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## Growth and Fertilization Responses of Hawaiian Tree Ferns<sup>1</sup>

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### ABSTRACT

Responses of a tree fern (*Cibotium glaucum*) to nutrient additions were examined in two rain forest sites in Hawaii Volcanoes National Park, Hawaii. In the younger forest (*ca* 200 yr old), separate additions of nitrogen and of phosphorus (but not additions of all other macro- and micronutrients) increased fern stem height growth. Nitrogen but not phosphorus increased leaf production, but fertilization had no effect on maximum leaf longevity (39 mo). In the older forest (>1000 yr old), nitrogen additions did not alter fern growth parameters; fern stem height growth and leaf production were greater in unfertilized plots of the >1000 yr old forest than in unfertilized plots in the younger forest; and leaf longevity (maximum of 34 mo) was shorter. Leaf production (February–April) and leaf mortality (August–November) were highly seasonal, with mortality occurring several months after expansion of new leaves. The asynchronous leaf recruitment and mortality resulted in cyclic monthly variability in leaves per fern. Our data support other studies suggesting that more rapid leaf turnover occurs in nutrient-rich sites, and that nitrogen appears to be the nutrient most limiting to growth in the early stages of primary succession.

*Key words:* *Cibotium glaucum*; fertilizer effects; Hawaii; nitrogen; phenology; phosphorus; tree ferns.

TREE FERNS ARE IMPORTANT COMPONENTS of tropical and south temperate rain forests (Ash 1987). They form a subcanopy in mature forests (Ash 1986, 1987), are common in very humid cloud forests (Conant & Cooper-Driver 1980, Seiler 1981, Tanner 1983), and colonize forest gaps (Holtum 1938), roadcuts (Conant & Cooper-Driver 1980), and exposed mineral soils found on landslides (Guariguata 1990) or under uprooted trees (L. Walker, pers. obs.). Relatively few studies of the ecology and demography of tree ferns have been conducted (but see Becker 1976), given their prominence in humid regions. Tree ferns grow slowly and may live for many decades. When tree ferns form dense, self-perpetuating thickets in disturbed areas (Seiler 1981), they may inhibit colonization and growth of other species (Wick & Hashimoto 1971, Page 1979, Burton & Mueller-Dombois 1984). They may also affect nutrient cycling in tropical forest soils, particularly where levels of soil nutrients are low (Mueller-Dombois *et al.* 1983).

This study examines the growth responses of *Cibotium glaucum* (J. Sm.) Hook. & Arn. to fertilization at two subtropical montane rain forest sites

in Hawaii. Each site represents a different stage (*ca.* 200 and >1000 yr, respectively) in forest development on soils derived from volcanic ash. Our study was designed to determine if growth of *C. glaucum* was nutrient-limited and to compare growth in the two successional sites.

### METHODS

**STUDY SITES.**—Our study was conducted at two rain forest sites in Hawaii Volcanoes National Park (HVNP), Hawaii, USA, between 1190 and 1220 m elevation and near the summit of Kilauea Volcano (19°20'N, 155°15'W). The younger site was in forest dating from a 1790 eruption of Kilauea near the Thurston lava tube; the older site was in the Olaa tract of HVNP where the forest vegetation had not been significantly disturbed by eruptions for at least 1000 yr. Mean annual precipitation is approximately 2500 mm at the younger site and 2900 mm at the older site (interpolated from Giambelluca *et al.* 1986); there is no distinct dry season. Mean January temperature is 14°C, and mean July temperature is 17°C. The tree fern *Cibotium glaucum* is common at both sites under either a dense (the younger site) or sparse (the older site) canopy of *Metrosideros polymorpha* Gaud. trees. The soil at the younger site is approximately 30 cm deep and

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is a well-drained, silty and sandy loam overlying pahoehoe lava (Gerrish *et al.* 1988). The soil at the older site is generally >1 m deep. Further site descriptions can be found in Vitousek *et al.* (1994).

**FERTILIZATION PROCEDURE.**—At the younger site, we conducted a complete factorial fertilization design with nitrogen (N)/phosphorus (P)/ and all other macro- and micronutrients (T) as part of a larger study of nutrient dynamics during post-volcanic succession (Vitousek *et al.* 1987, Vitousek & Walker 1989, Walker & Vitousek 1991, Vitousek *et al.*, 1994). The eight treatments were N, P, T, NPT, NP, NT, PT, and a control without fertilizer. Nitrogen fertilizer (50% urea, 50% (NH<sub>4</sub>)<sub>2</sub>S<sub>2</sub>O<sub>4</sub>) was applied initially (12/85) at a rate of 10.0 g m<sup>-2</sup>. Phosphorus (as P<sub>2</sub>O<sub>5</sub>), K (as K<sub>2</sub>SO<sub>4</sub>), Ca (as dolomite), and a micronutrient mix (Granusol) were each applied initially (12/85) at a rate of 5.0 g m<sup>-2</sup>. Magnesium (mostly as dolomite) was applied initially at 3.2 g m<sup>-2</sup>. Subsequent applications of each nutrient (at one-fourth initial levels) were applied at 6 mo intervals until 12/87 and again in 10/88. At the younger site, we established a grid of 40 20 × 20 m plots and then selected 32 plots that had minimal introductions of non-native woody plants. Each of the eight treatments was applied to four randomly chosen 15 × 15 m plots contained within the larger plots.

At the older site, N fertilizer was applied (at the same levels as at the younger site) to six 200 m<sup>2</sup> circular plots (8 m radius), each centered on a *Metrosideros polymorpha* tree. Applications of N at the older site were made every 6 mo for 2 yr (12/85 to 12/87) but were not made in 10/88. The six N plots and six control plots were scattered throughout a 1 ha area of forest.

**PLANT MEASUREMENTS.**—At both sites, stem height growth, leaf production, and leaf turnover on one *C. glaucum* individual per plot were monitored every 2 mo during the first 2 yr (12/85–12/87) and intermittently up to 3.5 yr total for the older site (7/89) and 6 yr total for the younger site (10/91). Change in stem height was measured from a nail (placed in the trunk about 50 cm above the ground) to the top of the lowest, unexpanded fiddlehead. Stem height growth per mo did not differ ( $P = 0.19$ ) at the younger site between the first 44 mo and the remaining 27 mo so height growth estimates for the younger site were based on means over 71 mo and were compared to means over 43 mo at the older site.

Leaf production was compared between treatments and between sites during the first and second complete years (1986, 1987). Leaf numbers per fern were compared in July 1987 because it was in the middle of the second year of fertilization. We also uniquely marked each new leaf cohort and assessed cohort survivorship at each visit. A leaf was considered to be alive as long as it still had any green or yellow tissue. Precipitation data were obtained from HVNP Resource Management (T. Tunison, pers. comm.) and compared against patterns of leaf emergence.

**DATA ANALYSIS.**—We used a factorial ANOVA (SAS 1988) to analyze the effects of fertilizer at the younger site and the *t* statistic for all other pairwise comparisons. Significance was determined at the 5 percent level. All data are reported as means ± standard error.

## RESULTS

**EFFECTS OF FERTILIZATION.**—At the younger site, stem height growth significantly increased from fertilization with N or with P (Table 1) but not with all nutrients except N and P (= T). Furthermore, there were no significant factorial interactions. Stem height growth at the older site was not significantly different between ferns fertilized with N and unfertilized controls. Unfertilized stems from the older site grew significantly more than unfertilized ferns from the younger site (Table 1).

Nitrogen fertilization significantly increased leaf production during the second year at the younger site (Table 1). No differences were found between treatments during the second year at the older site (Table 1) or during the first year at either site. Phosphorus fertilization had no effect on leaf production at the younger site during either year, and fertilization with all nutrients except N and P elicited no response. There were significantly higher rates of leaf production during the second year compared to the first at both sites and for both fertilized and unfertilized ferns. As with stem height growth, mean leaf production of unfertilized ferns at the older site was significantly higher than leaf production by unfertilized ferns from the younger site in 1987 (Table 1).

The higher leaf production under N fertilization at the younger site also increased the number of leaves per fern over unfertilized ferns (Table 1). Fertilized and unfertilized ferns did not differ in leaf number at the beginning of the study. No differences in leaves per fern were observed for P fertil-

TABLE 1. Mean ( $\pm$  SE) indices of growth of tree ferns in response to nutrient additions at two forest sites of different ages in Hawaii. Significant differences between means within columns are indicated by "S" ( $P < 0.05$ ), non-significant differences by "NS." Sample sizes are in parentheses.

Treatment N	Stem height growth (cm mo <sup>-1</sup> )	Leaf production in 1987 (leaves fern <sup>-1</sup> yr <sup>-1</sup> )	Leaf number in July 1987 (leaves fern <sup>-1</sup> )
200 yr-old site			
No nitrogen (16)	0.38 $\pm$ 0.03 S	3.6 $\pm$ 0.2 S	9.4 $\pm$ 0.5 S
Nitrogen (16)	0.60 $\pm$ 0.04	4.7 $\pm$ 0.2	11.7 $\pm$ 0.5
No phosphorus (16)	0.43 $\pm$ 0.03 S	4.0 $\pm$ 0.2 NS	10.5 $\pm$ 0.5 NS
Phosphorus (16)	0.55 $\pm$ 0.04	4.4 $\pm$ 0.3	10.6 $\pm$ 0.7
No fertilizer (4)	0.37 $\pm$ 0.04 S	3.7 $\pm$ 0.2 S	10.5 $\pm$ 1.2 NS
1000 yr-old site			
No fertilizer (6)	0.54 $\pm$ 0.04 NS	4.3 $\pm$ 0.2 NS	11.3 $\pm$ 0.6n NS
Nitrogen (6)	0.64 $\pm$ 0.05	4.7 $\pm$ 0.6	10.2 $\pm$ 0.8

ization at the younger site or for N fertilization at the older site (Table 1). Similarly, no differences were observed for leaf numbers between sites (Table 1). The minimum and maximum number of leaves found on any plant over the entire study were five and 16, respectively.

**PHENOLOGY.**—Leaves were mostly produced early in the calendar year. In the two years for which we have bimonthly data, unfertilized ferns from the younger site produced 91.6 percent of their leaves over the interval from February to April; ferns from the older site produced 90.3 percent of their leaves over the same interval. There was no fertilization effect on the timing of leaf production at either site. Only 14 of the 44 ferns followed in this study produced any leaves outside of the February–April period over the two years of bimonthly observation. Late producers in 1986 also tended to produce late leaves in 1987.

Most leaf mortality (70–75 percent) occurred between August and November, several months after the new leaves were fully expanded. The infrequent visits in the last half of the study period did not allow for exact determination of leaf longevity, but some estimates can be made by examining trajectories of leaf mortality (Fig. 1). Cohorts of leaves produced during February–April generally lived about 18 mo before beginning to die. At both sites, percent survivorship after 18 mo was still above 90 percent. Leaf mortality over the ensuing 15–20 mo resulted in cohort extinction in less than 40 mo. Our data suggest that maximum leaf longevity may

have been somewhat longer at the younger site (*ca* 39 mo) than at the older site (<34 mo), but no sign of a fertilization effect on longevity was evident at either site.

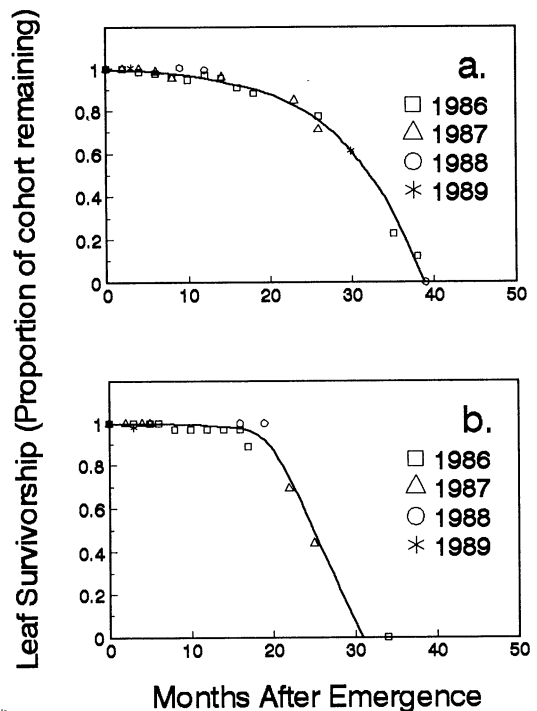


FIGURE 1. Survivorship of *Cibotium* leaves from all 32 ferns at the younger site (a), and all 12 ferns at the older site (b). Different symbols represent February–April cohorts from various years.

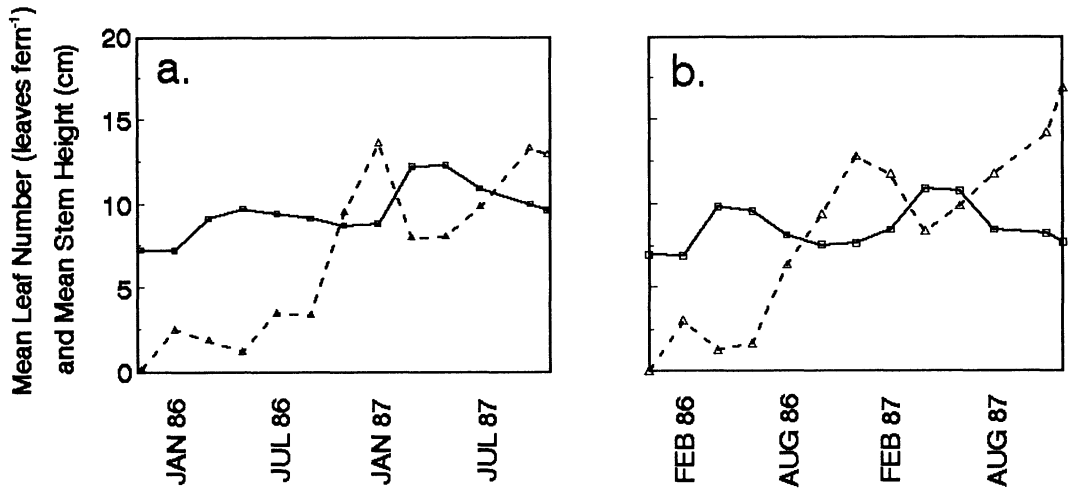


FIGURE 2. Mean number of leaves per fern (solid line) and mean stem height from a fixed reference point (dashed line) for all 32 ferns at the younger site (a), and all 12 ferns at the older site (b).

Asynchronous leaf recruitment and mortality resulted in cyclic monthly variability in leaves per fern (Fig. 2). Minimum leaf number occurred after high mortality between August and November but before the flush of new leaves between February and April; maximum number occurred between April and June. The difference between minimum and maximum leaf number within a calendar year can be quite high. For example, from January to May 1987, the average N-fertilized fern from the younger site increased from 8.75 to 13.06 leaves per fern. The highly periodic pattern of leaf production was not correlated with an erratic pattern of precipitation during the study period.

Stem height fluctuated directly out of phase with leaf production (Fig. 2). Because leaves emanate from the top of the stem, the apparent height of the stem dramatically increased as the fiddleheads emerged. Immediately following emergence, stem height appeared to drop. True stem height growth can only be determined by observing ferns over several years, as we have done here.

## DISCUSSION

The response of *Cibotium glaucum* to fertilization suggests that both nitrogen and phosphorus limit plant growth at the younger site, but nitrogen is not limiting at the older site. This is consistent with the results of Vitousek *et al.* (1987, 1994) who found that nitrogen limited diameter growth of the dominant tree *Metrosideros polymorpha* at the youn-

ger site but not at the older site. These data support the thesis that N becomes less limiting to plant growth during primary succession. Phosphorus limitation of growth at the younger site, however, was a surprising result, because Vitousek *et al.* (1987, 1994) found that P did not limit growth of *M. polymorpha* on the same site.

All measured phenological parameters are comparable to those recorded for other tree ferns throughout the world (Table 2) with the exception of tree ferns in Java (Jaag 1943 cited in: Holttum 1963) that had greater leaf production and shorter leaf longevity. Leaf production in Java was continuous and leaves were produced singly rather than in cohorts as described here. The study by Wick and Hashimoto (1971) is the only published work of which we are aware that examines *Cibotium* dynamics. Conducted over a 3 yr period, their study suggests a pattern of delayed leaf emergence with elevation (305–1524 m). At 1219 m, as in our study, 85 percent of leaf production occurred between February and April. Elevation also affected the month of maximum leaf occurrence: maximum number of leaves per fern at 305 m (7.75 leaves fern<sup>-1</sup>) occurred in May, and maximum number at 1524 m (6.33 leaves fern<sup>-1</sup>) occurred in August. In our study, maximum numbers of leaves occurred between March and May (Fig. 2). For other tree ferns, leaf production varies from highly seasonal to continuous (Holttum 1963). Some tree ferns actually lose all their leaves in an annual "resting period" (Maxon 1912).

TABLE 2. A comparison of tree fern studies (nd = no data).

Location	Species	Leaf longevity (mo)	Number of leaves (no. plant <sup>-1</sup> )	Leaf production (no. yr <sup>-1</sup> )	Stem growth (cm yr <sup>-1</sup> )
El Salvador <sup>a</sup>	<i>Alsophila salvinii</i>	24	6	3	8.3
Fiji <sup>b</sup>	<i>Leptopteris wilkesiana</i>	24–30	8–18	3–9	1.6
Fiji <sup>c</sup>	<i>Cyathea hornei</i>	13–19	3–11	3–9	1.5–40
Hawaii <sup>d</sup>	<i>Cibotium splendens</i>	21	4.3	3.6	5
Hawaii <sup>e</sup>	<i>Cibotium glaucum</i>	18–39	5–16	3–5	5–7
Jamaica <sup>f</sup>	<i>Cyathea pubescens</i>	17.5	7	8	6.7
Java <sup>g</sup>	<i>Cyathea contaminans</i>	5.5–6.6	6–10	15	nd
Java <sup>g</sup>	<i>Dicksonia blumei</i>	6.3	16–18	15	nd

<sup>a</sup> Seiler 1981.

<sup>b</sup> Ash 1986.

<sup>c</sup> Ash 1987.

<sup>d</sup> Wick and Hashimoto 1971.

<sup>e</sup> This study.

<sup>f</sup> Tanner 1983.

<sup>g</sup> Jaag 1943 (cited in Holttum 1963).

Wick and Hashimoto (1971) report an average leaf lifespan of 21 mo; this is consistent with the 18–39 mo range observed here. They also report an increase in leaf lifespan with elevation from 19 mo at 305 m to 24 mo at 1524 m. Slower leaf turnover with increasing elevation for *Cibotium* fits with a general pattern of lower foliar nutrient concentrations and increased nutrient conservation for *Metrosideros polymorpha* along the same elevation gradient (Vitousek *et al.* 1988, 1992).

Nitrogen availability may also explain the differences in leaf longevity between the younger site and the less N-limited older site (Vitousek *et al.* 1983). Nitrogen fertilization of *M. polymorpha* saplings at a 29 yr old site in HVNP tended to increase leaf production and decrease leaf longevity (Vitousek *et al.*, 1994), thereby increasing leaf turnover. Rapid leaf turnover is frequently associated with increases in nutrient status (Chapin 1980, Shaver 1983).

Although we did not measure overall fern height, many fern stems exceeded 2 m, and we have observed many ferns on other sites over 5 m tall. Employing an average height growth estimate of 5 cm yr<sup>-1</sup>, we can estimate that a 2 m tall tree fern is approximately 40 yr old. Furthermore, the upright part of these ferns often is only a small part of a much longer stem that has repeatedly grown

upright and fallen over. Many tree ferns of the Hawaiian rainforest must, therefore, exceed 100 yr of age. Other estimates of tree fern ages also exceed 100 yr (Maxon 1912, Tanner 1983).

*Cibotium glaucum* is the second most common species in the rain forests of windward Mauna Loa, contributing over 25 percent of aboveground biomass on some sites (Mueller-Dombois *et al.* 1983, Aplet & Vitousek 1994) and accounting for 70 percent of the N and 48 percent of the P in the aboveground biomass (Mueller-Dombois *et al.* 1983). Therefore, despite being dwarfed by *Metrosideros*, *Cibotium* has a disproportionate role in nutrient cycling in these forests. Such successful pre-emption of nutrients may be important in causing the eventual decline of *Metrosideros* on fertile soils in Hawaii (Mueller-Dombois *et al.* 1983, Burton & Mueller-Dombois 1984).

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