Survival, Growth, and Ecosystem Dynamics of Displaced Bromeliads in a Montane Tropical Forest[1]

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ABSTRACT

Epiphytes generally occupy arboreal perches, which are inherently unstable environments due to periodic windstorms, branch falls, and treefalls. During high wind events, arboreal bromeliads are often knocked from the canopy and deposited on the forest floor. In this study, we used a common epiphytic tank bromeliad, *Guzmania berteroniana* (R. & S.) Mez, to determine if fallen bromeliads can survive, grow, and reproduce on the forest floor and evaluate the potential impact of adult dispersal on plant and soil nutrient pools. Bromeliads were transplanted to and from tree stems and the forest floor and monitored intensively for six months; survival, growth, and impacts on ecosystem nutrient pools were followed on a subset of plants for 16 months. Six months after transplanting, bromeliad mortality was low (3%), and 19 percent of study individuals had flowered and produced new juvenile shoots. Mortality on the subset of plants followed for 16 months was 14–30 percent. Although survival rates were relatively high in all habitats, bromeliads transplanted to trees grew significantly more root length ($\bar{x} \pm$ SE: 189 ± 43 cm) than those moved to the forest floor (53 ± 15 cm) and experienced lower rates of leaf area loss. All transplanted bromeliads rapidly altered the substrate they occupied. Individuals transplanted to and among trees rapidly decreased base cation concentrations but significantly increased P concentrations of their underlying substrate. On the ground, bromeliads increased C, N, and P concentrations within nine months of placement. Our results suggest that in this montane tropical forest, bromeliads respond rapidly to displacement, locally modify their substrates, and can access the resources needed for survival regardless of habitat.

Key words: *epiphytes;* Guzmania berteroniana; *hurricanes; nutrient cycling; Puerto Rico; tropical montane forest.*

EPIPHYTES ARE A CONSPICUOUS COMPONENT of many tropical forests and have been shown to play an important role in ecosystem-level processes (Matelson *et al.* 1993). Most epiphytes occupy arboreal perches where they are subjected to different edaphic and microclimatic conditions than terrestrially rooted plants. The arboreal habitat is thought to supply epiphytes with higher inputs of atmospheric resources and light than the soil surface, but it also has lower storage capacity for water and nutrients, higher winds, and less stability. Epiphytes are particularly abundant in montane tropical forests, which can have high atmospheric inputs from rain and clouds but are also often high-wind environments (Asbury & McDowell 1994). In forests exposed to frequent high winds and hurricanes, epiphytes can fall from the canopy to the forest floor, either individually or with branch- and treefalls (Migenis & Ackerman 1993). These fallen epiphytes may not die immediately. Matelson *et al.* (1993) reported high survival rates for fallen epiphytic mats associated with branch falls in a cloud forest of Costa Rica. The consequences of displacement from the canopy for growth, reproduction,

and ecosystem nutrient pools have not been described.

Epiphytes contribute to ecosystem-level nutrient cycling by capturing atmospherically derived nutrients that constitute a net gain for terrestrial nutrient pools (Benzing 1990, Matelson *et al.* 1993). This is particularly true for bromeliads, which concentrate airborne nutrients via uptake through specialized trichrome cells located in leaf subaxils. Tank bromeliads can also access nutrients through a variety of symbiotic relationships with other organisms, some of which have been shown to fix atmospheric N (Bermudes & Benzing 1991). Soils that develop immediately beneath epiphytes may have high nutrient concentrations due to the combined nutrient inputs from decomposing epiphytic litter, impounded organic matter, and leakage of nutrient-rich waters (Paoletti *et al.* 1991). Most researchers agree, however, that bromeliads rarely access these soil resources via root uptake and instead have adapted to use leaves as their sole means of carbon, moisture, and ion gain (Benzing 1980).

The epiphytic community of the upper montane forests of Puerto Rico has developed under the influence of frequent high winds (Weaver 1994) and exposure to periodic hurricanes (Walker *et al.*

1991, 1996, 1999). These wind events often result in the displacement of arboreal bromeliads from canopy perches to the forest floor. In theory, displaced epiphytes should have the ability to survive, grow, and reproduce in new habitats as long as leaf tissue, the primary tissue for resource acquisition, remains undamaged and sufficient light resources remain available. We tested this theory by determining the effects of relocation on a common bromeliad *Guzmania berteroniana* (R. & S.) Mez. We also hypothesized that bromeliad growth on the forest floor would have a differential effect on plant tissue chemistry (reflecting a change in resource availability or uptake strategy) and/or substrate nutrients (through leaf senescence and leaching). To test these hypotheses, we used a reciprocal transplant experiment to address the following questions: (1) What are the effects of physical relocation on bromeliad growth and survival? (2) How does a change in substrate/habitat affect bromeliad tissue chemistry? and (3) How do bromeliads affect nutrient cycling in the substrate they occupy?

MATERIALS AND METHODS

The study was conducted in the palm forest-type of the Luquillo Experimental Forest (LEF), Puerto Rico (18°10′N, 65°50′W), as part of the NSF sponsored Long Term Ecological Research Program. This forest type is dominated by a single species of palm, *Prestoea montana* (R. Grah) Nichols, which grows to an average canopy height of 15 m (Weaver 1994) and occurs between 700 and 900 m elevation (Beard 1949, Brown *et al.* 1983). The average annual rainfall is 4450 mm, mean annual temperature is 18.7°C, and average relative humidity is 98 percent, with little or no seasonality (Weaver 1994). Tropical storms occur in this regional annually, and the hurricane return interval is approximately every 60 years.

We stratified our sampling on leeward and windward slopes where the tank bromeliad *G. berteroniana* is the dominant bromeliad species and abundant both above ground and at ground level. On palm stems, bromeliad density ranges from 1600 individuals/ha in the canopy, 3700 individuals/ha at the stem midpoint, to 800 individuals/ha at the stem base (Silver *et al.,* pers. obs.). In the montane forests of the LEF, ground-dwelling *G. berteroniana* occur in densities of up to 700 adult individuals/ha and are typically root-anchored in organic and/or mineral soil horizons. We refer to these ground-dwelling bromeliads as "terrestrial" throughout this paper in reference to the physical habitat these plants occupy, and the term does not imply a change in life history strategy. Adult reproductive *G. berteroniana* range in size from 40 to 120 cm across the longest leaf axis. Like most bromeliads, this species utilizes a dual-reproduction strategy: vegetative axillary offshoots are produced as well as brightly colored inflorescences (Fig. 1), which bear seeds that appear to be wind-dispersed.

RECIPROCAL TRANSPLANT EXPERIMENT.—Forty arboreal and 60 fallen individuals were randomly selected within two 450 m² plots, one leeward and one windward facing. Effort was taken to establish these plots under a continuous canopy of *P. montana*, without large gaps. Since no differences were found by aspect in any of the demographic or chemical variables we measured, data from leeward and windward sites were pooled by treatment. Each bromeliad was assigned to one of nine treatments, including six control categories (Table 1). We avoided using very small epiphytes (<20 cm diam.) in an attempt to eliminate immature plants from the data set. For aboveground samples, only individuals growing on palms and within 2 m of the ground were sampled. Transplanted bromeliads were carefully removed from tree stems or forest floor with tweezers, a flathead screwdriver, and/or a trowel to minimize damage to roots and the removal site. Transplanted bromeliads were relocated within plots using a stratified random design. To control for the effect of severing connections of the bromeliad to its substrate, 20 plants (10 on trees and 10 on the forest floor) were replaced in their original position after connections were severed. An additional 20 control plants (10 on trees and 10 on the forest floor) were not manipulated. We found no differences between the two types of controls, and so they were pooled for analyses by habitat location. All bromeliads transplanted to the forest floor were supported by small PVC stakes and a single nylon thread to keep them from tipping (Fig. 1). On trees, bromeliads were supported by a 1 cm wide, 10 cm diameter PVC ring that supported the base of the plant and was attached to the tree with a bungee cord (Fig. 1). As plants were reattached, a square piece of thin plastic mesh was placed between the substrate and the transplanted bromeliad base to facilitate measurements of root growth. We also located plants along roadsides, where bromeliads are rare or absent, in an effort to determine the effects of canopy removal. These roadsides were covered with grasses and low second-growth vegetation and characterized as high-light environments. Photosynthetically active

FIGURE 1.   *Guzmania berteroniana* specimen experimentally transplanted from the forest floor to a tree stem in an upper montane rain forest, Luquillo Experimental Forest, Puerto Rico. The PVC ring that supports this bromeliad is attached to the stem by an elastic cord. Between the bromeliad and the tree stem, blue plastic mesh has been inserted so that new root growth (extending through the mesh) can be measured.

radiation (PAR) ($mml/m^2/h$) in nearby forest and roadside plots was measured continuously for one week during our study period at 0.05 and 1 m heights. PAR measurements within the forest ranged from 1.3 to 4.7 $mml/m^2/h$ at 0.05 m off the ground to between 2.9 and 9.3 $mml/m^2/h$ at 1 m off the ground, while roadside plots averaged 34.8 and 33.0 $mml/m^2/h$ for the two heights, respectively (Olander *et al.* 1998).

Treatment and control bromeliads were sur-veyed every 2 weeks for 6 months to measure in-dices of health, growth, and mortality. Measure-ments included horizontal plant length and width (longest *x*- and *y*-axis); number of live leaves; num-ber of attached dead leaves; leaf damage by either herbivory or sun scorch; reproduction (flowering and number of juvenile shoots); vine, litter, or live leaf contact; and mortality. Under the canopy, her-bivory caused the majority of leaf tissue damage, whereas in open roadsides we observed leaves that

TABLE 1.   *Experimental and control treatments employed with* Guzmania berteroniana *specimens in the palm forest-type of an upper montane rain forest in the Luquillo Experimental Forest, Puerto Rico.*

Category	Label	N	Description
FF control	FC	10	forest floor control
FF (in place)	F	10	uprooted from forest floor and replaced in same location (control for uprooting)
FF → FF	FF	10	transplanted from one forest floor location to another
FF → Road	FR	20	transplanted from the forest floor to open roadside
FF → Tree	FT	10	transplanted from the forest floor to tree stem
Tree control	TC	10	tree stem control
Tree (in place)	T	10	removed from tree stem and replaced in same stem location (control for removal)
Tree → Tree	TT	10	transplanted from one tree stem location to another
Tree → FF	TF	10	transplanted from tree stem to forest floor

had dried and shriveled due to higher light intensity and temperature. We continued less intensive monitoring on a subset of plants for flowering and reproduction until month 9 ($N = 73$) but followed mortality and growth for the entire 16-month period ($N = 46$).

At 6, 9, and 16 months from the start of the experiment, we randomly selected three individuals per treatment to be harvested. All plants were remeasured just prior to harvesting. The harvested plants were separated into root and shoot tissues, washed individually to remove adhering soil and organic litter, dried at 65°C, weighed for biomass, and ground for nutrient analyses. For transplanted individuals, new root length was measured for roots that had grown through the mesh squares. For controls, total root length was measured. We used the following equation to estimate relative foliar growth rates assuming a constant leaf width: Relative foliar growth = $[L_L * L_{nl} * (1 - L_d)] T_f /$ $[L_L * L_{nl} * (1 - L_d)] T_o$, where L_L is the average leaf length calculated as half the average plant diameter (measured from leaf tip to leaf tip on both x- and y-axes), L_{nl} is the number of live leaves and L_d is the percent of damage to leaves as estimated by visual inspection. Plant growth or dieback was calculated as the relative change between the initial measurements (T_o) and those at the end of the monitoring period (T_f).

The soil, forest floor, or epiphytic organic matter (Ingram & Nadkarni 1993) beneath bromeliads selected for transplanting was sampled at the start of the experiment. Soils were sampled directly under bromeliads from 0 to 10 cm depth using a 2.5 cm wide soil corer. Soils were air-dried, sieved through a 2 mm mesh screen, and ground with a Wiley Mill. Forest floor litter was removed from a 10×10 cm^2 area directly beneath the bromeliad, dried at 65°C, weighed to determine mass, and ground in a Wiley mill. Samples of epiphytic organic matter, hereafter referred to as arboreal substrate, included bryophyte mats (which consisted of live and dead bryophytic tissue and arboreal soil) growing on tree stems in a 10×15 cm^2 area under the bromeliad base.

NUTRIENT ANALYSES.—We determined the exchangeable soil nutrient concentrations under bromeliads transplanted to and around the forest floor (including roadsides) and total nutrient content of forest floor and tree substrates under transplanted bromeliads. Both the original substrate (T_o) and the final substrate (T_f) were measured for bromeliads harvested within the first 9 months. No substrate samples were taken at 16 months. Exchangeable Ca, Mg, K, Mn, Fe, Zn, and Al concentrations were determined on a Perkin Elmer ICP at Yale University after extracting 5 g of air-dried and ground soil with 50 ml of NH_4Cl on a vertical vacuum extractor (Silver *et al.* 1994). Extractable soil P was determined after two successive extractions of 2 g air-dried and ground soil in 20 ml of Bray solution (0.003 M NH_4F and 0.025 M HCl; Olsen & Sommers 1982). Analyses were conducted on a Technicon Auto Analyzer at Yale University. Total C and N were determined for soil samples on a LECO CHN analyzer at Yale University. Soil moisture content was determined gravimetrically after drying at 105°C. All data reported here are on an oven-dry soil basis unless noted. Arboreal substrate samples and plant tissues were analyzed for total C and N at the University of California at Berkeley on a CE Elantec CN analyzer. For C and N analyses, three 0.3 g replicates of each sample were analyzed. Organic matter content was determined by loss on ignition (LOI) at 500°C. All analyses included blanks, reference samples, and sample replicates for quality control.

The total elemental composition of tree substrate, forest floor, and bromeliad tissue samples was estimated using a modified Kjeldahl procedure (Parkinson & Allen 1975). All samples were dried at 65°C and ground. Approximately 0.25 g samples were then digested in 8 ml H_2SO_4 and $LiSO_4$ using a block digestor. Solutions were analyzed on a Perkin Elmer ICP at Yale University and a Spectraspan V GCP at the International Institute of Tropical Forestry (IITF) for total Ca, Mg, K, P, Mn, Fe, Zn, and Al. A subset of solutions was analyzed both at IITF and Yale University and gave results within 5 percent of one another. All runs included blanks, standard reference material, and sample replicates for quality control.

STATISTICAL ANALYSES.—Data were analyzed using Systat 7.0 (Wilkinson 1991). Likelihood ratio chi-square tests were used to analyze effects of moving bromeliads on life history characteristics such as mortality and reproduction. We focus on the 6-month intensive data set. Analysis of covariance (ANCOVA) was used to compare regressions of plant growth over time. ANOVAs were used to determine (1) effects of transplanting bromeliads within and between forest floor, stems, and roadsides on root growth and nutrient content and (2) effects of location (stem vs. forest floor vs. roadside) on initial and final substrate nutrient concentrations and tissue mass and nutrient content. The

TABLE 2. *Life history characteristics of bromeliads used for transplant experiments in an upper montane rain forest, Luquillo Experimental Forest, Puerto Rico. See Table 1 for abbreviations. Numbers in parentheses indicate plants missing from a treatment and presumed dead at the end of 16 months.*

Treatment	N	Dead/absent specimens	Flowering plants	Plants w/juveniles
6 Months; $N = 100$				
FF control	10	0	3	3
FF (in place)	10	0	2	1
FF → FF	10	0	0	1
FF → Road	20	2	7	5
FF → Tree	10	0	3	2
Tree control	10	0	1	1
Tree (in place)	10	0	1	1
Tree → Tree	10	0	1	1
Tree → FF	10	1	1	1
16 Months; $N = 46$				
FF control	4	0 (1)	1	1
FF (in place)	4	0 (1)	1	1
FF → FF	4	0 (2)	0	1
FF → Road	12	5 (2)	4	3
FF → Tree	4	0	1	2
Tree control	4	0	0	0
Tree (in place)	4	0	0	0
Tree → Tree	4	0	1	1
Tree → FF	3	1 (1)	1	2

Tukey–Kramer least significant difference (LSD) multiple comparison test was used to determine where significant differences occurred, and log transformations were performed if necessary to meet the assumptions of ANOVA. We report data on life history characteristics for the 9- ($N = 73$) and 16-month ($N = 46$) samples, but we caution that sample sizes for these data are reduced. We used a power analysis to evaluate our ability to detect significant effects with a given sample size. Significance was determined as $P < 0.05$ unless otherwise noted.

RESULTS

HEALTH, GROWTH AND MORTALITY.—Total bromeliad mortality for the study was 3 percent after 6 months ($N = 100$) and 30 percent after 16 months of monitoring ($N = 46$; Table 2). The total mortality at 16 months included 7 individuals, from various treatments, that could not be located after the hurricane season of 1996. If these individuals are not included in the mortality calculations, total mortality was 14 percent for the 16-month period. At 6 months, transplant location had not significantly affected bromeliad survivorship (Table 3); however, location did have a significant effect by 16 months ($P < 0.01$, power = 0.84). Mortality occurred in individuals that were forest floor controls or transplants to the forest floor or roadside.

There was no mortality of individuals on trees, and there were no significant differences in mortality between forest floor and roadside plants.

During the first 6 months, 19 percent of the study bromeliads produced flowers (Table 2). In all cases, flowering was initiated between August and November and lasted for several weeks. None of the individuals we monitored flowered more than once during the experiment. While treatment appeared to have a weak effect on flowering during the initial 6 months of the study ($P < 0.1$), this pattern was not apparent for the subset of plants followed for 9 and 16 months (power = 0.70). Flowering was significantly correlated with production of juvenile offshoots for all time periods examined ($P < 0.01$, power = 1.0); the majority of juveniles were fully formed 2–4 months after cessation of flowering. Individuals transplanted to roadsides had slightly higher rates of flowering ($P < 0.1$) than those of other treatments (Table 2).

Herbivore damage was estimated by measuring loss of foliar tissue as a percent of total leaf area. Herbivory losses varied significantly with experimental treatment ($P < 0.01$) but were unaffected by measurement date for the first 6 months (Table 3). In particular, forest floor and tree stem controls, and plants moved from one forest floor site to another experienced higher rates of herbivore damage than other transplanted individuals (Table 4). Plants transplanted to roadsides were relatively un-

TABLE 3. *The effects of treatment and time on growth and life history measures of* Guzmania berteroniana *in an upper montane rain forest, Luquillo Experimental Forest, Puerto Rico. No significant differences existed between untouched controls and "in place" controls (FC and F; TC and T); so these treatments were pooled by location (T or F) for analyses. (A) chi-square results for bromeliad status at 6-month harvest date.* G^2 *is the likelihood chi-square statistic. (B) ANOVA and ANCOVA results for herbivory and plant growth after 6 months of monitoring.*

(A) Source of variation	G^2	N	df	P
Mortality × Treatment	7.44	100	6	0.28
Flowering × Treatment	10.63	100	6	0.10
Juvenile prod. × Treatment	5.39	100	12	0.94
Juvenile prod. × Flowering	39.00	100	2	0.00
(B) Source of variation	F	N	df	P
Herbivory (%)				
Treatment	9.53	1220	6	0.00
Date	0.79	1220	11	0.65
Treatment × Date	3.94	1220	17	0.00
Relative plant growth				
Treatment	5.71	1156	6	0.00
Date	1.33	1156	12	0.20
Treatment × Date	2.82	1156	18	0.00

affected by herbivory over the study period but initially experienced a high degree of leaf damage due to desiccation from sun exposure. The majority of these individuals responded by growing new leaves or juvenile shoots soon after sun damage occurred, and thereafter appeared unaffected by high light intensity. At the 9- and 16-month harvest dates, leaf area affected by herbivory had increased.

There were no statistically significant differences in the size of bromeliads growing on the ground or in trees at the start of the experiment. After 6 months, forest floor bromeliads had lost a significant amount of leaf area relative to bromeliads growing on trees (Tables 3, 4). This trend continued to be evident on the subset of individuals monitored for 16 months. Plants moved to the roadside also lost considerable leaf area ($\bar{x} \pm$ SE: $-22.5 \pm$ 8%), primarily due to sun scorching. In the forest, the majority of leaf area loss was due to physiological senescence as opposed to herbivore or sun damage. Relative foliar growth of individuals transplanted to or among forest floor sites was less than 1, indicating a loss of leaf area, while individuals transplanted to or among trees had higher relative foliar growth rates close to or greater than 1, indicating net growth (Fig. 2). The size of individuals

TABLE 4. *Growth and health characteristics of bromeliads used for transplant experiments in an upper montane rain forest, Luquillo Experimental Forest, Puerto Rico. Standard errors are indicated by parentheses. Treatments with different lowercase letters are significantly different at the 95 percent level using a Tukey-Kramer LSD multiple comparison test. No significant differences existed between untouched controls and "in place" controls (FC and F; TC and T); so these treatments were pooled by location (T or F) for analyses. Root growth was measured for new roots only at 6, 9, and 16 months on harvested specimens. No root growth data (nd) are included for forest floor and tree stem controls because new growth could not be determined on undisturbed individuals. See Table 1 for abbreviations.*

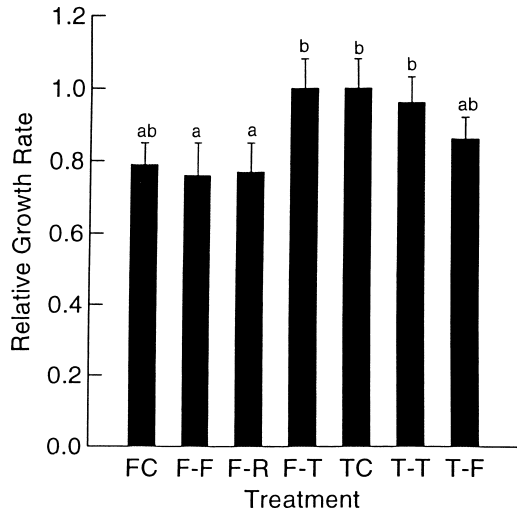| Treatment	N	Herbivory at 6 months (%) $\bar{x}$ (SE)	Δ Plant leaf area at 6 months (%) $\bar{x}$ (SE)	N	Root growth rate (cm/d) $\bar{x}$ (SE)
FF control	20	6.6 (0.3)ab	−18.5 (7.0)a	16	nd
FF → FF	10	7.1 (0.4)a	−24.2 (9.1)ab	7	0.28 (0.13)b
FF → Road	20	5.2 (0.4)bc	−22.5 (8.0)b	13	0.56 (0.15)a
FF → Tree	10	5.9 (0.3)c	0.4 (8.3)c	10	0.71 (0.18)ab
Tree control	20	7.3 (0.3)a	−0.3 (6.1)c	20	nd
Tree → Tree	10	4.9 (0.5)c	−3.7 (7.4)c	10	0.62 (0.15)a
Tree → FF	10	5.4 (0.5)c	−13.9 (6.0)a	8	0.23 (0.05)bc

FIGURE 2. The relative bromeliad growth rate (RGR) in seven experimental treatments six months after transplanting in an upper montane rain forest, Luquillo Experimental Forest, Puerto Rico. See Table 1 for abbreviations. No significant differences existed between untouched controls and "in-place" controls (FC and F; TC and T); so these treatments were pooled by location (T or F) for analyses. When RGR = 1, there was no change from initial size. Different lowercase letters indicate significant differences at the 95 percent level.
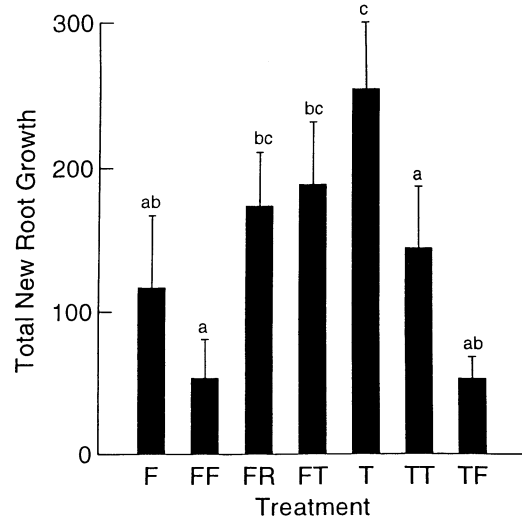
FIGURE 3. Mean total new root length (cm) for bromeliads harvested after 6 to 9 months of experimental treatments in an upper montane rain forest, Luquillo Experimental Forest, Puerto Rico. See Table 1 for abbreviations. No significant differences existed between untouched controls and "in place" controls (FC and F; TC and T); so these treatments were pooled by location (T or F) for analyses. Different lowercase letters indicate significant differences at the 95 percent level.

moved to tree stems and tree controls stayed relatively constant over the study period (Table 4).

For the combined pool of bromeliads harvested on all three dates ($N = 84$), average root growth rates $\pm$SE ranged from 0.23 ± 0.05 cm/day to 0.71 ± 0.18 cm/day (Table 4) and total new root length was significantly affected by treatment ($P < 0.05$, power = 0.79). Bromeliads moved to the forest floor from trees and those moved to a new location on the forest floor showed significantly less new root growth than individuals moved to trees or to roadsides, regardless of harvest date (Fig. 3). After 6 months, bromeliads transplanted to the forest floor had a low amount of total new root length ($\bar{x} \pm$ SE: 53 ± 15 cm), while those moved to tree stems grew an average 189 ± 43 cm new root length.

TISSUE AND SUBSTRATE CHEMISTRY.—Overall, element concentrations were significantly higher in foliar tissues than in roots; the exceptions were C and Fe, which were lower in leaves than in roots, and Al, which did not differ significantly between these two tissue types (Table 5). Foliar element concentrations were not significantly influenced by treatment in most cases; however, control plants grow-

ing on trees contained significantly higher leaf C than plants from all other treatments ($P < 0.1$). In addition, foliar Mg was 29 percent lower in plants growing by roadsides than those growing in the forest. In root tissues, forest floor controls had significantly lower Mg, K, and P than plants from most other treatments, but had higher concentrations of Al and Fe relative to arboreal controls (Table 5). Bromeliads transplanted from forest sites to roadsides gained Ca, Mg, K, and P ($P < 0.01$) relative to forest floor controls. While root C was low in roadside plants, it was also highly variable and differed significantly only from arboreal controls (Table 5). There were no additional patterns in foliar or root element content when plant mass was considered.

Arboreal substrate P concentrations were higher (Fig. 4a) and K was lower in samples collected beneath bromeliads than in samples collected from unoccupied substrates sampled at the beginning of the study ($P < 0.1$; Table 6a). We also found that arboreal substrates under control plants contained significantly higher Fe ($P < 0.1$) and lower Ca and Mg than initially unoccupied transplant sites (Table 6a). Arboreal substrates were composed of decaying bryophytes, sloughed tree bark, and undis-

TABLE 5. Total elemental concentrations in foliar and root tissues of Guzmania berteroniana transplanted among forest floor, tree, and roadside locations in an upper montane rain forest, Luquillo Experimental Forest, Puerto Rico. Values are means of 6- and 9-month harvests (N = 5–7). No significant differences existed between untouched controls and "in place" controls (FC and F; TC and T); so these treatments were pooled by location (T or F) for analyses. Standard errors are in parentheses. Different lowercase letters within a nutrient among sample types indicate significant differences at the 95 percent level using a Tukey–Kramer LSD test and are included when the overall ANOVA model was significant at the 95 percent level. An * indicates model significance at the 90 percent level. Uppercase letters denote significant differences between average concentrations of foliar and root samples (treatments combined). See Table 1 for abbreviations.

| Sample type	Total C (%)	Total N (%)	Nutrient concentration (mg/g 65°C dry wt.)					
			Ca	Mg	K	Al	P	Fe
Foliage								
FF control	45.61 (0.32)a*	1.07 (0.17)	3.22 (0.33)	3.42 (0.36)ab	16.04 (1.37)	0.12 (0.02)	2.27 (0.57)	0.09 (0.03)
FF → FF	45.74 (0.39)a	1.09 (0.14)	3.16 (0.22)	3.57 (0.31)ab	18.05 (0.83)	0.20 (0.07)	2.83 (0.52)	0.19 (0.11)
FF → Road	45.39 (0.33)a	0.86 (0.12)	3.14 (0.36)	2.53 (0.07)c	14.00 (0.79)	0.08 (0.02)	1.52 (0.18)	0.04 (0.01)
FF → Tree	43.62 (1.21)a	0.94 (0.13)	3.16 (0.13)	3.82 (0.25)b	17.34 (1.19)	0.14 (0.01)	2.42 (0.41)	0.12 (0.01)
Tree control	48.28 (2.59)b	0.88 (0.54)	3.39 (0.37)	3.92 (0.39)ab	17.81 (1.38)	0.12 (0.03)	2.39 (0.32)	0.12 (0.03)
Tree → Tree	45.55 (0.41)a	0.74 (0.08)	2.95 (0.13)	3.41 (0.32)ab	16.36 (1.82)	0.13 (0.02)	1.84 (0.28)	0.07 (0.01)
Tree → FF	44.97 (0.36)a	0.87 (0.03)	2.98 (0.24)	3.67 (0.17)ab	16.75 (1.00)	0.15 (0.04)	2.22 (0.24)	0.09 (0.02)
x̄	45.59 (0.80)A	0.92 (0.17)A	3.17 (0.27)A	3.52 (0.29)A	16.69 (1.23)A	0.13 (0.02)A	2.24 (0.38)A	0.10 (0.03)A
Roots								
FF control	47.45 (0.60)ab*	0.74 (0.04)	1.58 (0.23)a	0.32 (0.08)a	0.90 (0.14)a*	0.50 (0.20)a*	0.72 (0.05)a	0.36 (0.16)a
FF → FF	46.32 (0.76)ab	0.82 (0.09)	1.96 (0.19)ab	0.42 (0.10)ab	1.48 (0.38)b	0.58 (0.16)a	0.93 (0.08)b	0.61 (0.11)a
FF → Road	45.18 (2.64)a	0.83 (0.07)	2.94 (0.49)c	0.58 (0.08)bc	1.67 (0.31)b	1.25 (0.87)a	0.96 (0.10)b	1.47 (0.96)a
FF → Tree	46.09 (2.52)ab	0.74 (0.08)	1.75 (0.19)ab	0.52 (0.15)bc	1.31 (0.31)ab	0.17 (0.08)ab	0.91 (0.11)b	0.23 (0.12)ab
Tree control	49.68 (1.52)c	0.91 (0.10)	1.56 (0.27)a	0.51 (0.09)b	1.49 (0.34)b	0.16 (0.06)b	0.94 (0.10)b	0.11 (0.04)b
Tree → Tree	47.95 (0.84)ac	0.81 (0.08)	1.89 (0.42)ab	0.57 (0.18)b	1.86 (0.41)b	0.13 (0.08)b	1.03 (0.10)b	0.11 (0.06)b
Tree → FF	48.83 (0.95)bc	0.83 (0.08)	2.28 (0.21)b	0.72 (0.13)c	1.35 (0.21)b	0.32 (0.08)ab	0.96 (0.11)b	0.32 (0.10)a
x̄	47.36 (1.40)B	0.81 (0.08)B	1.89 (0.28)B	0.50 (0.11)B	1.38 (0.29)B	0.42 (0.20)A	0.90 (0.03)B	0.41 (0.19)B
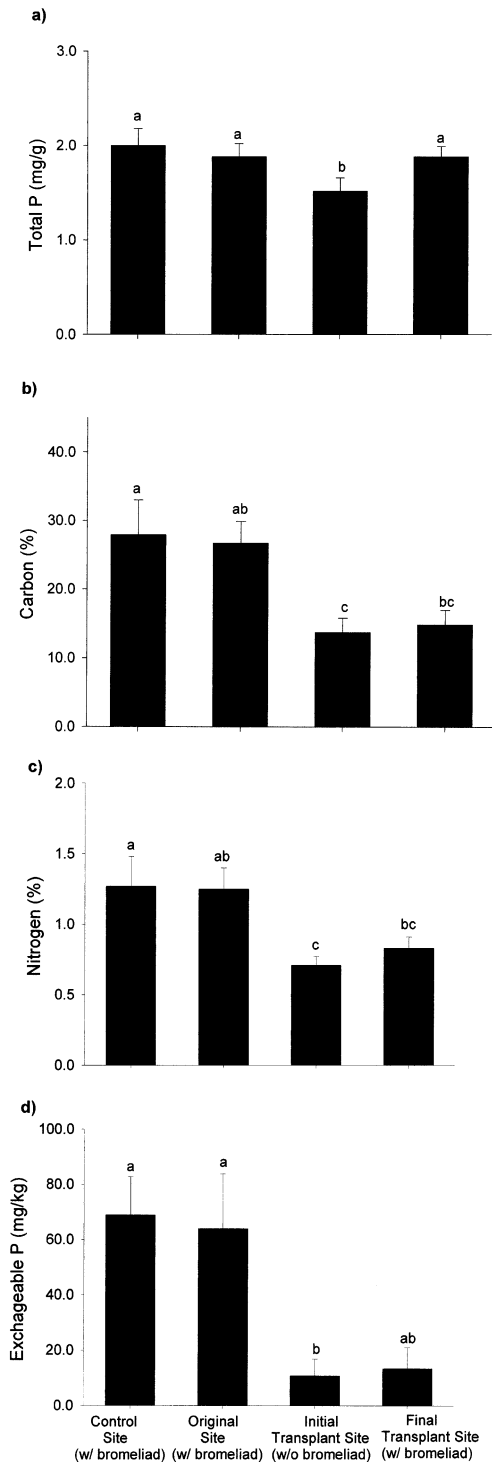
FIGURE 4. (a) Total arboreal substrate P (mg/g); (b) total terrestrial substrate C (%); (c) total terrestrial substrate N (%); and (d) terrestrial substrate exchangeable P (mg/kg) in samples collected beneath bromeliads trans-

tinguishable organic matter, and had significantly higher organic matter concentrations in sites beneath bromeliads than in tree substrates with no bromeliad colonization. When we corrected for high variability in organic matter content of arboreal substrates (by calculating concentrations on an ash weight basis), we still found higher P ($P <$ 0.01) in substrates of control and transplanted bromeliads relative to substrates collected in unoccupied sites. Total K concentrations continued to show the opposite trend ($P < 0.01$) and were highest in unoccupied substrates sampled at the beginning of the study.

We compared total C and N and exchangeable elements in terrestrial bromeliad substrates (soil plus litter) with similar substrate materials from unoccupied sites. Substrates sampled from beneath control plants and plants prior to removal contained significantly more C ($P < 0.01$), N ($P <$ 0.01), and extractable P ($P < 0.05$) than unoccupied sites (Fig. 4b, c, d). Terrestrial substrate samples collected at the end of the study beneath transplanted bromeliads had gained C (Fig. 4b) and N (Fig. 4c) and were no longer significantly different than either control or unoccupied sites. Similarly, substrates under terrestrial bromeliads had slightly higher exchangeable P (Fig. 4d) compared to unoccupied sites. Phosphorus concentrations were substantially higher than reported literature values for soils in the mountains of the LEF (Frangi & Lugo 1985; Silver *et al.* 1994, 1999; Table 6b). Of the other exchangeable elements we measured, only Al varied consistently ($P < 0.1$), and was higher in substrates of controls and transplant bromeliads prior to their removal (Table 6b).

DISCUSSION

There is relatively little known about the life history characteristics of most bromeliad species, and *G. berteroniana*, the most common bromeliad in the upper montane forests of the LEF, is no exception. Most authors describe bromeliads as obligate

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planted among forest floor, tree stems, and roadsides in the Luquillo Experimental Forest, Puerto Rico. "Control" substrate was collected beneath non-transplanted plants at the end of the study. "Original" substrate was collected prior to transplanting; "Transplant" substrate was sampled in the new transplant location; and "Final Transplant" substrate was collected at the transplant location at the end of the study. Different lowercase letters indicate significant differences among substrate groups at the 95 percent level.

TABLE 6. *(A) Total element and organic matter concentrations as measured by loss on ignition (LOI) of arboreal substrates and (B) exchangeable elements in terrestrial substrates. "Original site T_o" substrate samples collected at start of study at initial bromeliad locations. "Transplant site T_o" substrate samples collected at start of study at previously uncolonized transplant locations. "Control T_f" substrate samples collected beneath controls during 6- and 9-month harvests. "Transplant T_f" substrate samples collected beneath transplanted bromeliads after 6 and 9 months of growth in new location. Values are means with standard errors within an element among substrate groups indicate significant differences at the 95 percent level using a Tukey–Kramer LSD multiple comparisons test and are included when the overall ANOVA model was significant at the 95 percent level. An * denotes model significance at the 90 percent level.*

(A)

Arboreal substrate total element concentration (mg/g)

Substrate group	N	Ca	Mg	K	Al	Fe	P	percent LOI
Control T_f	16	2.98 (0.31)a	1.10 (0.11)a	3.60 (0.32)a*	0.65 (0.32)a*	0.52 (0.29)a*	2.19 (0.19)a*	91.58 (1.37)a
Original site T_o	28	4.49 (1.29)b	2.61 (0.58)b	4.76 (0.86)ab	0.35 (0.07)a	0.22 (0.05)b	2.13 (0.33)a	90.01 (1.30)a
Transplant site T_o	22	3.05 (0.43)b	1.55 (0.13)c	5.33 (0.53)b	0.23 (0.05)ab	0.16 (0.05)b	1.56 (0.15)b	86.20 (1.53)b
Transplant site T_f	14	2.85 (0.30)a	1.13 (0.15)a	3.57 (0.47)a	0.22 (0.09)b	0.18 (0.08)b	1.93 (0.12)a	92.06 (1.18)a

(B)

Terrestrial substrate exchangeable elements (cmol/kg)

Substrate group	N	Ca	Mg	K	Al	Fe	Exchangeable P (mg/kg)
Control T_f	11	6.87 (2.31)	3.77 (1.02)	0.70 (0.12)a	4.59 (1.32)a*	0.52 (0.12)	68.88 (43.35)a
Original site T_o	31	7.47 (1.52)	3.02 (0.69)	1.03 (0.19)b	2.83 (0.22)a	0.26 (0.05)	64.06 (19.82)a
Transplant site T_o	40	6.79 (1.02)	2.15 (0.48)	0.61 (0.19)a	2.12 (0.38)b	0.21 (0.04)	10.84 (6.03)b
Transplant site T_f	19	6.70 (1.43)	2.43 (0.39)	0.54 (0.13)a	2.02 (0.44)b	0.35 (0.07)	13.33 (7.62)ab

arboreal epiphytes (Kress 1986, Benzing 1990). While bromeliads have been noted on the forest floor (Matelson *et al.* 1993, Richardson *et al.* 2000), it is often assumed that they cannot persist, and thus are functionally equivalent to litterfall. The common assumption that tropical tank bromeliads are adapted only to an arboreal environment is misleading, however, because their requirements for growth (atmospheric nutrients, humidity, and low to medium light levels) may be available in both arboreal and terrestrial habitats. This is particularly true in short-statured montane forests that are frequently characterized by high humidity and inputs from cloud- and rainwater, but this may also occur in other tropical forests.

In the LEF, mature bromeliads commonly occur on the forest floor, achieving densities as high as 700 individuals/ha. The absence of single juvenile bromeliads on the forest floor, however, indicates that *G. berteroniana* is unable to germinate on the forest floor; that very small plants are not as susceptible to displacement; and/or that seeds and small propagules suffer lethal disturbance caused by falling litter and woody debris. Adult bromeliads on the forest floor probably established there after displacement from arboreal sites during semiannual tropical storms or hurricanes. Their ability to persist long after being knocked from the canopy may be due to the relatively low canopy (15 m) and steep slopes that allow light to enter from the side during part of the day. The large size and the ability to expand through vegetative reproduction contribute to the abundance and high survivorship of adult *G. berteroniana*. Indeed, the low mortality rate of transplanted and control bromeliads during our 16-month experiment suggest that these epiphytes are not obligately dependent on arboreal habitats for survival and growth. Although bromeliads on trees had higher survival and root growth rates than forest floor bromeliads, we observed many *G. berteroniana* that maintained substantial leaf area, produced flowers, and reproduced vegetatively (producing juvenile offshoots) after being moved to the ground. It is possible that we overestimated growth and survival by loosely supporting the bromeliads we transplanted to the ground. Under natural disturbance conditions, some plants are likely to fall inverted and may suffer higher mortality or have to allocate more resources to root growth to right themselves. Our disturbance control treatments ("FF in place" and "Tree in place") did not have significantly different mortality or relative growth from undisturbed controls, suggesting that this species is fairly resilient to mechanical perturbation.

Longevity of arboreal and terrestrial epiphytes has not been well documented, although Oberbauer *et al.* (1996) noted that several *Tillandsia* spp. survived at least 10 months following hurricane disturbance in southern Florida. Our results suggest that bromeliad longevity can exceed 16 months following a major disturbance event. In addition, the *G. berteroniana* that we moved to new habitats quickly grew new securing roots on the scale of tens of millimeters per day. Plants that were moved to tree stems, which represents a very unstable habitat, grew the most new root length. The ability to quickly prioritize C allocation to new tissues such as roots has been suggested as a response to a lack of specific resources (Bloom *et al.* 1985). In this case, physical stability may be the limiting resource stimulating plant responses. Individuals that were moved to roadsides, characterized by drier and sunnier conditions, responded by allocating resources to new shoots and roots instead of established tissues. Roadside plants also produced more flowers than forest plants, suggesting that in this species, allocation to reproduction is possible under stressful conditions. Other bromeliad species also have been shown to respond to disturbance with the production of juvenile shoots (Oberbauer *et al.* 1996). The correlation we found between flowering and axillary shoot production supports the assumption that individual bromeliad shoots are determinate (Richardson *et al.* 2000). Our results showed that after being moved to the forest floor, *G. berteroniana* did not exhibit a shade-stress response by increasing leaf area, but instead lost many older leaves to senescence and herbivory. This is partly because light levels are not significantly different in this forest type between the forest floor and mid–low canopy levels (Olander *et al.* 1998) and partly because the higher degree of disturbance on the forest floor may overwhelm the plant's leaf turnover capacity.

The effects of herbivory on our study bromeliads varied with habitat. In particular, plants growing along roadsides experienced less herbivory than control bromeliads on the forest floor. Bromeliads that were moved to or relocated among trees and those moved from trees to the forest floor had less herbivore damage than stationary controls. This may have been due to a lag time following relocation before plants were discovered by herbivores. If this is the case, the ability to successfully relocate or "be mobile" may have an added benefit of reduced risk of herbivory, at least over the first year;

however, some of the events that lead to bromeliad displacement can also result in canopy openings, which increase light and temperature and can lead to leaf desiccation (as evidenced by the high degree of sun damage to roadside bromeliad).

We hypothesized that habitat (terrestrial or arboreal) would have a significant impact on C and nutrient concentrations in bromeliad tissues. Some bromeliads have been shown to switch uptake and allocation strategies as resource availability changes (Nadkarni & Primack 1989). Here, *G. berteroniana* generally allocated more nutrients (except Fe) to leaves than to root tissues. Bromeliads did not respond to different microenvironments by changing nutrient allocation to leaves. Arboreal bromeliads, however, contained higher levels of Mg, K, and P in root tissues than the forest floor controls. This resource allocation to support structures may be related to bromeliads' increased need for stability when growing suspended against a tree stem. While these patterns of tissue concentrations could be controlled by differential root uptake in arboreal versus terrestrial habitats, to show this conclusively, further study using substrate fertilization and/or isotopic tracers needs to be conducted. Higher Fe and Al in root tissues on the forest floor is likely to result from mineral plaques precipitating on root surfaces of newly rooted bromeliads.

In addition to altering plant nutrient content, displaced bromeliads also changed the nutrient content of their substrate. Tank bromeliads, with their ability to impound water and floral and faunal detritus, are effective repositories for decomposing organic matter, which often leads to the formation of arboreal soil. We found that arboreal substrate (a combination of bryophytes and arboreal soil) that developed directly beneath *G. berteroniana* had higher organic matter content, P, and Fe, and lower K than similar material from sites uncolonized by bromeliads. These patterns result both from nutrient capture by bromeliads and the effects of nutrient inputs from bromeliads to their substrate. Bromeliads influence arboreal soil by capturing nutrients from atmospheric sources, intercepting tree litterfall and promoting decay in tank impoundments, leaking nutrients from tanks, disrupting stemflow, and producing bromeliad leaf/root litter. Nutrients that are mineralized in arboreal environments may be taken up by microorganisms, other epiphytes, or leached to other parts of the ecosystem (Nadkarni & Matelson 1991). Epiphyte nutrient cycling is difficult to quantify at an ecosystem scale due to high spatial and temporal variability. For example, in a Costa Rican cloud forest, epiphyte-derived litter decay and nutrient dynamics were highly sporadic in space and time but generally exhibited fast decay rates and slow nutrient turnover times (Nadkarni & Matelson 1992).

Fallen epiphytes affected ecosystem nutrient cycles differently than litterfall. Beneath terrestrial bromeliads, we measured increased substrate C, N, and P. This was likely a result of nutrient-rich bromeliad litter inputs (Nadkarni & Matelson 1992) and leakage from the tank. It is not surprising that for forest floor-dwelling *G. berteroniana*, the material impounded in the plant's tank, together with its senesced tissues, will eventually contribute to the terrestrial ecosystem nutrient cycle when the plant dies (Veneklaas 1990, Nadkarni & Matelson 1992). Our results, however, indicate that under terrestrial bromeliads, increased soil C and nutrient pools may develop while the plants are alive, augmenting the eventual inputs that will occur with plant death. Thus, fallen bromeliads not only contribute appreciably to the forest floor nutrient capital through their eventual death and decay but also affect the timing of nutrient release because of the lag time between falling and plant death.

The high concentrations of P we found in bromeliad substrates are particularly intriguing. In Puerto Rican floodplain forests, Frangi and Lugo (1985) found that concentrations of P were eight times higher in epiphyte-derived arboreal soil than in terrestrial soil. This may have been a result of high organic matter content, as well as high atmospheric nutrient inputs to these systems from trade winds containing high concentrations of Saharan dust (Talbot *et al.* 1986). It could also have been caused by lower Fe in arboreal soil relative to terrestrial soil. Phosphorus can be rapidly occluded in tropical soils by Fe and Al oxides and hydroxides (Sanchez 1976), removing it from the soil exchange complex. Phosphorus is commonly a limiting element in tropical forests. Phosphorous added through epiphytic soil results in hot spots of P availability on the landscape.

Our results showed that bromeliads are capable of surviving drastic changes in their habitat conditions caused by displacement and relocation. Most plants are static with regard to location throughout their life cycle. In high wind environments, however, epiphytes can move to new locations, effectively dispersing as adults and colonizing new habitats. In this study, the successful colonization of new habitats was augmented by the ability to allocate resources to new root growth, as well as the production of new shoots. As with all plants, bromeliads modified their environment; but unlike most plants, which tend to deplete nutrients in

their rhizosphere, transplanted bromeliads locally concentrated C, N, and P in their substrate over a relatively short period of time. These resources were probably derived from atmospheric sources and can be considered a net input to the ecosystem as opposed to a recycling of resources already present. In summary, our results showed that bromeliads can successfully disperse as adults surviving to reproduce vegetatively, and that the presence of bromeliads can locally enrich substrate nutrient capital. We found that *G. berteroniana* is adapted to the dynamic nature of montane tropical forests with its ability to relocate to new environments and successfully reestablish.

ACKNOWLEDGMENTS

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