

Leilani Z. Durand · Guillermo Goldstein

Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii

Received: 28 December 1999 / Accepted: 28 August 2000 / Published online: 15 November 2000
© Springer-Verlag 2000

Abstract Photosynthetic gas exchange, chlorophyll fluorescence, nitrogen use efficiency, and related leaf traits of native Hawaiian tree ferns in the genus *Cibotium* were compared with those of the invasive Australian tree fern *Sphaeropteris cooperi* in an attempt to explain the higher growth rates of *S. cooperi* in Hawaii. Comparisons were made between mature sporophytes growing in the sun (gap or forest edge) and in shady understories at four sites at three different elevations. The invasive tree fern had 12–13 cm greater height increase per year and approximately 5 times larger total leaf surface area per plant compared to the native tree ferns. The maximum rates of photosynthesis of *S. cooperi* in the sun and shade were significantly higher than those of the native *Cibotium spp* (for example, 11.2 and 7.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and 5.8 and 3.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ respectively for the invasive and natives at low elevation). The instantaneous photosynthetic nitrogen use efficiency of the invasive tree fern was significantly higher than that of the native tree ferns, but when integrated over the life span of the frond the differences were not significant. The fronds of the invasive tree fern species had a significantly shorter life span than the native tree ferns (approximately 6 months and 12 months, respectively), and significantly higher nitrogen content per unit leaf mass. The native tree ferns growing in both sun and shade exhibited greater photoinhibition than the invasive tree fern after being experimentally subjected to high light levels. The native tree ferns recovered only 78% of their dark-acclimated quantum yield (F_v/F_m), while the invasive tree fern recovered 90% and 86% of its dark-acclimated F_v/F_m when growing in sun and shade, respectively. Overall, the invasive tree fern appears to be more efficient at capturing and utilizing light than the native *Cibotium* species, particularly in high-light environments such as those associated with high levels of disturbance.

Keywords Tree ferns · Photoinhibition · Invasive species · Photosynthesis · Hawaii

Introduction

Isolated island ecosystems, such as the Hawaiian archipelago, have evolved a biota which is highly vulnerable to invasion (Carlquist 1980; Loope and Mueller-Dombois 1989; Loope 1992). Invasive species are usually characterized by high growth rates, thereby imposing a large demand on limiting resources. A successful invasive species should either capture limiting resources more efficiently (use more resources at a lower carbon cost) than native species, or use them at a time when they are unavailable to native species (Vitousek 1986; Harrington et al. 1989). The availability of resources may change with time or with microsites in a heterogeneous environment. For example, light levels in the understory of a forest will change depending on gap openings and seasonal variations in leaf area index. This variation may be very pronounced in chronically disturbed habitats (Chazdon et al. 1996). If an invasive species is to be successful in this type of environment, it should be able to adjust its level of physiological activity to the spatial and temporal changes in resource availability. A recent study in Hawaii of native and invasive species found that invasive species had higher maximum photosynthetic rates and a wider range of photosynthetic and dark respiration rates under different light environments (Pattison et al. 1998). In addition, the invaders had lower dark respiration rates and a higher leaf area ratio at low light levels. These traits indicate that the invaders were more plastic in their response to different light levels than the native species. Even though plasticity is expected to enhance growth under varying environmental conditions, in certain habitats plasticity does not necessarily lead to increased growth rates (Walters and Reich 1999). Successful invasive species in forest ecosystems might also be expected to acclimate more readily to openings in the canopy by exhibiting less susceptibility to photoinhibition. Photoinhibition

L.Z. Durand (✉) · G. Goldstein
Department of Botany, University of Hawaii,
3190 Maile Way, Honolulu, HI 96822, USA
e-mail: ldurand@hawaii.edu
Fax: +1-808-9563923

has not been studied in Hawaiian native and invasive species.

Of the more than 800 introduced plant species that have become naturalized in the Hawaiian Islands, 30 are ferns (Vitousek et al. 1987; Wagner 1995). Native ferns make up a relatively large percentage of Hawaii's plant species, in part due to the dispersability of their small, lightweight spores, and in part due to the low species diversity of the Hawaiian flora (Carlquist 1980). The ratio of native pteridophyte to native angiosperm taxa in Hawaii averages roughly 1:6, compared to an average of 1:14 for most continental floras (Wagner 1995). In the Hawaiian forests, native tree ferns are keystone species that shape the community dynamics of the forest around them. They promote the establishment of native plants by supporting them as epiphytes on their trunks during the first part of their life cycle (Medeiros et al. 1993). In addition, they influence nutrient cycling by sequestering disproportionately high levels of nitrogen and phosphorus in their leaves (Vitousek et al. 1995).

Sphaeropteris cooperi, a tree fern native to Australia, has recently become an invasive species of concern in the Hawaiian Islands (Medeiros et al. 1992; Wilson 1996). *S. cooperi* forms dense stands, displacing native species (Medeiros et al. 1992), including the native tree ferns in the genus *Cibotium*, the dominant tree ferns in Hawaii. This study investigated what leaf-level and whole-plant-level traits make the Australian tree fern a successful invader in the Hawaiian Islands. Three native *Cibotium* species were chosen for comparison based on their similar growth form and phylogenetic relatedness to the Australian tree fern. By studying co-occurring native and invasive species of similar growth form, conclusions as to which leaf and whole-plant traits are conferring invasive ability can be drawn. The main objectives of this study were: (1) to determine whether the invasive Australian tree fern *S. cooperi* exhibited greater plasticity to different light environments than the three native Hawaiian *Cibotium* species; (2) to determine the degree of photoinhibition of tree ferns growing under different light regimes; and (3) to study growth patterns, and leaf-level physiological and morphological traits of the invasive and native tree ferns.

Materials and methods

Species

The invasive Australian tree fern, *S. cooperi* (W.J. Hooker ex F. Mueller) Tryon [syn. *Cyathea cooperi* (W.J. Hooker ex. F. Mueller Domin)], was introduced to the Hawaiian Islands as a horticultural plant and first escaped from cultivation in the 1950s (Wilson 1996). *Sphaeropteris cooperi* is now naturalized on the islands of Oahu, Maui, Kauai, and Hawaii (Wilson 1996). The Hawaiian representatives of the tree fern genus *Cibotium* comprise four species, three of which [*C. chamissoi* (Kaulf.), *C. menziesii* (Hook.), *C. glaucum* (J.E. Smith) Hook. and Arn.] are found on all of the major islands. The fourth, *C. nealii* (Degener), is found only on the island of Kauai (Palmer 1994). These endemic ferns grow in wet forests from an elevation of 40 to 1,800 m, and at mean annual temperatures ranging from 13 to 23°C (Becker 1976). Sporophytes in all species were studied as this is the larger and more enduring phase of the ferns' life cycle. While the gametophyte may play an important role in the invasive spread of *S. cooperi*, the sporophyte is the only generation that can potentially compete with co-occurring plants as it places a much higher demand on limiting resources than the gametophyte.

Study sites

Four sites were selected for this study based on accessibility and species composition (Table 1). The sites ranged in elevation from 200 to 1,250 m, and encompass much of the altitudinal range of the native Hawaiian tree ferns. Rainfall at the study sites was similar (Giambelluca et al. 1986), with the exception of the low-elevation site which had a higher mean annual rainfall. Due to management efforts to control *S. cooperi*, the low-elevation site was the only accessible site with sympatric native and invasive tree ferns. No mid-elevation site with *S. cooperi* was available. A mid-elevation site with only native tree ferns was included in this study because it could provide valid insights into tree fern responses at varying elevations. The high-elevation site on Oahu contained only native tree ferns, so a study site on the island of Kauai at a similar elevation and rainfall where the invasive tree fern was found was selected for comparison.

Photosynthetic gas exchange

Net CO₂ responses to photosynthetic photon flux density (PPFD) were studied on *C. chamissoi* and *S. cooperi* at the low-elevation site (Lyon Arboretum), on *C. chamissoi*, *C. menziesii*, and *C. glaucum* at the high-elevation site on Oahu (Mt. Kaala), and on *S. cooperi* at the high-elevation site on Kauai (Waineke Swamp). The mid-elevation site was very remote, and thus not accessible for measuring photosynthesis because of the weight of the equipment. One fully mature, recently expanded frond from each of five mature sporophytes (those with a trunk over 40 cm in height) of each species from plants growing under both sun (forest edge or gap) and shade (understory) conditions was selected for photosynthetic

Table 1 Elevation (m), annual precipitation (mm), and tree fern species present at the sites used for this study. Lyon Arboretum, Wa'ahila Ridge and Mt. Ka'ala are on the island of O'ahu, Waineke Swamp is on the island of Kauai

Site	Elevation	Rainfall	Species
Low elevation (Lyon Arboretum)	155	4,000	<i>Sphaeropteris cooperi</i> <i>Cibotium chamissoi</i>
Mid elevation (Wa'ahila Ridge)	430	2,000	<i>C. chamissoi</i> <i>C. menziesii</i>
High elevation (Mt. Ka'ala)	1,225	2,000	<i>C. chamissoi</i> <i>C. menziesii</i> <i>C. glaucum</i>
High elevation (Waineke Swamp)	1,250	2,000	<i>S. cooperi</i>

measurements at each site. Representative tree ferns were chosen based on stem size, height and accessibility. A portion of frond without spores approximately 20 cm² was enclosed in a Licor 6200 0.25 l cuvette (Licor, Inc., Lincoln, Neb., USA). A QBeam external light source (Quantum Devices, Barneveld, Wis., USA) was attached to the cuvette. Photosynthetic gas exchange was measured at 14 light levels ranging from 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The leaf was allowed to acclimate to each light level for 10 min under ambient CO₂ concentration and temperature (17–20°C) before gas exchange was measured. Measurements of gas exchange were used to generate a response curve of net CO₂ assimilation (*A*) to PPFD. The curve-fitting program Photosyn Assistant (Dundee Scientific, Scotland, UK) was used to analyze photosynthetic data.

Leaf traits

The mean surface area per frond was calculated for each species by multiplying the total number of pinnules per frond by the average surface area of a pinnule. Ten pinnules per frond were collected, and the surface area of each pinnule was measured with a Licor 3000A area meter (Li-Cor, Inc.) and averaged. The surface area of the tip of each frond was measured separately, as the pinnules in this region were smaller than those over the rest of the frond. The surface area per frond was multiplied by the number of mature living fronds per plant to estimate the total leaf surface area per plant.

Fresh leaf samples were collected in the field for leaf mass per area (LMA) estimates and kept on ice for less than 24 h at which time the area was measured using a LI-3000A leaf area meter. The leaf samples were then dried at 60°C for 5 days and weighed to determine LMA (the ratio of dry weight to projected surface area of the leaves).

For measurements of chlorophyll content, leaf samples were collected in the field and stored on ice for less than 24 h; then 0.025 g of leaf material was crushed in 80% acetone using a mortar and pestle. 1.5 ml of the acetone extract was removed and centrifuged for 10 min. The supernatant was extracted, a 1:4 dilution with 80% acetone was made, and absorbances were measured at 646, 664 and 720 nm using a diode array spectrophotometer (Hewlett-Packard Co., Waldbronn, Germany). Chlorophyll content was determined following the protocol of Arnon (1949).

Growth and leaf life span

Measurements of stem growth and frond production were obtained on mature sporophytes of the same size class at the low, middle, and high-elevation sites on Oahu from November 1997 through October 1998. Due to management efforts to control *S. cooperi*, only a limited number of individuals, all of which were growing in the shade, were available for the length of time necessary to conduct growth and leaf life span measurements. Therefore, measurements of growth and leaf life span on native tree ferns were conducted on plants growing in the same light environment as the available invasive tree ferns. A point at the soil surface on one side of five individuals of each species at each site was permanently marked and measurements of stem height from the meristem to this point were obtained monthly. The total number of living fronds was counted monthly. A frond was counted as living as long as 10% green tissue remained. All newly emerging fronds were flagged, dated and monitored until senescence. The number of months between frond emergence and senescence was recorded as the leaf life span of the frond. Growth and leaf life span were not measured on *S. cooperi* at the high-elevation site as attempts at management of this species resulted in its removal before measurements could be completed.

Chlorophyll fluorescence and nitrogen content

In situ chlorophyll fluorescence was measured using a Mini-PAM fluorometer (Mini-PAM, Walz, Germany), on both gap and under-

story plants. A portion of an attached leaf was dark adapted for 10 min, and minimum fluorescence (F_0) of the leaf sample was measured by illuminating the upper leaf surface with 0.15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. Maximum fluorescence (F_m) was measured on the same dark-adapted leaf portion by an actinic pulse of 4,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (Basu et al. 1998). Three measurements of dark-adapted quantum yield (F_v/F_m) were obtained, where F_v ($F_m - F_0$) is the variable fluorescence. F_v/F_m is correlated with the efficiency of photosystem II (Kraus and Weis 1991). Plants were then subjected to high light (2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) from a 20-W halogen lamp for 20 min. After the 20-min treatment at high light, the light level was reduced to 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and recovery of F_v/F_m was monitored for 50 min.

Leaf samples were analyzed for nitrogen content using an automated elemental analyzer (Fry et al. 1992). Leaf samples were collected and dried at 60°C for at least 48 h and then crushed in liquid nitrogen. Samples of approximately 0.550 mg of tissue were weighed and nitrogen concentration was determined. Instantaneous photosynthetic nitrogen use efficiency (PNUE) was calculated as maximum mass-based net CO₂ assimilation rate (A_{mass}) divided by leaf nitrogen content. Integrated PNUE was calculated as PNUE of fully expanded fronds multiplied by their leaf life span. Because photosynthetic rates are not always light-saturated in the field, and because maximum *A* declines with leaf age, using maximum *A* will result in overestimation of both instantaneous and integrated PNUE. Nevertheless, it will still provide reliable comparative estimates of nutrient use efficiency.

Statistical analysis

Because the sample design was not a full factorial, a one-way ANOVA among all species at all sites was performed, followed by pre-planned contrasts. Contrasts were used to compare native and invasive species at the same elevation, and between all natives and invasive regardless of elevation. Contrasts based on ANOVA were used to analyze significance of maximum *A*, dark respiration, light compensation and the percent recovery of F_v/F_m for sun and shade plants separately.

Results

Photosynthetic gas exchange

As expected, area based net CO₂ assimilation (A_{area}) increased with increasing PPFD. Light saturation was attained at about 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD for sun-grown plants and at about 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD for shade-grown plants (Fig. 1). The maximum A_{area} of the sun-grown invasive tree fern, *S. cooperi*, at both high and low elevation, was significantly higher ($P < 0.001$) than that of native tree ferns (Fig. 1a). Similarly, maximum A_{area} of *S. cooperi* growing in the shade at both high and low elevation was significantly higher ($P < 0.001$) than that of the native tree ferns growing under the same light conditions (Fig. 1b).

The photosynthetic light compensation point of sun-grown *S. cooperi* was not significantly different from that of the native tree ferns at low and at high elevation ($P = 0.25$ and $P = 0.03$ respectively, Table 2). Similarly, for shade-grown plants, the light compensation point of *S. cooperi* was not significantly different from that of the native tree ferns at low and at high elevation ($P = 0.40$ and $P = 0.08$ respectively, Table 2). The dark respiration rate of sun-grown *S. cooperi* was significantly lower

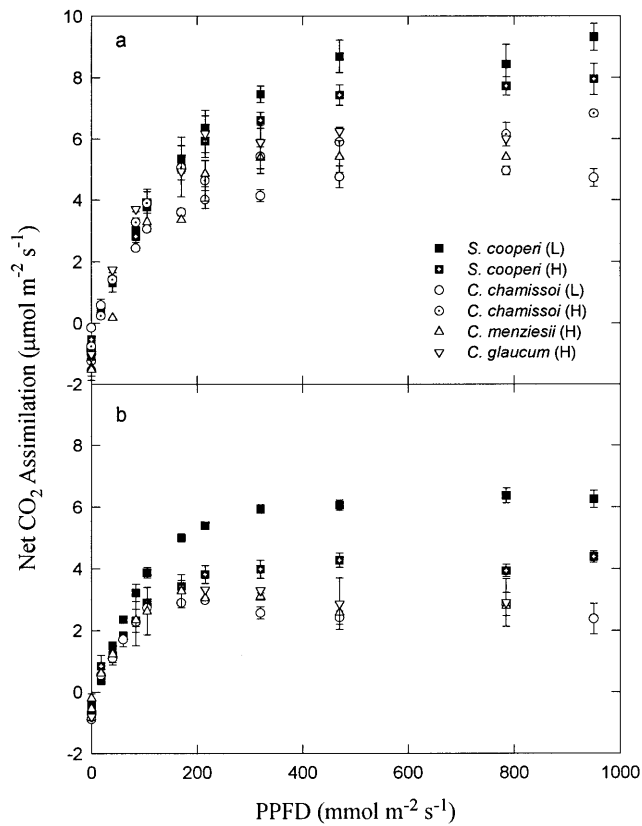


Fig. 1 Net CO₂ assimilation as a function of photosynthetic photon flux density (PPFD) of native (*Cibotium* spp.) and invasive (*Sphaeropteris cooperi*) tree ferns at low (L) and high (H) elevation for **a** plants growing in sun and **b** plants growing in shade. All measurements were taken on mature, fully expanded leaves. Symbols represent mean ($n=5$) \pm SE. Statistics for parameters estimated from these light response curves are given in Table 2

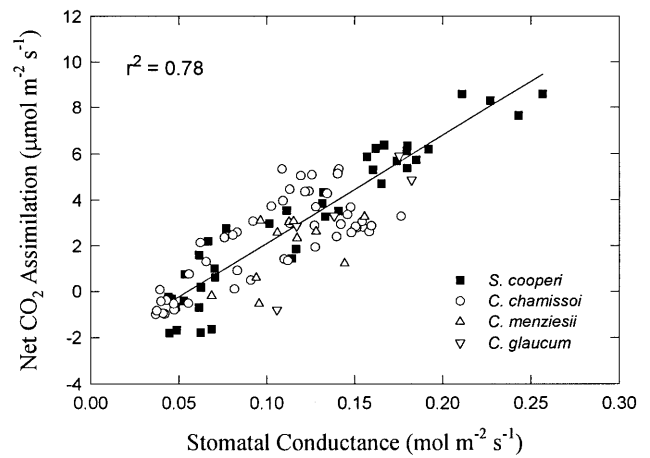


Fig. 2 Net CO₂ assimilation as a function of stomatal conductance for native and invasive tree ferns. Data shown is from low- and high-elevation plants growing in sun and shade. Each symbol represents an individual measurement

than that of native tree ferns only at high elevation (Table 2). If comparisons are made within a species across different light conditions, maximum A_{area} , light compensation point and dark respiration rate were generally lower for shade plants compared to sun plants (Table 2).

All tree fern species at all sites conformed to the same linear relationship between net CO₂ assimilation and stomatal conductance (Fig. 2), but *S. cooperi* had a greater range of net CO₂ assimilation and stomatal conductance. The maximum stomatal conductance for *S. cooperi* was 0.26 mol m⁻² s⁻¹, while the maximum stomatal conductance for the native tree fern species ranged from 0.16 to 0.18 mol m⁻² s⁻¹.

Table 2 Maximum net CO₂ assimilation (A_{area}), light compensation point, and dark respiration of native and invasive tree ferns at two elevations for plants growing in sun and in shade conditions. Values are means \pm SE ($n=5$)

		A_{area} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Light compensation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
Sun				
Low elevation				
Invader	<i>S. cooperi</i>	11.2 \pm 0.69 ^a	11.1 \pm 3.4	0.85 \pm 0.2
Native	<i>C. chamissoi</i>	5.75 \pm 0.51	8.21 \pm 1.5	0.54 \pm 0.1
High elevation				
Invader	<i>S. cooperi</i>	8.92 \pm 0.51 ^a	9.75 \pm 2.3	0.53 \pm 0.2 ^a
Natives	<i>C. chamissoi</i>	7.01 \pm 0.65	12.6 \pm 0.6	0.79 \pm 0.1
	<i>C. menziesii</i>	6.43 \pm 0.51	26.2 \pm 0.5	1.62 \pm 0.2
	<i>C. glaucum</i>	6.75 \pm 0.19	12.2 \pm 1.7	1.04 \pm 0.1
Shade				
Low elevation				
Invader	<i>S. cooperi</i>	7.11 \pm 0.31 ^a	10.1 \pm 1.8	0.53 \pm 0.1
Native	<i>C. chamissoi</i>	3.59 \pm 0.19	10.1 \pm 3.3	0.64 \pm 0.2
High elevation				
Invader	<i>S. cooperi</i>	4.56 \pm 0.11 ^a	5.23 \pm 2.2	0.29 \pm 0.1
Natives	<i>C. menziesii</i>	3.38 \pm 0.0	7.57 \pm 1.1	0.30 \pm 0.1
	<i>C. glaucum</i>	3.96 \pm 0.02	14.5 \pm 1.2	0.78 \pm 0.1

^a Indicates statistical significance ($P \leq 0.01$) of the difference between the invasive and native ferns within that group

Table 3 Leaf chlorophyll content, leaf mass per area (LMA), leaf life span ($n=10$), annual height increase, and mean leaf surface area per plant ($n=5$) for native and invasive tree ferns at three different elevations. Values are means \pm SE

		Chlorophyll (mg g ⁻¹)	LMA (g m ⁻²)	Leaf life span (months)	Annual ht. increase (cm)	Mean leaf surface area (m ²)
Low elevation						
Invader	<i>S. cooperi</i>	2.50 \pm 0.16 ^a	37.9 \pm 2.1 ^a	6.0 \pm 0.15 ^a	15.4 \pm 2.49 ^a	344.8 \pm 9.3 ^a
Native	<i>C. chamissoi</i>	1.73 \pm 0.07	54.7 \pm 2.8	11.0 \pm 0.30	2.99 \pm 0.81	63.7 \pm 1.1
Mid elevation						
Natives	<i>C. chamissoi</i>	2.21 \pm 0.10	50.9 \pm 3.1	12.0 \pm 0.71	2.55 \pm 0.97	37.5 \pm 0.9
	<i>C. menziesii</i>	1.81 \pm 0.07	78.9 \pm 4.0	10.8 \pm 1.1	1.93 \pm 0.49	38.7 \pm 1.9
High elevation						
Invader	<i>S. cooperi</i>	2.95 \pm 0.13 ^a	34.7 \pm 1.8 ^a	n/a	n/a	n/a
Natives	<i>C. chamissoi</i>	1.12 \pm 0.08	120.3 \pm 7.2	10.6 \pm 0.42	n/a	22.2 \pm 1.3
	<i>C. menziesii</i>	1.13 \pm 0.05	127.5 \pm 3.8	12.0 \pm 0.50	2.95 \pm 1.76	42.6 \pm 1.0
	<i>C. glaucum</i>	1.19 \pm 0.07	135.2 \pm 3.0	12.6 \pm 0.73	3.21 \pm 0.63	61.4 \pm 1.2

^a Indicates statistical significance ($P\leq 0.01$) of the difference between the invasive and native ferns within that group

Leaf traits and growth

The chlorophyll content on a dry weight basis of *S. cooperi* was 70% higher than that of the native tree ferns at low elevation, and more than double that of the native tree ferns at high elevation (Table 3). The differences between the invasive and the natives were in both cases significant at $P<0.001$. The LMA of *S. cooperi* was significantly lower than that of the native tree ferns at low and high elevation ($P<0.001$, Table 3). The LMA of *S. cooperi* was nearly the same at the low and high-elevation sites, while the LMA of the native tree ferns increased with increasing elevation. The leaf life span of *S. cooperi* was significantly shorter ($P<0.001$) than that of native tree ferns (Table 3). Differences in chlorophyll content and LMA between shade and sun plants at each elevation were not statistically different ($P\geq 0.39$ and $P\geq 0.13$ respectively, for all species at each elevation).

Annual height increase of *S. cooperi* growing at low elevation was significantly greater ($P<0.001$) than that of the native tree fern growing at the same site (Table 3). *S. cooperi* had a 12–13 cm greater height increase per year than the native tree ferns. In ferns, height growth is closely linked to rates of leaf production. *S. cooperi* maintained between 12 and 18 fronds per plant, and averaged 2.7 new fronds per month, over the course of 1 year. The native ferns maintained only between 3 and 6 fronds per plant over the same time period, and produced an average of 0.2–0.4 new fronds per month (data not shown). This contributed to the nearly 5 times greater leaf surface area per plant of *S. cooperi* (Table 3).

Chlorophyll fluorescence

F_v/F_m of dark adapted leaves was similar for plants growing in sun and shade, and similar between invasive and native species (Fig. 3). For *S. cooperi* and native

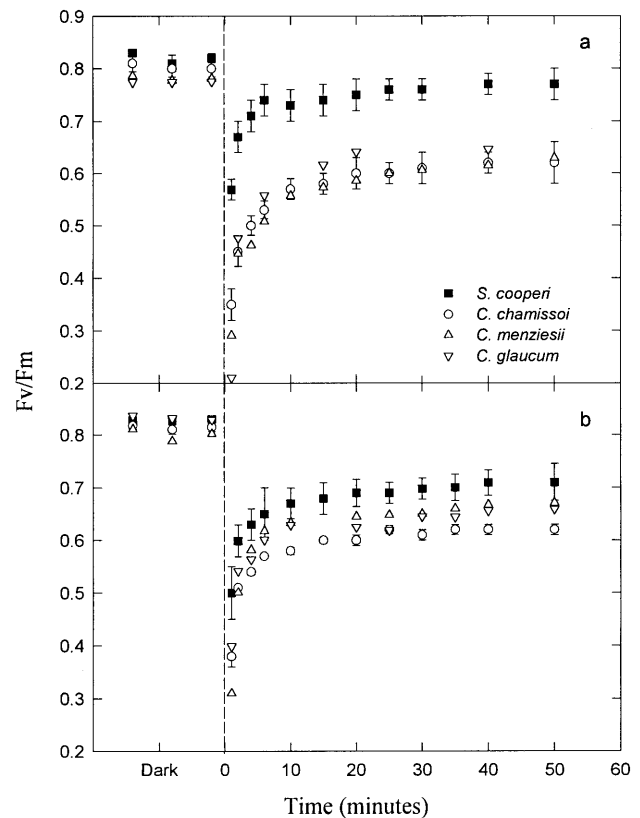


Fig. 3a, b The F_v/F_m ratio of native and invasive tree fern leaves during dark-acclimation and after exposure to saturating light levels. Symbols represent mean \pm SE ($n=3$). F_v/F_m of dark-adapted leaves was measured three times at 5-min intervals after which a saturating beam of actinic light ($2,000 \mu\text{mol m}^{-2} \text{s}^{-1}$) was applied for 20 min (dashed line). Recovery of F_v/F_m was measured at a PPFD of $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ over 50 min for **a** plants growing in sun and **b** plants growing in shade

Table 4 Leaf N content per unit mass (% d.m.), leaf N content per unit area, photosynthetic nitrogen use efficiency (PNUE) and integrated photosynthetic nitrogen use efficiency of native and invasive tree ferns at three different elevations. Values are means \pm SE ($n=10$)

		Nitrogen % d.m.	Nitrogen g m ⁻²	PNUE (mol C s ⁻¹ mol N ⁻¹)	Integrated PNUE (mol C mol N ⁻¹)
Low elevation					
Invader	<i>S. cooperi</i>	2.63 \pm 0.2 ^a	0.99 \pm 0.1	13.5 \pm 1.0 ^a	2.1 \pm 0.2 $\times 10^{-8}$
Native	<i>C. chamissoi</i>	2.03 \pm 0.1	1.05 \pm 0.1	6.69 \pm 0.6	1.9 \pm 0.2 $\times 10^{-8}$
Mid elevation					
Natives	<i>C. chamissoi</i>	2.20 \pm 0.1	1.25 \pm 0.1	n/a	n/a
	<i>C. menziesii</i>	1.80 \pm 0.1	1.47 \pm 0.2	n/a	n/a
High elevation					
Invader	<i>S. cooperi</i>	2.44 \pm 0.2 ^a	1.08 \pm 0.1 ^a	9.16 \pm 0.8 ^a	n/a
Natives	<i>C. chamissoi</i>	1.64 \pm 0.1	2.05 \pm 0.2	4.93 \pm 0.4	1.4 \pm 0.1 $\times 10^{-8}$
	<i>C. menziesii</i>	1.60 \pm 0.1	2.11 \pm 0.2	3.34 \pm 0.3	1.0 \pm 0.1 $\times 10^{-8}$
	<i>C. glaucum</i>	1.50 \pm 0.1	2.07 \pm 0.2	3.70 \pm 0.2	1.2 \pm 0.1 $\times 10^{-8}$

^a Indicates statistical significance ($P\leq 0.01$) of the difference between the invasive and native ferns within that group

ferns growing in the sun, F_v/F_m ranged from 0.78 to 0.83 (Fig. 3a). In the shade, these values ranged from 0.79 to 0.84 (Fig. 3b). Recovery of F_v/F_m after exposure to saturating light was significantly lower in native tree ferns growing in the sun compared to *S. cooperi* ($P<0.001$, Fig. 3a). Sun-grown *S. cooperi* recovered 90% of the initial dark-adapted F_v/F_m value after only 20 min, while the native tree ferns only recovered 72 to 78% of initial F_v/F_m after 50 min. Recovery of shade-grown native tree ferns was significantly lower ($P<0.001$) than that of *S. cooperi* grown under similar light conditions (Fig. 3b). After a 50-min recovery period, *S. cooperi* recovered 86% of the initial F_v/F_m value, while the native tree ferns only recovered 76–82% of the initial F_v/F_m .

Nitrogen content and functional relationships

Leaf nitrogen content on a per weight basis (N_{mass}) of *S. cooperi* was significantly higher than that of native tree ferns at both low and high elevation ($P<0.001$, Table 4). Differences in N content between shade and sun plants at each elevation were not statistically different ($P>0.49$ for all species at each elevation). LMA and N_{mass} appear to be functionally related, as N_{mass} decreased in a linear fashion with increasing LMA ($N_{\text{mass}}=2.72-9.3 \text{ LMA}$, $r^2=0.88$). Leaf nitrogen content on a per area basis (N_{area}) was not significantly different between the invader and natives at low elevation ($P=0.37$, Table 4). At high elevation, however, the natives had a significantly higher N_{area} ($P<0.001$). Photosynthetic nitrogen use efficiency (PNUE) was significantly higher for *S. cooperi* growing at low and high elevation ($P<0.001$) than for the native tree ferns (Table 4). Integrated PNUE was not significantly different ($P=0.23$) between *S. cooperi* and the native tree fern growing at low elevation (Table 4). Chlorophyll content and A_{mass} increased linearly with increasing N_{mass} (Fig. 4). *S. cooperi* had a higher N_{mass} , chlorophyll content, and A_{mass} than the native tree ferns independent of elevation and light conditions.

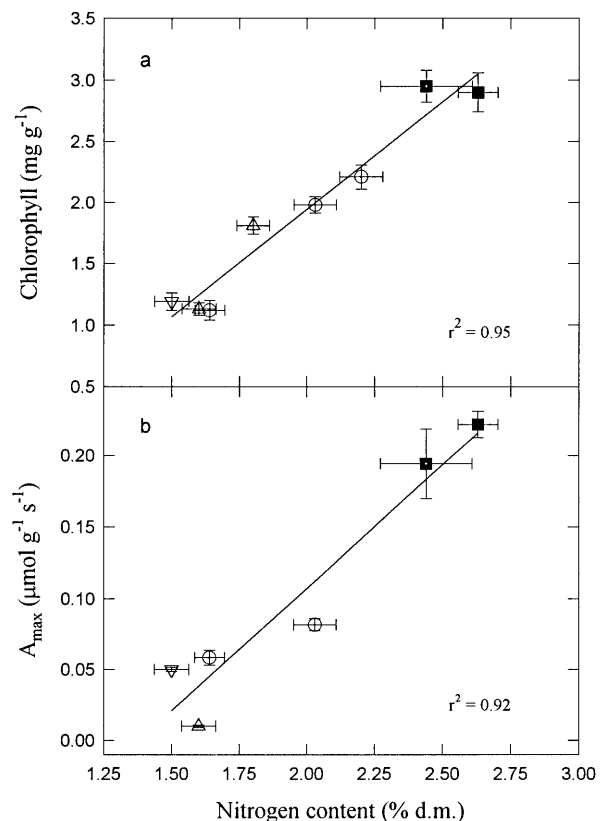


Fig. 4 Relationships between **a** chlorophyll content on a dry weight (*d.m.*) basis and **b** maximum net CO₂ assimilation (A_{max} , on a mass basis) and nitrogen content of native and invasive tree ferns (symbols as in Fig. 1). **a** Includes mean \pm SE of tree ferns from low, middle and high elevations, **b** includes mean \pm SE of tree ferns from low and high elevations

Discussion

Photosynthetic gas exchange

Light is one of the most important limiting resources to plant growth in the understory of tropical rainforests (Yates et al. 1988). Therefore, the ability of plants to

capture and utilize light is an important determinant of growth potential and fitness in this type of environment (Givnish 1988; Chazdon et al. 1996). The native *Cibotium* tree ferns reach heights of 3–7 m and therefore spend the sporophytic portion of their life cycle in the understory or as subcanopy plants. The invasive *S. cooperi* reaches heights of up to 12 m in its native range in northeastern Australia where it grows in gullies and along stream banks (Jones and Clemensha 1978). Little is known about the ecology or physiology of *S. cooperi* in its native habitat. In Hawaii, the sporophytes of *S. cooperi* have been observed reaching heights of up to 8 m, and are found in the subcanopy, or in gaps or along forest edges where the fronds are exposed to relatively high light levels. Plants growing or acclimated to low light levels tend to have lower photosynthetic capacity than plants growing in sunny conditions, as well as low light compensation points and dark respiration rates (e.g., Bjorkman et al. 1972). These differences in photosynthetic light response reflect differences in leaf physiology, anatomy, and biochemistry. For both the invasive and native tree ferns, the photosynthetic rates at light saturation were higher for plants growing under sunny than under shaded conditions, regardless of elevation. The light compensation points and dark respiration rates of the tree ferns growing under sunny conditions tended to be relatively high when compared to the tree ferns growing in the shade.

When comparisons are made across species rather than across light conditions, the photosynthetic rates of the invasive *S. cooperi* in the sun and shade at light saturation were always significantly higher than those of the native *Cibotium* species. Differences in leaf-level photosynthesis, however, may not translate into differences in whole-plant growth because patterns of resource allocation can have a substantial effect on growth and development (e.g., Givnish 1988; Poorter and Remkes 1990). When plant species with a similar growth habit are compared, individuals with a higher photosynthetic capacity (a leaf-based trait) and higher allocation of carbon to total leaf surface area (a whole-plant trait) will tend to exhibit higher growth rates under similar light conditions (Kitajima 1994). In this study, the invasive tree fern had a much higher total leaf surface area per plant, which together with higher photosynthetic rates could partially account for the nearly 5 times greater height growth rate of the invasive tree fern compared to the native tree ferns.

It is generally assumed that the photosynthetic rates of ferns are relatively low compared to other groups of vascular plants (Nobel et al. 1984). In this study, the relative differences in CO_2 assimilation between the native and invasive species of tree ferns, as well as the maximum photosynthetic rates, were comparable to those of native and invasive angiosperm species in mesic Hawaiian forests (Pattison et al. 1998). The photosynthetic rates of the invasive tree fern were as much as double those of the native tree ferns when expressed on a mass basis. Similar differences, though not as large,

were observed when A was expressed on a leaf surface area basis. Photosynthesis expressed on a per leaf mass basis, representing a rate of energy capture per unit investment, provides a better prediction of whole-plant growth than when photosynthesis is expressed per unit leaf area (Givnish 1988; Tilman 1988). The greater photosynthetic rates of *S. cooperi* suggests that this species is either more efficient at utilizing light energy, or has more carboxylating enzymes, or both, than native tree ferns. This has important implications for the relative success of the invasive fern under a range of growing conditions.

Although the photosynthetic rate at light saturation was substantially higher in *S. cooperi* compared to the three native tree fern species, the light compensation points were not statistically different between the two groups of ferns. The light compensation points of all tree ferns however, were lower than light compensation points measured on other invasive and native Hawaiian species (Pattison et al. 1998). Low light compensation points are advantageous for plants growing in the shade because they may help maintain a positive carbon balance under low light conditions (Boardman 1977), such as those found in the understory of Hawaiian rainforests. The light compensation points of the studied species were low enough that it is unlikely they played a significant role in daily carbon balance differences between native and the invasive tree fern species.

There was a strong linear relationship between stomatal conductance and net CO_2 assimilation of both the invasive and native tree ferns (Fig. 2). The invasive tree ferns, however, had a greater range of values of both A_{area} and stomatal conductance. Within the range of A_{area} and stomatal conductance that was common for invasive and native ferns, similar stomatal conductance will result in the same A_{area} , regardless of whether the fern is the invasive or one of the native *Cibotium* species. Thus, differences in photosynthetic rates between the invasive and native species cannot be attributed to differences in stomatal regulation of gas exchange.

Photoinhibition

The greater reduction in F_v/F_m exhibited by native tree ferns after exposure to high light levels, in both sun and shade plants, suggests that these species are not as efficient at dissipating excess light as the invasive tree fern, and may be sustaining photoinhibitory damage. Shade-tolerant plants tend to have a reduced capacity to acclimate to high light and thus are more susceptible to photoinhibition in comparison to species that are known to require high light levels for growth. This increased susceptibility to photoinhibition is rarely responsible for plant mortality (Lovelock et al. 1994). However, if other stresses, such as water deficit or low soil nitrogen, exist in conjunction with photoinhibition, plants are likely to incur severe photoinhibitory damage and undergo reductions in growth (Osmond 1983; Bjorkman and Powles

1984). Both the temporary reduction in light harvesting capability and the cost of repairing damage to the photosystems can cause a substantial loss in net daily carbon gain in a plant undergoing photoinhibition (Raven 1989). Overall, the native tree ferns appear to be shade-adapted plants that are not able to adjust quickly or efficiently to a high-light environment, and thus are less likely to survive in gaps or disturbed areas than the invasive tree fern.

Leaf traits and functional relationships

When compared across diverse ecosystems and biomes, short leaf life spans are associated with higher photosynthetic rates, higher leaf nitrogen content, and a lower LMA (Chabot and Hicks 1982; Reich 1993; Reich et al. 1997). The trends observed in this study with invasive and native tree ferns are consistent with these global patterns of functionally based leaf trait relationships observed in higher plants. The invasive tree fern had a 50% shorter leaf life span than the native tree ferns and a correspondingly lower LMA, but higher photosynthetic rates and higher nitrogen content per unit mass. This combination of morphological and functional traits can result in higher growth rates (Reich et al. 1997), and may have contributed to the substantially higher growth rates of the invasive compared to the native fern species. In addition, the shorter leaf life span in *S. cooperi* may have contributed to a faster recovery from photoinhibition. In gap-grown species, there is a relationship between higher yields of photosystem II electron transport and shorter leaf life span (Lovelock et al. 1998).

Numerous studies have linked the regulation of leaf life span to the initial leaf construction costs and carbon assimilation potential (e.g., Kikuzawa 1991; Kitajima et al. 1997). The general pattern observed is that leaves with higher photosynthetic rates and/or lower construction costs have a shorter leaf life span than leaves with lower photosynthetic rates and/or higher construction costs. Generally, the construction cost of a thin leaf (low LMA) is lower than that of a thicker leaf (high LMA). In a broad survey of 34 natives and 30 invasive species on the island of Hawaii, the invasive species, regardless of elevation or life form, had lower LMA, higher net CO₂ assimilation, and a lower leaf construction cost (measured by combustion of ash free leaves) than the native species (Baruch and Goldstein 1999). The lower leaf construction costs of the invasive species suggest that these species utilized carbon resources more efficiently than native species by investing less energy per unit of leaf mass produced, which potentially can contribute to high growth rates (Lambers and Poorter 1992). While leaf construction cost was not measured on the native and invasive tree ferns in this study, the shorter leaf life span, lower LMA and higher net CO₂ assimilation of the invasive tree ferns suggest a lower leaf construction cost for this species. A lower leaf construction cost could be a

factor in the faster height growth rate measured for the invasive tree fern.

Nitrogen content and nitrogen use efficiency

Consistent with its higher photosynthetic rate, the invasive tree fern had higher N content on a mass basis, at both high and low elevations, than the native tree ferns. On a per area basis, however, nitrogen content was not different between the natives and invasive at low elevation. The photosynthetic rates tended to be more closely associated with N expressed on a mass basis rather than on an area basis, perhaps better reflecting the economy of nitrogen and carbon allocation and the amount and activity of carboxylating enzymes (Field and Mooney 1986). A linear relationship between nitrogen and chlorophyll content, expressed on a mass basis, among all tree ferns was observed in this study, suggesting that the pattern of nitrogen allocation to the light harvesting system was similar in all studied species (Fig. 4a).

The higher instantaneous PNUE in the invasive tree fern reflected the relatively high A_{mass} in this species compared to the native tree fern species, rather than lower leaf nitrogen content. Nutrient use efficiency of plants can be better described as the total carbon gain per unit of foliar nutrient integrated over the life of the leaf (Chapin 1991). Integrated PNUE was similar between the invasive and native tree ferns. The native tree ferns had a leaf life span twice as long as the invasive tree fern, thereby increasing the nutrient use efficiency when carbon assimilation is integrated over the life of the fronds. Greater leaf longevity is one mechanism that can enhance nutrient use efficiency (Loveless 1961; Chabot and Hicks 1982). Similar integrated PNUE, furthermore, suggests that all tree ferns studied, both native and invasive, have similar access to soil nitrogen in the study sites and that nitrogen source may not contribute to the invasive success of *S. cooperi* in Hawaii.

Conclusions

There are many traits in plants that can confer invasive ability to a species. This study examined only a subset of these traits on the sporophytic stage of an invasive and three native Hawaiian tree fern species. Other traits, such as reproductive potential and damage from herbivores, could also be of importance. Furthermore, it may be possible that traits of the gametophyte stage could be playing a role in the increasing presence of *S. cooperi* in Hawaii. Successful completion of the life cycle in ferns requires both stages, and further studies on the gametophyte stage would help advance our understanding of the invasive success of this species. The results of this study suggest that the sporophytes of the invasive tree fern, *S. cooperi*, have higher growth rates than the native tree ferns in the genus *Cibotium* as a consequence of higher photosynthetic capacity and higher total leaf surface area

per plant. The invasive tree fern achieved higher photosynthetic rates at a lower leaf carbon cost (lower LMA and lower dark respiration rates), and with comparable return on the investment in leaf nitrogen (similar integrated PNUE). In addition, *S. cooperi* recovered more rapidly from photoinhibition resulting from high light levels than the native tree fern species. The invasive tree fern appears to be more suited than the native *Cibotium* species for capturing and utilizing light resources, particularly in environments with changing light levels, such as those characterized by relatively high levels of disturbance.

Acknowledgements We thank C. Smith from the Cooperative Research Program at the University of Hawaii and the B. Krauss Fellowship in Botany for providing funds for this research. We also gratefully acknowledge The Joseph Souza Center at Kokee State Park, Lyon Arboretum, and the Oahu Natural Area Reserves staff for their support. Mike Clearwater provided useful comments on the manuscript.

References

- Arnon DI (1949) Copper enzymes in isolated chloroplasts, polyphenoloxidase in *Beta vulgaris*. *Plant Physiol* 24:1:1–15
- Baruch Z, Goldstein G (1999) Leaf construction cost, nutrient concentration, and net CO₂ assimilation of native and invasive species in Hawaii. *Oecologia* 121:183–192
- Basu PS, Sharma A, Sukumaran NP (1998) Changes in net photosynthetic rate and chlorophyll fluorescence in potato leaves induced by water stress. *Photosynthetica* 35:13–19
- Becker RE (1976) The phytosociological position of tree ferns (*Cibotium* spp.) in the montane rainforests on the island of Hawaii. PhD dissertation, University of Hawaii at Manoa
- Bjorkman O, Powles SB (1984) Inhibition of photosynthetic reactions under water stress: interaction with light level. *Planta* 161:490–504
- Bjorkman O, Ludlow MM, Morrow PA (1972) Photosynthetic performance of two rainforest species in their native habitat and analysis of their gas exchange. *Carnegie Inst Washington Yearb* 71:94–102
- Boardman NK (1977) Comparative photosynthesis of sun and shade plants. *Annu Rev Plant Physiol* 28:355–377
- Carlquist S (1980) Hawaii: a natural history. Natural History Press, Garden City
- Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. *Annu Rev Ecol Syst* 13:229–59
- Chapin FS (1991) Integrated response of plants to stress. *BioScience* 41:29–36
- Chazdon RL, Pearcy RW, Lee DW, Fetcher N (1996) Photosynthetic responses of tropical forest plants to contrasting light environments. In: Mulkey S, Chazdon RL, Smith AP (eds) *Tropical plant ecophysiology*. Chapman and Hall, New York, pp 5–55
- Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givnish TJ (ed.) *On the economy of plant form and function*. Cambridge University Press, Cambridge, pp 25–55
- Fry B, Brand W, Mersch FJ, Tholke K, Garritt R (1992) Automated analysis system for coupled $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements. *Anal Chem* 64:288–291
- Giambelluca TW, Nullet MA, Schroeder TA (1986) Rainfall atlas of Hawaii (Report R76). University of Hawaii, State of Hawaii Department of Land and Natural Resources, Honolulu
- Givnish TJ (1988) Adaptation to sun and shade: a whole-plant perspective. *Aust J Plant Physiol* 15:63–92
- Harrington RA, Brown BJ, Reich PB (1989) Ecophysiology of exotic and native shrubs in southern Wisconsin. *Oecologia* 80:356–367
- Jones DL, Clemensha SC (1978) Australian ferns and fern allies with notes on their cultivation. Reed, Sydney
- Kikuzawa K (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *Am Nat* 138:1250–1263
- Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428
- Kitajima K, Mulkey SS, Wright J (1997) Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five tropical canopy tree species. *Am J Bot* 84:702–708
- Kraus GH, Weis E (1991) Chlorophyll fluorescence and photosynthesis: the basics. *Annu Rev Plant Physiol Plant Mol Biol* 42:301–313
- Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv Ecol Res* 23:188–261
- Loope LL (1992) An overview of problems with introduced plant species in national parks and biosphere reserves of the United States. In: Stone CP, Smith CW, Tunison JT (eds) *Alien plant invasion in native ecosystems of Hawaii, management and research*. Cooperative National Park Resources Study Unit, University of Hawaii Press, Honolulu, pp 3–28
- Loope LL, Mueller-Dombois D (1989) Characteristics of invaded islands, with special reference to Hawaii. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FH, Rejmanek M, Williamson M (eds) *Biological invasions: a global perspective*. Wiley, New York, pp 257–280
- Loveless AR (1961) A nutritional interpretation of sclerophyllous based on differences in the chemical composition of sclerophyllous and mesophytic leaves. *Ann Bot* 25:168–184
- Lovelock CE, Jebb M, Osmond, CB (1994) Photoinhibition and recovery in tropical plant species: response to disturbance. *Oecologia* 97:297–307
- Lovelock CE, Kursar TA, Skillman JB, Winter K (1998) Photoinhibition in tropical forest understorey species with short- and long-lived leaves. *Funct Ecol* 12:553–560
- Medeiros AC, Loope LL, Flynn T, Anderson SJ, Cuddihy LW, Wilson KA (1992) Notes on the status of an invasive Australian tree fern (*Cyathea cooperi*) in Hawaiian rain forests. *Am Fern J* 82:27–33
- Medeiros AC, Loope LL, Anderson SJ (1993) Differential colonization by epiphytes on native (*Cibotium* spp.) and alien (*Cyathea cooperi*) tree ferns in a Hawaiian rain forest. *Selbyana* 14:71–74
- Nobel PS, Calkin HW, Gibson AC (1984) Influences of PAR, temperature and water vapor concentration on gas exchange by ferns. *Physiol Planta* 62:527–534
- Osmond CB (1983) Interactions between irradiance, nitrogen nutrition, and water stress in the sun-shade responses of *Solanum dilemaria*. *Oecologia* 57:316–321
- Palmer DD (1994) The Hawaiian species of *Cibotium*. *Am Fern J* 84:73–85
- Pattison RR, Goldstein G, Ares A (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* 117:449–459
- Poorter H, Remkes C (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* 83:553–567
- Raven JA (1989) Fight or flight: the economics of repair and avoidance of photoinhibition of photosynthesis. *Funct Ecol* 3:5–9
- Reich PB (1993) Reconciling apparent discrepancies among studies relating life span, structure and function of leaves in contrasting plant life forms and climates: “the blind man and the elephant” retold. *Funct Ecol* 7:721–725
- Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. *Ecology* 94:13730–13734
- Tilman D (1988) Resource competition and community structure. Princeton University Press, Princeton

- Vitousek PM (1986) Biological invasions and ecosystem properties: can species make a difference? In: Mooney HA, Drake JA (eds) *Ecology of biological invasions of North America and Hawaii*. Springer, Berlin Heidelberg New York, pp 163–176
- Vitousek PM, Loope LL, Stone CP (1987) Introduced species in Hawaii: biological effects and opportunities for ecological research. *Trends Ecol Evol* 2:224–227
- Vitousek PM, Gerrish G, Turner DR, Walker LR, Mueller-Dombois D (1995) Litterfall and nutrient cycling in four Hawaiian montane rainforests. *J Trop Ecol* 11:189–203
- Wagner WH Jr (1995) Evolution of Hawaiian ferns and fern allies in relation to their conservation status. *Pac Sci* 49:31–41
- Walters MB, Reich PB (1999) Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broadleaved evergreen species differ? *New Phytol* 143:143–154
- Wilson KA (1996) Alien ferns in Hawaii. *Pac Sci* 50:127–141
- Yates DJ, Unwin GL, Doley D (1988) Rainforest environment and physiology. *Proc Ecol Soc Aust* 15:31–37

Copyright of *Oecologia* is the property of Kluwer Academic Publishing / Academic and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.