47	12.89	138.43	0.00	4			
10	1/95	7.60	16.74	148.88	0.13				
11	1/95	7.93	20.09	162.37	0.00	25			
12	1/95	9.67	18.44	180.09	0.53	15			
13	1/95	8.87	21.44	196.92	0.67	32.5			
14	1/95	10.67	16.81	186.63	0.00	22.5			
15	1/95	9.00	16.30	151.39	0.07	30			
16	1/95	9.60	21.33	212.20	0.27	32.5			
17	1/95	10.67	24.51	273.18	0.27	32.5			
18	1/95	9.27	22.34	216.95	0.53	40			
1	5/95	5.64	11.68	75.77	0.00	7	4	130	-0.08
2	5/95	6.71	21.86	131.86	0.43	25	8	130	-0.79
3	5/95	9.08	21.54	201.29	0.58	35	3	130	-0.92
4	5/95	8.77	17.19	175.38	1.23	30	2	130	-0.88
5	5/95	10.31	18.50	203.85	1.23	25	0	130	-0.57
6	5/95	7.71	15.68	126.71	0.00	7	1	130	-0.25
7	5/95	8.87	15.73	145.00	0.00	10	0	130	0.09
8	5/95	9.33	17.17	167.54	0.00	5	2	130	0.24
9	5/95	6.25	13.75	105.58	0.00	5	3	130	-0.25
10	5/95	6.42	17.42	131.54	0.08	7	3	130	-0.13
11	5/95	6.31	21.50	136.31	0.00	15	2	130	-0.20
12	5/95	9.87	14.77	148.93	0.47	20	0	130	-0.24
13	5/95	7.77	16.12	133.88	0.46	25	2	130	-0.48
14	5/95	11.93	17.97	235.83	0.00	30	0	130	0.38
15	5/95	14.07	17.90	263.10	0.00	15	0	130	0.86
16	5/95	8.29	22.21	204.71	0.21	45	1	130	-0.06
17	5/95	9.00	23.68	226.00	0.29	40	1	130	-0.36
18	5/95	7.57	18.11	159.75	0.43	40	1	130	-0.44

APPENDIX B-2. Continued.

plot number	date measured	number of leaves	stem length	leaf number * stem length	number of flowers	percent cover	deaths over meas. interval	days in meas. interval	absolute growth rate
1	7/95	5.63	12.31	68.00	0.00	8	3	65	-0.12
2	7/95	8.80	24.50	209.50	0.00	35	3	65	1.19
3	7/95	9.73	24.18	254.59	0.00	35	1	65	0.82
4	7/95	8.20	18.80	208.60	0.00	30	8	65	0.51
5	7/95	11.78	20.00	265.67	0.44	15	6	65	0.95
6	7/95	7.42	17.17	137.00	0.00	7	2	65	0.16
7	7/95	9.93	17.18	182.57	0.00	10	1	65	0.58
8	7/95	9.17	17.54	169.13	0.00	6	0	65	0.02
9	7/95	7.20	16.15	130.55	0.00	5	2	65	0.38
10	7/95	6.00	18.63	141.21	0.00	5	0	65	0.15
11	7/95	6.08	22.13	140.33	0.00	15	1	65	0.06
12	7/95	8.91	16.05	164.50	0.09	20	4	65	0.24
13	7/95	4.90	13.40	85.90	0.00	20	3	65	-0.74
14	7/95	15.31	20.88	375.96	0.00	20	2	65	2.16
15	7/95	14.47	21.43	333.20	0.00	20	0	65	1.08
16	7/95	11.82	26.59	381.00	0.00	35	3	65	2.71
17	7/95	11.08	30.88	362.54	0.08	30	1	65	2.10
18	7/95	8.25	18.42	185.88	0.00	35	2	65	0.40
1	1/95	11.50	24.20	281.95	0.00	7	6	162	1.32
2	1/95	16.00	38.10	682.20	0.00	45	4	162	2.92
3	1/95	10.80	29.76	381.96	1.00	45	6	162	0.79
4	1/95	6.00	8.00	48.00	0.00	20	4	162	-0.99
5	1/95	12.00	24.60	302.30	1.00	12	7	162	0.23
6	1/95	8.00	12.75	103.55	0.00	7	7	162	-0.21
7	1/95	14.60	27.73	430.17	0.10	25	3	162	1.53
8	1/95	12.00	20.88	248.03	0.00	5	9	162	0.49
9	1/95	10.50	19.15	210.25	0.00	5	6	162	0.49
10	1/95	6.80	19.54	148.40	0.00	5	7	162	0.04
11	1/95	11.33	16.97	205.90	0.00	15	9	162	0.40
12	1/95	14.00	25.50	352.06	0.00	25	6	162	1.16
13	1/95	13.33	26.33	368.50	0.00	40	7	162	1.74
14	1/95	57.57	51.18	3618.43	0.00	70	6	162	20.02
15	1/95	31.63	42.89	1711.30	0.00	55	7	162	8.51
16	1/95	29.50	27.45	1111.85	0.50	55	6	162	4.51
17	1/95	18.40	57.04	1130.50	0.80	65	8	162	4.74
18	1/95	21.80	39.45	1027.15	1.00	70	7	162	5.19

APPENDIX B-3. *Pilea* growth rate data. All length measurements are in cm. Absolute growth rate calculated as the change total leaf number*area of largest leaf divided by the number of days in the measurement interval

plot number	date measured	number of juvenile leaves	total number of leaves	length of largest leaf	width of largest leaf	leaf length *leaf width (area)	leaf number* area	number of flowers	total plant density	days in meas. interval	deaths over meas. interval	absolute growth rate
1	1/95	0.53	8.60	4.90	3.89	19.04	163.78	0.00	80			
2	1/95	0.47	7.67	4.67	3.31	15.43	118.31	0.00	63			
3	1/95	0.60	8.00	6.94	4.95	34.38	275.01	0.00	19			
4	1/95	0.13	8.13	5.31	3.80	20.19	164.22	0.00	21			
5	1/95	0.15	7.85	4.46	3.25	14.48	113.63	0.00	13			
6	1/95	0.40	7.67	5.25	3.49	18.29	140.25	0.00				
7	1/95	0.43	7.36	6.54	4.54	29.68	218.33	0.00	59			
8	1/95	1.27	6.93	4.71	3.43	16.18	112.20	0.00	42			
9	1/95	0.73	7.20	5.07	3.57	18.09	130.28	0.00	55			
10	1/95	0.54	6.15	4.15	2.66	11.06	68.03	0.00	13			
11	1/95	0.40	5.40	4.34	2.85	12.38	66.87	0.00	23			
12	1/95	0.60	6.20	7.04	4.94	34.78	215.62	0.00	51			
1	5/95	1.29	7.79	4.93	3.86	19.01	148.01	0.86	132	130	1	-0.12
2	5/95	0.50	7.25	4.92	3.25	15.98	115.85	1.17	80	130	3	-0.02
3	5/95	0.31	7.77	7.46	5.19	38.74	301.00	0.46	21	130	3	0.20
4	5/95	0.64	7.79	5.43	3.68	19.97	155.48	0.64	24	130	0	-0.07
5	5/95	1.00	8.67	4.92	3.42	16.80	145.59	0.08	14	130	1	0.25
6	5/95	1.64	8.71	5.07	3.32	16.84	146.79	0.07	37	130	1	0.05
7	5/95	0.86	7.14	5.46	3.89	21.27	151.94	0.50	60	130	1	-0.51
8	5/95	0.40	6.53	5.00	3.47	17.33	113.24	0.53	50	130	0	0.01
9	5/95	0.38	8.85	6.85	4.38	30.02	265.54	0.92	50	130	1	1.04
10	5/95	1.13	6.25	3.63	2.25	8.16	50.98	0.00	11	130	5	-0.13
11	5/95	1.00	5.00	4.33	3.30	14.30	71.50	0.00	16	130	5	0.04
12	5/95	0.73	12.27	7.87	5.30	41.69	511.44	1.07	60	130	2	2.28
1	7/95	0.86	7.21	5.00	3.79	18.93	136.56	0.43	148	65	0	-0.18
2	7/95	1.00	7.00	4.59	3.14	14.40	100.79	0.36	97	65	1	-0.23
3	7/95	0.38	7.15	6.75	4.58	30.94	221.32	0.17	24	65	0	-1.23
4	7/95	0.38	8.31	5.65	4.00	22.62	187.88	0.69	25	65	1	0.50
5	7/95	0.25	8.17	4.92	3.42	16.80	137.19	0.33	15	65	0	-0.13
6	7/95	0.42	9.92	4.96	3.21	15.91	157.75	0.08	53	65	2	0.17
7	7/95	0.43	6.64	5.64	3.79	21.36	141.91	0.14	74	65	0	-0.15
8	7/95	1.00	7.46	5.38	3.73	20.09	149.89	0.00	58	65	2	0.56
9	7/95	0.71	9.79	7.29	4.71	34.35	336.11	0.36	95	65	0	1.09
10	7/95	0.33	6.00	4.17	2.25	9.38		0.33	10	65	2	-0.78
11	7/95	0.33	4.67	4.83	3.00	14.50		0.00	18	65	4	-1.10
12	7/95	0.92	13.31	8.04	5.46	43.90	584.24	0.08	82	65	2	1.12
1	1/96	0.50	8.00	4.25	3.45	14.66	117.30	0.00	157	162	10	-0.12
2	1/96	0.00	6.33	4.27	3.03	12.94	81.97	0.00	67	162	8	-0.12
3	1/96	0.89	8.56	6.73	4.71	31.72	271.39	0.00	28	162	3	0.31
4	1/96	0.22	8.44	6.53	4.54	29.69	250.72	0.00	33	162	5	0.39
5	1/96	0.40	8.90	5.14	3.84	19.74	175.66	0.00	17	162	4	0.24
6	1/96	0.86	6.71	5.69	3.51	19.98	134.16	0.00	35	162	5	-0.15
7	1/96	0.17	7.50	6.23	4.33	27.01	202.58	0.00	66	162	2	0.37
8	1/96	0.57	18.00	5.99	4.37	26.17	470.99	0.00	87	162	6	1.98
9	1/96	2.83	34.58	7.59	5.48	41.56	1437.43	0.00	163	162	2	6.80
10	1/96	0.00	6.33	5.47	3.30	18.04	114.25	0.00	6	162	3	0.71
11	1/96	1.00	3.00	3.50	2.80	9.80	29.40	0.00	5	162	5	0.18
12	1/96	0.57	22.43	6.51	4.56	29.69	665.83	0.00	170	162	6	0.50

APPENDIX C

APPENDIX C-1. Raw biomass data measured on individual plants. All length measurements are in cm. All weight measurements are in g. Refer to methods for further information.
Dieffenbachia seguine

plot number	plant number	stem length	number of leaves (total)	fresh weight	dry weight	percent water content	circumference at stem top	circumference at stem bottom
5	9	15.0	2	12	0.978	1126.99	2.0	3.0
5	10	18.0	2	21	1.415	1384.10	3.0	4.0
5	4	36.2	4	72	5.164	1294.27	2.5	8.6
5	3	39.3	3	93	6.203	1399.27	3.0	7.2
5	1	51.0	3	139	9.090	1429.15	4.5	9.5
5	8	54.8	3	200	14.286	1299.97	5.0	13.5
5	7	36.0	3	80	5.080	1474.80	3.0	9.0
5	5	20.5	4	29	1.889	1435.20	2.5	4.5
5	6	49.4	3	135	9.139	1377.19	3.0	8.0
5	2	44.3	2	133	9.888	1245.06	2.5	9.0
4	2	94.8	2	405	25.614	1481.17	4.5	13.1
4	10	50.0	3	125	13.942	796.57	3.5	9.3
4	9	37.3	2	77			3.5	7.0
4	8	105.0	2	660	39.909	1553.76	6.5	11.8
4	13	20.9	3	15	0.768	1853.13	1.5	4.0
4	7	23.2	4	30	1.630	1740.49	2.5	3.5
4	1	87.0	4	220	11.597	1797.04	4.0	7.6
4	4	52.0	1	148	10.321	1333.97	3.5	8.5
4	12	84.7	3	246	15.691	1467.78	4.5	10.2
4	3	20.6	3	29	1.636	1672.62	2.5	6.0
8	1	113.0	4	2730	158.768	1619.49	8.0	18.0
8	4	127.5	4	940	48.255	1847.98	7.5	11.5
8	3	78.2	3	182	15.006	1112.85	4.0	7.5
8	2	103.5	4	505	31.041	1526.88	5.0	9.0
8	5	29.0	2	29	1.811	1501.33	2.5	4.0
8	U1	12.5	2	17	1.031	1548.88	2.0	8.0
7	7	68.5	3	165	10.125	1529.63	5.0	8.0
7	5	172.0	4	1648	85.174	1834.86	8.0	16.0
7	1	221.0	3	2325	128.885	1703.93	10.0	15.8
7	U1	105.0	3	390	19.881	1861.67	6.0	10.0
7	3	114.0	2	559	28.904	1833.99	7.5	11.5
7	4	11.0	2	3.5	0.216	1520.37	0.5	0.5
7	2	119.0	4	862	46.226	1764.75	7.0	13.5
9	2	65.5	4	200	10.559	1794.12	4.0	8.5
9	5	138.8	4	1095	53.599	1942.95	8.0	14.0
9	4	174.0	4	1660	94.002	1665.92	8.0	15.5
9	1	207.0	3	2065	114.952	1696.40	8.5	17.0
9	7	160.0	4	1070	53.770	1889.96	8.0	12.0
9	6	9.0	0	2.7	0.239	1029.71	0.5	3.0
9	3	44.0	3	70	3.915	1687.99	2.5	5.0
9	8	281.5	3	3201	174.480	1734.59	8.0	16.0
9	9	163.5	4	1243	60.066	1969.39	8.0	14.5
9	U1	17.0	3	10	0.473	2014.16	1.5	2.5
3	12	202.0	5	2289	135.587	1588.21	9.0	13.0
3	15	139.5	5	1257	85.428	1371.41	9.5	11.3
3	8	165.0	0	1153	102.542	1024.42	9.0	11.0
3	11	157.0	4	1527	89.216	1611.58	8.5	13.0
3	14	167.0	5	1630	86.489	1784.63	9.0	11.5
3	1	75.5	3	350	20.689	1591.72	5.5	9.5
3	13	51.0	1	99	6.562	1408.69	3.5	6.0
3	5	21.0	0	6	0.274	2089.78	0.5	2.0
3	4	28.5	1	19	1.347	1310.54	2.0	3.0

APPENDIX C-1. *Continued.*
Dieffenbachia seguine

plot number	plant number	stem length	number of leaves (total)	fresh weight	dry weight	water content	circumference at stem top	circumference at stem bottom
3	3	36.5	2	90	5.708	1476.73	5.5	5.5
1	12	187.5	5	3143	218.079	1341.22	12.0	15.0
1	15	159.5	5	3159	239.993	1216.29	13.0	17.5
1	21	88.0	1	143	8.919	1503.32	3.0	6.0
1	5	123.0	6	1523	112.437	1254.54	9.5	13.0
1	13	58.0	2	236	16.440	1335.52	6.0	8.0
1	14	12.0	0	5	0.408	1125.49	2.0	3.0
1	4	53.0	1	57	3.300	1627.27	3.0	4.0
1	1	107.0	5	750	54.414	1278.32	8.0	12.0
1	3	58.5	2	125	6.840	1727.49	3.5	6.5
1	7	99.5	3	589	34.939	1585.80	7.0	10.5
2	5	180.0	4	1681	100.532	1572.10	10.0	10.0
2	6	125.0	5	2897	189.937	1425.24	12.5	20.5
2	3	242.0	6	4855	361.189	1244.17	12.0	16.0
2	4	151.5	4	1205	78.403	1436.93	8.0	11.5
2	7	90.5	1	437	26.872	1526.23	6.0	9.0
2	9	181.0	5	1975	122.126	1517.18	11.0	12.0
2	8	89.5	1	168	10.527	1495.90	4.0	5.0
2	25	78.5	1	147	10.052	1362.40	5.0	5.5
2	10	19.5	0	9	0.768	1071.88	1.5	3.5
2	12	61.5	5	695	42.596	1531.61	9.0	11.0
6	1	205.0	7	3112	172.381	1705.30	11.0	16.0
6	8	121.0	5	890	44.837	1884.97	8.5	12.0
6	15	94.5	3	532	27.049	1866.80	7.0	11.5
6	9	115.0	2	854	42.098	1928.60	7.0	13.5
6	12	89.5	3	300	13.089	2192.00	5.0	8.0
6	7	39.5	2	50	2.038	2353.39	2.5	5.0
6	11	62.5	3	133	6.872	1835.39	2.5	6.5
6	6	38.5	2	105	5.487	1813.61	2.0	7.5
6	14	16.0	0	10	0.380	2531.58	1.5	3.5
6	13	63.0	2	223	11.184	1893.92	6.0	10.0

APPENDIX C-2. Raw biomass data measured on individual plants. All length measurements are in cm. All weight measurements are in g. Refer to methods for further information.

Ichnanthus pallens

plot number	plant number	stem length	number of leaves (total)	fresh weight	dry weight	percent water content
13	U1	13.6	11	0.311	0.102	204.90
13	U2	20.4	13	0.818	0.207	295.17
13	U3	14.4	13	0.603	0.146	313.01
13	13	22.5	17	0.495	0.206	140.29
13	U4	47.4	24	2.055	0.461	345.77
13	U5	21.0	13	0.625	0.139	349.64
13	1	17.4	7	0.269	0.065	313.85
13	2	27.8	17	0.849	0.288	194.79
13	U6	22.5	10	0.363	0.083	337.35
13	U7	21.1	9	0.839	0.178	371.35
1	U1	5.7	3	0.083	0.014	492.86
1	U2	26.3	12	0.777	0.225	245.33
1	U3	19.8	14	1.359	0.298	356.04
1	U4	23.7	17	1.216	0.273	345.42
1	U5	5.3	5	0.129	0.035	268.57
1	2	33.4	12	0.746	0.222	236.04
1	U6	18.3	10	0.532	0.135	294.07
1	U7	10.1	8	0.150	0.048	212.50
1	U8	14.4	5	0.098	0.047	108.51
1	14	18.4	11	0.246	0.104	136.54
3	6	42.6	15	2.077	0.600	246.17
3	5	14.0	5	0.243	0.075	224.00
3	U1	37.7	12	1.612	0.371	334.50
3	U2	41.1	13	1.479	0.393	276.34
3	U3	33.3	12	1.339	0.339	294.99
3	U4	40.2	6	0.938	0.263	256.65
3	2	21.4	11	0.749	0.298	151.34
3	7	18.8	6	0.438	0.150	192.00
3	U5	32.2	10	0.854	0.225	279.56
3	9	29.0	4	0.534	0.163	227.61
12	U1	28.2	9	0.582	0.178	226.97
12	10	30.2	20	0.876	0.233	275.97
12	9	19.2	14	0.703	0.211	233.18
12	6	25.2	20	1.138	0.327	248.01
12	U2	21.8	12	0.823	0.202	307.43
12	5	33.1	12	0.680	0.212	220.75
12	U3	23.2	15	0.997	0.258	286.43
12	U4	23.7	17	0.721	0.223	223.32

APPENDIX C-2. *Continued.*
Ichnanthus pallens

plot number	plant number	stem length	number of leaves (total)	fresh weight	dry weight	percent water content
12	U5	31.2	19	0.857	0.236	263.14
12	12	14.0	8	0.354	0.092	284.78
5	2	32.0	13	1.103	0.312	253.53
5	U1	34.6	10	1.125	0.297	278.79
5	U2	24.5	14	1.101	0.225	389.33
5	U3	26.4	11	0.909	0.237	283.54
5	U4	21.5	13	1.445	0.356	305.90
5	U5	23.0	13	0.766	0.152	403.95
5	U6	19.4	10	0.664	0.166	300.00
5	U7	31.3	10	1.612	0.364	342.86
5	U8	40.3	16	1.291	0.336	284.23
5	13	18.0	13	1.040	0.190	447.37
5	U9	44.5	12	2.141	0.510	319.80
2	10	80.0	30	3.731	0.746	400.13
2	U1	60.5	13	2.749	0.642	328.19
2	3	25.6	10	0.544	0.166	227.71
2	U2	24.8	9	0.703	0.159	342.14
2	U3	39.2	11	1.770	0.469	277.40
2	U4	31.3	10	1.636	0.491	233.20
2	U5	14.9	9	0.461	0.101	356.44
2	U6	41.5	15	2.075	0.579	258.38
2	U7	11.6	6	0.145	0.052	178.85
2	U8	31.2	7	0.679	0.176	285.80
4	10	8.7	6	0.113	0.043	162.79
4	U1	33.0	16	1.589	0.398	299.25
4	U2	21.9	6	0.661	0.149	343.62
4	U3	37.5	14	2.202	0.456	382.89
4	U4	55.0	22	4.237	0.884	379.30
4	U5	21.9	11	1.069	0.288	271.18
4	U6	46.7	17	2.228	0.551	304.36
4	U7	39.2	6	2.492	0.612	307.19
4	U8	23.4	9	1.171	0.378	209.79
4	U9	47.0	13	2.139	0.568	276.58
18	10	8.7	6	6.876	1.477	365.54
18	7	33.0	16	1.673	0.405	313.09
18	15	21.9	6	3.092	0.721	328.85
18	U1	37.5	14	0.705	0.149	373.15
18	U2	55.0	22	0.357	0.107	233.64
18	U3	21.9	11	1.255	0.302	315.56

APPENDIX C-2. *Continued.*
Ichnanthus pallens

plot number	plant number	stem length	number of leaves (total)	fresh weight	dry weight	percent water content
18	U4	46.7	17	1.135	0.261	334.87
18	U5	39.2	6	0.540	0.138	291.30
18	2	23.4	9	1.580	0.364	334.07
18	6	47.0	13	0.237	0.070	238.57
8	U1	17.8	8	0.516	0.115	348.70
8	U2	5.4	8	0.147	0.042	250.00
8	10	18.2	11	0.562	0.129	335.66
8	U3	11.2	7	0.301	0.073	312.33
8	2	27.8	17	0.643	0.158	306.96
8	12	27.9	12	0.852	0.192	343.75
8	7	26.0	10	0.883	0.194	355.15
8	U4	12.4	10	0.356	0.082	334.15
6	U1	19.1	9	0.453	0.110	311.82
6	U2	12.7	8	0.291	0.065	347.69
6	5	11.9	7	0.156	0.044	254.55
6	14	16.7	9	0.426	0.113	276.99
6	U3	12.8	10	0.339	0.081	318.52
6	U4	24.8	10	0.475	0.127	274.02
6	U5	28.2	10	0.680	0.171	297.66
6	U6	7.6	4	0.061	0.018	238.89
6	U7	19.2	12	0.496	0.128	287.50
6	U8	42.0	11	1.641	0.413	297.34
9	7	32.5	11	0.784	0.205	282.44
9	U1	17.2	8	0.452	0.105	330.48
9	12	24.3	14	0.384	0.131	193.13
9	U2	9.1	8	0.152	0.044	245.45
9	U3	13.9	6	0.050	0.023	117.39
9	U4	16.3	8	0.226	0.059	283.05
9	13	36.4	11	0.696	0.229	203.93
9	U5	34.6	18	0.986	0.283	248.41
9	11	16.3	7	0.166	0.053	213.21
10	8	6.7	8	0.201	0.065	209.23
10	U1	13.3	7	0.424	0.114	271.93
10	14	16.1	1	0.098	0.052	88.46
10	U2	33.7	17	1.442	0.342	321.64
10	U3	19.5	7	0.481	0.110	337.27
10	15	23.0	10	0.625	0.165	278.79
10	U4	5.7	7	0.107	0.035	205.71
10	U5	20.3	10	1.042	0.223	367.26

APPENDIX C-2. *Continued.*
Ichnanthus pallens

plot number	plant number	stem length	number of leaves (total)	fresh weight	dry weight	percent water content
10	6	31.7	10	1.009	0.284	255.28
10	5	21.3	5	0.383	0.119	221.85
17	U1	18.6	11	0.558	0.156	257.69
17	U2	37.2	13	2.132	0.522	308.43
17	U3	62.8	13	2.994	0.710	321.69
17	U4	12.4	8	0.283	0.073	287.67
17	U5	138.0	24	7.457	1.780	318.93
17	4	60.2	12	2.429	0.582	317.35
17	7	32.5	10	1.673	0.387	332.30
17	1	55.5	13	2.069	0.544	280.33
17	6	39.4	20	1.592	0.384	314.58
11	U1	18.5	9	0.422	0.125	237.60
11	U2	26.0	11	0.846	0.256	230.47
11	1	12.9	9	0.429	0.133	222.56
11	U3	173.1	32	9.802	1.783	449.75
11	7	33.2	16	1.388	0.374	271.12
11	U4	46.3	16	1.829	0.425	330.35
11	15	13.0	9	0.308	0.093	231.18
11	U5	20.0	9	0.762	0.168	353.57
11	U6	9.6	6	0.157	0.038	313.16
11	U7	53.1	19	3.117	0.653	377.34
7	2	44.2	15	1.703	0.477	257.02
7	7	22.5	12	0.781	0.228	242.54
7	11	42.6	16	1.357	0.424	220.05
7	3	265.2	14	0.895	0.278	221.94
7	9	26.6	11	1.011	0.269	275.84
7	15	28.3	14	1.064	0.324	228.40
7	1	31.0	15	1.339	0.394	239.85
7	6	15.4	11	0.440	0.141	212.06
7	14	19.8	11	0.556	0.173	221.39
7	10	24.9	15	0.828	0.230	260.00
16	U1	5.4	15	1.609	0.300	436.33
16	U2	63.9	20	3.410	0.576	492.01
16	U3	43.6	10	0.725	0.183	296.17
16	U4	28.2	13	1.221	0.194	529.38
16	U5	31.4	11	1.604	0.246	552.03
16	U6	35.2	21	0.786	0.155	407.10
16	3	109.5	50	4.026	0.821	390.38
16	13	12.0	8	0.265	0.056	373.21

APPENDIX C-2. *Continued.*
Ichnanthus pallens

plot number	plant number	stem length	number of leaves (total)	fresh weight	dry weight	percent water content
16	U7	26.5	13	0.775	0.189	310.05
16	U8	45.0	20	2.114	0.414	410.63
14	3	385.5	129	26.028	4.138	529.00
14	U1	59.5	21	3.179	0.563	464.65
14	U2	40.5	13	1.230	0.228	439.47
14	U3	102.4	32	6.077	0.909	568.54
14	12	224.0	65	14.157	2.272	523.11
14	U4	80.0	36	4.027	0.703	472.83
14	4	83.1	36	4.615	0.714	546.36
14	8	27.6	14	1.108	0.217	410.60
14	15	68.3	25	4.285	0.738	480.62
14	2	40.2	25	1.889	0.313	503.51
15	3	164.0	51	9.067	1.717	428.07
15	6	54.5	20	1.761	0.314	460.83
15	U1	35.2	12	2.211	0.338	554.14
15	U2	55.5	25	3.206	0.520	516.54
15	2	43.0	15	1.507	0.417	261.39
15	13	31.2	9	0.664	0.142	367.61
15	15	45.5	22	2.351	0.399	489.22
15	14	125.8	52	6.958	1.162	498.80
15	7	60.4	30	3.043	0.508	499.02
15	5	80.0	32	4.048	0.778	420.31

APPENDIX C-3. Raw biomass data measured on individual plants. All length measurements are in cm. All weight measurements are in g. Refer to methods for further information.
Pilea inaequalis

plot number	plant number	stem length	number of leaves (total)	leaf length (largest)	leaf width (largest)	fresh weight	dry weight	percent water content
1	U5	31.3	9	4.8	4.2	2.514	0.286	779.02
1	U7	29.0	13	4.8	3.0	1.854	0.214	766.36
1	U3	30.8	10	6.3	5.3	4.553	0.511	791.00
1	13	60.4	10	6.2	4.6	6.181	0.610	913.28
1	U4	51.3	6	4.7	3.5	5.107	0.521	880.23
1	15	42.9	8	2.3	1.6	2.733	0.253	980.24
1	7	32.1	7	4.0	3.0	6.455	0.603	970.48
1	U6	46.2	8	4.4	3.6	5.420	0.589	820.20
1	U2	26.4	6	3.4	3.1	2.199	0.217	913.36
1	U1	37.9	7	6.1	5.5	4.913	0.491	900.61
2	U1	25.8	4	3.5	2.4	1.507	0.133	1033.08
2	U2	27.1	5	5.4	4.4	2.646	0.284	831.69
2	U3	28.2	7	4.2	2.7	2.473	0.225	999.11
2	U4	34.6	8	5.3	3.6	4.517	0.383	1079.37
2	U5	36.0	7	4.6	2.9	3.649	0.385	847.79
2	U6	34.0	6	4.8	2.8	2.864	0.290	887.59
2	U7	35.2	8	4.6	3.5	2.739	0.304	800.99
2	10	33.9	6	3.7	2.6	1.612	0.169	853.85
2	13	111.8	23	4.3	3.6	10.990	1.093	905.49
2	6	66.5	11	5.0	3.8	5.411	0.505	971.49
3	7	24.6	2	6.5	3.8	1.985	0.201	887.56
3	2	28.9	7	3.8	3.0	2.801	0.257	989.88
3	12	19.5	6			2.883	0.321	798.13
3	U1	26.3	10	6.5	4.5	9.547	0.908	951.43
3	U2	12.2	2	11.8	8.6	0.687	0.067	925.37
3	11	61.6	29	4.7	3.4	14.982	1.262	1087.16
3	10	28.8	11	9.8	7.0	9.422	0.915	929.73
3	13	27.7	7	9.3	6.2	3.597	0.402	794.78
3	14	62.3	14	7.5	4.7	14.656	1.447	912.85
3	5	23.1	0			2.060	0.195	956.41
4	4	7.4	6	4.2	3.3	0.782	0.073	971.23
4	7	18.5	9	6.1	4.5	3.749	0.452	729.42
4	14	8.6	9	5.4	3.6	1.252	0.206	507.77
4	13	19.2	8	6.7	4.8	3.304	0.328	907.32
4	5	21.2	14	6.0	4.6	4.337	0.544	697.24
4	4	21.5	10	7.8	5.9	3.179	0.331	860.42
4	3	8.3	1	3.3	1.4	0.339	0.068	398.53
4	11	11.6	10	7.2	5.2	3.319	0.365	809.32
4	U1	9.4	5	4.7	3.1	0.798	0.111	618.92
4	12	22.3	14	8.5	6.5	7.467	0.903	726.91
5	5	48.7	31	8.1	5.8	8.590	1.125	663.56
5	9	9.1	5	4.6	3.2	0.520	0.118	340.68
5	8	25.0	11	7.1	5.3	3.788	0.440	760.91
5	4	15.2	8	4.1	3.2	1.338	0.216	519.44
5	11	13.9	3	5.7	4.4	1.423	0.191	645.03
5	13	20.8	8	3.7	2.6	1.623	0.214	658.41
5	3	6.1	5	2.5	1.8	0.210	0.037	467.57
5	1	14.0	8	6.1	4.4	2.047	0.322	535.71
5	12	10.8	6	2.4	1.9	0.580	0.093	523.66
5	10	21.3	6	5.1	3.5	2.249	0.387	481.14
6	7	14.5	0			1.753	0.189	827.51
6	3	94.2	15	7.4	5.8	15.668	1.502	943.14

APPENDIX C-3. *Continued.*
Pilea inaequalis

plot number	plant number	stem length	number of leaves (total)	leaf length (largest)	leaf width (largest)	fresh weight	dry weight	percent water content
6	U3	42.3	7	6.8	4.4	5.898	0.555	962.70
6	2	34.8	7	5.7	4.2	5.107	0.524	874.62
6	U2	9.2	6	2.4	1.8	0.405	0.036	1025.00
6	1	33.2	0			4.280	0.399	972.68
6	U1	16.5	7	4.5	3.4	0.779	0.076	925.00
6	9	67.0	9	8.7	5.4	7.450	0.714	943.42
6	6	51.4	14	9.3	5.8	9.601	0.983	876.70
6	4	42.4	10	4.5	3.5	4.685	0.532	780.64
7	6	53.6	15	7.9	5.1	6.323	0.781	709.60
7	12	26.6	13	7.8	6.0	6.595	0.730	803.42
7	13	42.6	10	7.0	5.3	8.334	0.832	901.68
7	15	25.8	9	7.4	5.0	4.419	0.477	826.42
7	3	62.1	9	8.6	4.7	8.815	0.842	946.91
7	2	15.1	10	5.9	4.5	1.540	0.173	790.17
7	8	35.6	4	3.8	2.7	2.735	0.230	1089.13
7	14	22.2	6	4.4	3.4	2.180	0.222	881.98
7	9	42.1	4	5.8	4.1	4.118	0.398	934.67
7	4	31.7	10	5.0	4.3	4.800	0.579	729.02
8	4	27.4	7	6.1	4.9	2.122	0.220	864.55
8	14	140.2	47	5.0	4.1	14.300	1.170	1122.22
8	8	55.2	6	4.1	3.3	4.314	0.329	1211.25
8	15	18.1	5	3.9	2.4	1.156	0.109	960.55
8	9	42.0	9	5.5	5.4	5.161	0.511	909.98
8	U2	36.4	18	9.0	6.8	12.991	1.339	870.20
8	U1	19.2	10	7.0	4.6	3.273	0.350	835.14
8	11	187.9	43	6.1	4.6	20.431	1.652	1136.74
8	10	52.7	11	5.2	4.3	5.447	0.511	965.95
9	13	51.0	27	7.3	5.4	7.295	0.800	811.88
9	5	108.4	34	8.1	6.9	16.870	1.567	976.58
9	3	79.9	24	7.2	5.1	9.630	0.975	887.69
9	8	34.5	12	7.1	5.5	6.359	0.660	863.48
9	12	34.5	12	5.1	3.3	2.454	0.258	851.16
9	14	235.6	99	7.8	5.0	44.852	3.999	1021.58
9	4	148.1	62	8.5	6.3	20.823	2.026	927.79
9	7	48.8	23	8.6	5.8	8.079	0.890	807.75
9	6	37.6	20	7.3	4.6	5.274	0.609	766.01
9	1	57.7	25	9.0	6.4	12.869	1.171	998.98
10	U3	3.2	2	3.8	1.3	0.116	0.026	346.15
10	5	17.0	4	5.5	3.3	1.401	0.165	749.09
10	6	38.1	7	4.7	3.3	2.017	0.217	829.49
10	2	13.9	6	4.7	2.7	1.158	0.156	642.31
10	U1	4.3	3	1.5	1.0	0.027	0.006	350.00
10	U2	17.1	3	3.6	2.7	1.054	0.168	527.38
11	U2	1.0	4	0.3	0.2	0.006	0.001	500.00
11	U1	14.8	9	2.2	1.8	0.589	0.092	540.22
11	U4	2.0	4	3.8	2.6	0.506	0.068	644.12
11	11	23.7	9	3.2	2.6	0.790	0.113	599.12
11	U3	2.0	4	1.0	0.5	0.009	0.008	12.50
12	11	392.3	84	7.2	5.2	63.404	5.125	1137.15
12	U4	19.0	7	4.2	3.4	1.682	0.159	957.86
12	U3	18.1	7	4.3	3.3	1.400	0.135	937.04
12	U2	41.8	8	6.3	4.5	4.717	0.330	1329.39
12	16	210.3	18	5.6	4.6	26.836	1.756	1428.25

APPENDIX C-3. *Continued.*
Pilea inaequalis

plot number	plant number	stem length	number of leaves (total)	leaf length (largest)	leaf width (largest)	fresh weight	dry weight	percent water content
12	17	112.6	21	6.3	3.4	10.446	0.742	1307.82
12	U1	129.4	43	5.1	4.1	14.783	1.206	1125.79
12	7	25.8	2	1.9	1.5	2.490	0.152	1538.16
12	1	81.8	31	9.0	6.1	19.935	1.652	1106.72
12	2	59.4	17	8.2	5.5	10.257	0.830	1135.78

APPENDIX D

APPENDIX D. Total biomass and water content values from each growth plot.
All weights are in g.

species	plot number	total fresh weight	total dry weight	total number of plants	total percent water content
<i>Dieffenbachia</i>	1	21519	1501.919	33	1332.77
<i>Dieffenbachia</i>	2	46994	3117.707	40	1407.33
<i>Dieffenbachia</i>	3	18513	1220.053	23	1417.39
<i>Dieffenbachia</i>	4	3641	229.846	23	1484.10
<i>Dieffenbachia</i>	5	916.6	63.297	11	1348.09
<i>Dieffenbachia</i>	6	12710	637.962	22	1892.28
<i>Dieffenbachia</i>	7	5952.5	319.411	7	1763.59
<i>Dieffenbachia</i>	8	4403	255.912	6	1620.51
<i>Dieffenbachia</i>	9	10616.7	566.055	10	1775.56
<i>Ichnanthus</i>	1	6.315	1.692	12	273.23
<i>Ichnanthus</i>	2	112.617	23.630	87	376.58
<i>Ichnanthus</i>	3	93.350	18.844	88	395.38
<i>Ichnanthus</i>	4	82.997	16.546	44	401.61
<i>Ichnanthus</i>	5	35.735	7.443	37	380.12
<i>Ichnanthus</i>	6	11.483	2.677	26	328.95
<i>Ichnanthus</i>	7	38.528	8.699	40	342.90
<i>Ichnanthus</i>	8	4.260	0.985	8	332.49
<i>Ichnanthus</i>	9	3.896	1.132	9	244.17
<i>Ichnanthus</i>	10	8.669	2.242	21	286.66
<i>Ichnanthus</i>	11	41.356	8.651	47	378.05
<i>Ichnanthus</i>	12	30.759	7.482	41	311.11
<i>Ichnanthus</i>	13	41.574	9.013	65	361.27
<i>Ichnanthus</i>	14	264.308	40.492	118	552.74
<i>Ichnanthus</i>	15	145.093	23.087	83	528.46
<i>Ichnanthus</i>	16	135.744	21.766	149	523.65
<i>Ichnanthus</i>	17	206.107	40.205	170	412.64
<i>Ichnanthus</i>	18	234.100	42.597	196	449.57
<i>Pilea</i>	1	410.400	40.410	173	915.59
<i>Pilea</i>	2	80.336	7.565	50	961.94
<i>Pilea</i>	3	84.705	8.169	22	936.91
<i>Pilea</i>	4	79.398	10.663	34	644.61
<i>Pilea</i>	5	29.933	4.204	15	612.01
<i>Pilea</i>	6	134.034	12.568	44	966.47
<i>Pilea</i>	7	210.424	20.555	73	923.71
<i>Pilea</i>	8	263.059	23.027	83	1042.39
<i>Pilea</i>	9	566.398	51.668	148	996.23
<i>Pilea</i>	10	5.773	0.738	6	682.25
<i>Pilea</i>	11	1.900	0.282	5	573.76
<i>Pilea</i>	12	785.645	58.572	165	1241.33

VITA

Amy Elizabeth Arnold was born in Maryville, Tennessee on January 1, 1967 to Evelyn H. and William O. Bledsoe. She graduated from William Blount High School in May 1985. She attended the University of Tennessee, Knoxville, where she earned bachelor of science degrees in Biology (concentration in Ecology) and Zoology (minor in Political Science) in December 1989. In August 1990 she entered the University of Tennessee graduate program in Public Health while working in the Industrial Hygiene Section at Oak Ridge National Laboratory, Oak Ridge, Tennessee. In August 1992, she received a Master of Public Health degree with a concentration in Occupational and Environmental Health and Safety. She entered the graduate program in Ecology at the University of Tennessee in August 1993.