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Leaf construction cost, nutrient concentration, and net CO₂ assimilation of native and invasive species in Hawaii

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Abstract The effects of biological invasions are most evident in isolated oceanic islands such as the Hawaiian Archipelago, where invasive plant species are rapidly changing the composition and function of plant communities. In this study, we compared the specific leaf area (SLA), leaf tissue construction cost (CC), leaf nutrient concentration, and net CO₂ assimilation (*A*) of 83 populations of 34 native and 30 invasive species spanning elevation and substrate age gradients on Mauna Loa volcano in the island of Hawaii. In this complex environmental matrix, where annual precipitation is higher than 1500 mm, we predicted that invasive species, as a group, will have leaf traits, such as higher SLA and *A* and lower leaf CC, which may result in more efficient capture of limiting resources (use more resources at a lower carbon cost) than native species. Overall, invasive species had higher SLA and *A*, and lower CC than native species, consistent with our prediction. SLA and foliar N and P were 22.5%, 30.5%, and 37.5% higher, respectively, in invasive species compared to native ones. Light-saturated photosynthesis was higher for invasive species (9.59 μmol m⁻² s⁻¹) than for native species (7.31 μmol m⁻² s⁻¹), and the difference was larger when *A* was expressed on a mass basis. Leaf construction costs, on the other hand, were lower for the invasive species (1.33 equivalents of glucose g⁻¹) than for native species (1.37). This difference was larger when CC was expressed on an area basis. The trends in the above traits were maintained when groups of ecologically equivalent native and invasive species (i.e., sharing similar life

history traits and growing in the same habitat) were compared. Foliar N and P were significantly higher in invasive species across all growth forms. Higher N may partially explain the higher *A* of invasive species. Despite relatively high N, the photosynthetic nitrogen use efficiency of invasive species was 15% higher than that of native species. These results suggest that invasive species may not only use resources more efficiently than native species, but may potentially demonstrate higher growth rates, consistent with their rapid spread in isolated oceanic islands.

Key words Cost of construction · Life forms · Nitrogen use efficiency · Photosynthesis · Specific leaf area

Introduction

Oceanic islands are composed of ecosystems highly susceptible to biological invasions (Elton 1958; Mueller-Dombois et al. 1981; Vitousek et al. 1987a). The relative number of non-indigenous invasive species on islands is usually high, and their rate of introduction can also be very rapid (Wester 1992). Invasive species can drastically change ecosystem-level processes (Vitousek et al. 1987b) or even entirely replace native plant species in certain island ecosystems (Mueller-Dombois et al. 1981; Shimizu and Tabata 1985; Itow 1992). No other group of islands can better exemplify the effects of invasive species than the Hawaiian Islands. There are currently over 4600 non-native plant species in Hawaii, of which approximately 800 are spreading and reproducing independent of direct human intervention (Stone et al. 1992). Eighty-six of these naturalized species are invasive and are believed to represent serious threats to native ecosystems (Vitousek et al. 1987a; Stone et al. 1992).

Research in invasion biology has historically focused on methods and technology to prevent the spread of the invasive species, rather than attempting to understand why invasions succeed or fail, knowledge which could potentially help prevent future invasions (Carey et al.

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1996; Luken and Thieret 1997). Several traits have been theorized to be more important in explaining the success of a particular invasive species in a given habitat. Differences in reproductive efforts, seed dispersal, seedling establishment capabilities, growth and carbon fixation rate, acclimation potential, susceptibility to herbivory and pathogens, phenology, age of reproductive maturity, and genetics can all act as important predictors of invasive ability (Bazzaz 1986; Rejmanek 1996; Williamson and Fitter 1996; Pysek 1997). When certain life history characteristics are similar between invasive and native species, such as overall reproductive potential, growth form, and susceptibility to herbivory, successful invading species must either capture limiting resources more efficiently (use more resources at a lower carbon cost) than native species, or use the resources at times when they are unavailable to the latter (Vitousek 1986). Higher resource utilization efficiency should promote faster growth rates. In addition, invasive species in island ecosystems free of specific herbivores and parasites may devote more resources to growth and reproduction rather than to defense mechanisms.

Several physiological and morphological traits in plants are related to growth and efficiency of resource utilization. Photosynthetic rates (A) may reflect the potential of an organism to assimilate CO_2 . Higher A may lead to higher rates of biomass accumulation and growth, particularly if the allocation of photoassimilates to the leaves and to non-photosynthetic stems and roots remains constant (Lambers and Poorter 1992). Specific leaf area (SLA, leaf area per unit leaf mass) tends to be positively related to growth and efficiency. A greater SLA may increase the capacity of the plant to assimilate CO_2 because more leaves are produced for a given mass of carbon invested in photosynthetic tissues (Lambers and Poorter 1992; Reich et al. 1997). When species of the same life form are compared, faster growing plants are positively correlated with higher SLA (Lambers and Poorter 1992; Reich et al. 1997).

Leaf construction cost (CC) is a measure of the energy invested by plants to synthesize carbon skeletons and nitrogenous compounds. This cost can also be indirectly related to the efficiency of resource utilization (Williams et al. 1987; Lambers and Poorter 1992; Griffin 1994). Leaf nutrient concentrations, mainly N and P, are important determinants of growth potential. Low leaf N and P concentrations characterize plants with relatively high nutrient use efficiency (Chapin 1980). Although plants with low leaf nutrient concentration tend to be nutrient use efficient, high leaf nutrient concentration, especially N, promotes growth and allows a more efficient use of radiant energy by increasing the instantaneous photosynthetic nitrogen use (Field and Mooney 1986).

This research was carried out on the east slopes of Mauna Loa volcano on the island of Hawaii. The eastern flank of Mauna Loa receives abundant precipitation from the prevailing northeast trade winds and exhibits little seasonal variation. The incipient soils on new lava flows are poor in nutrients, particularly N, compared to

the more developed soils of older lava flows (Vitousek et al. 1992). Invasive species can be found in most plant communities in this matrix of elevation/temperature, soil age and parent material, particularly at lower elevations, on older substrates and in ruderal sites (Wester and Juvik 1983). In this environmental matrix, where precipitation is non-limiting, we predicted that invasive species will possess a suite of traits that favor efficient use of resources and high potential growth rates, such as foliage with higher SLA and A and lower leaf CC than native species. These differences among sympatric native and invasive plant species may partially explain the success of the invasive species in mesic Hawaiian environments.

Materials and methods

Study sites and plant material

Plant material was collected during January and February 1997 from several sites located along an elevational gradient on the eastern slopes of the Mauna Loa volcano on the island of Hawaii, from the Kalapana Bay area (about 300 m) to the top of the divide (~2000 m) between Mauna Loa and Mauna Kea volcanoes. Mauna Loa is a large (4169 m) active shield volcano. Annual precipitation increased from the lowlands to a maximum at ~650 m and then decreased gradually as elevation increased (Wester and Juvik 1983; Gianbelluca et al. 1986). Air temperature decreased with elevation with a lapse rate of $5.8^\circ\text{C}/1000$ m. Soils were mostly acidic and the nutrient concentration tended to be higher in the old lava flows and ruderal sites. In addition, three species were collected from a relatively dry lowland site on the island of Oahu.

Thirty-four native and 30 invasive species from a total of 83 populations differing in life history characteristics and habitat preference were studied (Table 1). These species belong to 34 families of angiosperms and three pteridophytes. One species in particular, the dominant native tree *Metrosideros polymorpha* Gaud., has a wide altitudinal/ecological range, and therefore ten populations were initially sampled. *M. polymorpha* grows from sea level to the treeline (located at 2500 m) and from recent lava flows to old weathered soils, with large intraspecific morphological and physiological variation (Kitayama et al. 1997; Cordell et al. 1998). Some of the large intraspecific variability in this species is genetically determined (Cordell et al. 1998). To avoid pseudoreplication in the data analysis, only two randomly selected *M. polymorpha* populations with contrasting morphological and physiological traits (one glabrous and one pubescent) were included in the comparative study with all the species. The same was done with other species for which more than one population was sampled.

Collection sites were divided according to elevation ranges of lowland (0–500 m), mid-elevation (500–1200 m) and high-elevation sites (>1200 m). According to the substrate and soil age, the sites were classified as old lava flows (>150 year), recent lava flows (<150 year) and ruderal sites (along the roads) (Table 2). Lava flow age was obtained from geological maps (US Geological Survey 1986; Lockwood et al. 1988). At each site, leaves of native and invader species were collected under similar environmental conditions of forest, ecotone, and open sites. Therefore, the resources available to them (light, soil water, and nutrients) were essentially the same. For all species the youngest fully developed leaves were sampled. Studied species were classified either as herbs, shrubs, or trees, while the geographic origin or source of each species was identified either as native or invasive according to Wagner et al. (1990) and D. Mueller-Dombois (personal communication). Here, we refer to native plants as those that arrived on Hawaii before European settlement and to invasives as those introduced later, either purposefully or inadvertently, and which have established breeding populations without human interference.

Table 1 Geographical origin, life form, elevation, and age of substrate of the plants selected for the study. Origin refers to native (*N*) and invasive (*I*) plants. Life form refers to herbs (*H*), shrubs (*S*), and trees (*T*). Elevation ranges were *LOW* (0–500 m), medium (*MED* 500–1200) and *HIGH* (>1200 m). Substrate refers to lava flows aged >150 years (*OLD*), younger or aged <150 years

(*REC*), while those disturbed along roads and paths are ruderal sites (*RUD*). *glab* and *pub* refer to glabrous and pubescent ecotypes, respectively, of *Metrosideros polymorpha*. Nomenclature follows Wagner et al. (1990). *Asterisks* denote three species collected from a low-elevation site on the island of Oahu

Species	Family	Origin	Life form	Elevation	Substrate
<i>Acacia koa</i>	Fabaceae	N	T	MED	RUD
<i>Albizia chinensis</i>	Fabaceae	I	T	LOW	RUD
<i>Alpinia mutica</i>	Zingiberaceae	I	H	LOW	RUD
<i>Andropogon virginicus</i>	Poaceae	I	H	LOW	RUD
<i>Antidesma pulvinatum</i>	Euphorbiaceae	I	T	HIGH	OLD
<i>Araliaceae</i> sp.	Araliaceae	I	S	LOW	OLD
<i>Arundina graminifolia</i>	Orchidiaceae	I	H	MED	REC
<i>Bromus</i> sp.	Poaceae	I	H	HIGH	OLD
<i>Brussaia arguta</i>	Hidrangeaceae	N	S	MED	OLD
<i>Buddleia asiatica</i>	Loganiaceae	I	S	LOW	OLD
<i>Carex kauaiensis</i>	Cyperaceae	N	H	HIGH	REC
<i>Cecropia obtusifolia</i>	Cecropiaceae	I	T	LOW	RUD
<i>Cheirodendron tryginum</i>	Araliaceae	N	T	HIGH	OLD
<i>Chenopodium oahuense</i>	Chenopodiaceae	N	S	HIGH	OLD
<i>Cibotium glaucum</i>	Pteridophyta	N	T	MED	OLD
<i>Clermontia montes-loa</i>	Lobeliaceae	N	S	MED	OLD
<i>Clidemia hirta</i>	Melastomataceae	I	S	LOW	OLD
<i>Coprosma ernodeoides</i>	Ochraceae	N	S	MED	REC
<i>Coprosma ochracea</i>	Ochraceae	N	S	MED	REC
<i>Coprosma ochracea</i>	Ochraceae	N	S	HIGH	OLD
<i>Dicranopteris linearis</i>	Pteridophyta	N	H	LOW	OLD
<i>Dicranopteris linearis</i>	Pteridophyta	N	H	MED	REC
<i>Dodonea viscosa</i>	Sapindaceae	N	S	HIGH	REC
<i>Dubautia scabra</i>	Asteraceae	N	S	MED	REC
<i>Freycinetia arborea</i>	Pandanaceae	N	H	MED	OLD
<i>Hedychium gardnerianum</i>	Zingiberaceae	I	H	MED	OLD
<i>Hedyotis centranthoides</i>	Rubiaceae	N	S	MED	REC
<i>Heteropogon contortus</i> (*)	Poaceae	N	H	LOW	OLD
<i>Holcus lanatus</i>	Poaceae	I	H	HIGH	REC
<i>Hypochoeris radicata</i>	Asteraceae	I	H	MED	REC
<i>Ilex anomala</i>	Aquifoliaceae	N	T	MED	OLD
<i>Leucaena leucocephala</i> (*)	Fabaceae	I	S	LOW	OLD
<i>Metrosideros polymorpha</i> (glab)	Myrtaceae	N	T	LOW	OLD
<i>M. polymorpha</i> (glab)	Myrtaceae	N	T	LOW	REC
<i>M. polymorpha</i> (glab)	Myrtaceae	N	T	MED	OLD
<i>M. polymorpha</i> (glab)	Myrtaceae	N	T	MED	REC
<i>M. polymorpha</i> (pub)	Myrtaceae	N	T	LOW	OLD
<i>M. polymorpha</i> (pub)	Myrtaceae	N	T	LOW	REC
<i>M. polymorpha</i> (pub)	Myrtaceae	N	T	MED	OLD
<i>M. polymorpha</i> (pub)	Myrtaceae	N	T	MED	REC
<i>M. polymorpha</i> (pub)	Myrtaceae	N	T	HIGH	OLD
<i>M. polymorpha</i> (pub)	Myrtaceae	N	T	HIGH	REC
<i>Machaerina mariscoides</i>	Cyperaceae	N	H	MED	REC
<i>Melastoma candidum</i>	Melastomataceae	I	S	LOW	OLD
<i>Melinis minutiflora</i>	Poaceae	I	H	LOW	RUD
<i>Melinis minutiflora</i>	Poaceae	I	H	MED	RUD
<i>Melochia umbellata</i>	Sterculiaceae	I	T	LOW	REC
<i>Miconia calvescens</i>	Melastomataceae	I	T	LOW	RUD
<i>Myoporum sandwicense</i>	Myoporaceae	N	T	HIGH	OLD
<i>Myrica faya</i>	Myricaceae	I	T	HIGH	OLD
<i>Myrica faya</i>	Myricaceae	I	T	MED	REC
<i>Myrsine lessertiana</i>	Myrsinaceae	N	T	HIGH	OLD
<i>Myrsine sandwicense</i>	Myrsinaceae	N	S	LOW	OLD
<i>Nephrolepis</i> sp.	Pteridophyta	N	H	HIGH	REC
<i>Nephrolepis</i> sp.	Pteridophyta	N	H	LOW	OLD
<i>Pandanus tectorius</i>	Pandanaceae	N	H	LOW	RUD
<i>Pennisetum setaceum</i> (*)	Poaceae	I	H	LOW	OLD
<i>Pennisetum setaceum</i>	Poaceae	I	H	HIGH	OLD
<i>Pelea</i> sp.	Rutaceae	N	T	HIGH	OLD
<i>Peperomia</i> sp.	Piperaceae	N	H	MED	OLD
<i>Pipturus albidus</i>	Urticaceae	N	S	LOW	OLD
<i>Pipturus albidus</i>	Urticaceae	N	T	LOW	OLD
<i>Pluchea indica</i>	Asteraceae	I	S	LOW	OLD

Table 1 (contd.)

Species	Family	Origin	Life form	Elevation	Substrate
<i>Psidium cattleianum</i>	Myrtaceae	I	T	LOW	OLD
<i>Psidium cattleianum</i>	Myrtaceae	I	T	MED	OLD
<i>Psidium guajava</i>	Myrtaceae	I	T	LOW	OLD
<i>Psychotria</i> sp.	Rubiaceae	N	S	LOW	OLD
<i>Rhus sandwicensis</i>	Anacardiaceae	N	T	HIGH	OLD
<i>Rubus argutus</i>	Rosaceae	I	S	MED	RUD
<i>Rubus hawaiiensis</i>	Rosaceae	N	S	HIGH	OLD
<i>Senecio mikanioides</i>	Asteraceae	I	H	HIGH	OLD
<i>Setaria palmifolia</i>	Poaceae	I	H	LOW	REC
<i>Sophora chrysophylla</i>	Fabaceae	N	T	HIGH	OLD
<i>Spathodea campanulata</i>	Bignoniaceae	I	T	LOW	RUD
<i>Styphelia tameiameia</i>	Epacridaceae	N	S	HIGH	OLD
<i>Tibouchina floribunda</i>	Melastomataceae	I	S	MED	OLD
<i>Tibouchina herbacea</i>	Melastomataceae	I	H	LOW	OLD
<i>Tibouchina urvelliana</i>	Melastomataceae	I	S	LOW	RUD
<i>Trema orientalis</i>	Ulmaceae	I	T	MED	OLD
<i>Trema orientalis</i>	Ulmaceae	I	T	LOW	RUD
<i>Vaccinium chalicinum</i>	Ericaceae	N	S	HIGH	OLD
<i>Vaccinium reticulatum</i>	Ericaceae	N	S	HIGH	OLD
<i>Verbascum thapsus</i>	Scrophulariaceae	I	H	HIGH	OLD

Table 2 Environmental characteristics of the study sites: age of substrate refers to sites older than 150 years (*Old*), younger than 150 years (*Rec*; the year of the flow is also given) and ruderal sites (*Rud*); elevation; annual average rainfall and air temperature; pH, and nutrient content from the soils. *A'a'* is rough clinker lava, whereas *pahoehoe* lava flows are characterized by a smooth surface.

Both have the same chemical composition. *Tephra* is volcanic cinder. *Kipuka* refers to vegetation islands among recent lava flows. Rainfall and temperature were interpolated from Gianbelluca et al. (1986) and from Wester and Juvik (1983). Substrate age is from a US Department of the Interior Geological Survey Topographic Map (US Geological Survey 1986) and Lockwood et al. (1988)

Site	Age of substrate	Elevation (m)	Rainfall (mm)	Air temperature (°C)	pH	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	N (%)
Kalapana (forest)	Old	300	3000	23.0	5.9	64	100	1120	360	0.38
Kalapana (a'a' flow)	Rec (1955)	300	3000	33.0	5.3	28	200	3500	1020	0.61
Kalapana Kipuka (forest)	Old	300	3000	23.0	5.7	22	120	4400	780	1.28
Pahoe (main road)	Rud	300	1500	23.0	5.8	58	160	5600	2000	1.37
Saddle Road (forest)	Old (2500 years)	1000	4400	17.5	3.9	37	160	2200	460	2.89
Saddle Road (pahoehoe)	Rec (1850)	1000	4400	17.5	4.6	23	240	3900	420	1.18
Volcano (forest)	Old (2000 years)	1200	2200	16.5	5.5	103	100	1300	300	0.50
Volcano (tephra)	Rec (1959)	1200	2200	16.5	5.4	28	40	280	40	0.14
PTA site (kipuka)	Old (2500 years)	2000	2200	12.0	6.8	482	480	7300	680	1.24
Top Saddle Road (kipuka)	Old (2500 years)	2000	2200	12.0	4.9	27	160	1500	160	1.44

Photosynthetic gas exchange, nutrients, and cost of construction

Net CO₂ assimilation (*A*) and stomatal conductance (*g_s*) were measured in the field with a Li-Cor 6200 gas exchange system (Li-Cor, Lincoln, Neb.) on young fully expanded leaves of three individuals of 65% of all populations sampled. Each leaf was acclimated for 3–5 min to 1000 μmol m⁻² s⁻¹ of photosynthetic photon flux density (PPFD) prior to the gas exchange measurement. Light was provided by a QBEAM 2000 lamp (Quantum Devices, Barneveld, Wisc.). During measurements, cuvette air temperature, humidity, and CO₂ partial pressure were similar to that of the surroundings. Leaf temperature differed less than 1°C from air temperature, whereas PPFD was maintained at 1000 μmol m⁻² s⁻¹. During measurements, air temperature ranged from 21.9°C at high elevation to 32.1°C at low-elevation sites.

A composite soil sample was obtained by mixing three individual subsamples taken at a depth of 10–20 cm from each site. In recent lava flow sites, soils were obtained from the lava surface. Soils were analyzed for pH and for P, K, Ca, Mg, and total available N content. The first four elements were determined by inductively coupled plasma spectroscopy (Isaac and Johnson 1983),

whereas N concentration was analyzed with a micro-Kjeldahl procedure (Nelson and Sommers 1972).

At each site, local populations of native and invasive species were identified and ~100 g of recently expanded mature leaves from 10–20 randomly selected individuals from each species were collected, sealed in plastic bags, brought to the laboratory and kept in cold storage until processing, which took place within 48 h. In the laboratory, the leaves were gently washed with distilled water. The surface area of three leaves per species was measured with a Li-Cor leaf area meter (Model 3000) and their weight determined after drying at 60°C for 48 h. SLA was calculated as the ratio of leaf area to dry weight. The remaining leaves were dried and a 2 to 3 g aliquot of dry leaf per species was analyzed for N, P, and K concentration with the methods described above. Another 5 g aliquot was employed for the determination of the energy concentration (GE) of the tissues on an ash-free dry weight basis by bomb calorimetry (Parr Instruments, Moline, Ill.) following the manufacturer's recommended methods (Parr Instruments 1975). From N, GE, and ash content, leaf CC was calculated as in Williams et al. (1987), considering ammonium as the sole source of N, which corresponds to the mostly acidic soils found at the study sites. Instantaneous photosynthetic nitrogen use efficiency (PNUE) was

calculated as $A/[N]$. Intrinsic water use efficiency was calculated as A/g_s .

Statistical analysis

Statistical analysis was performed for all species with one- and two-way ANOVAs considering geographic plant origin or source, plant life form, elevation, and age of substrate as main factors. Differences between means were tested with a Tukey HSD method (SYSTAT 1997). In addition, comparisons between native and invasive species were done for the few families that had species of the same life form in both groups, and pairs of ecologically equivalent species were also selected and compared. Here, we consider as ecological equivalents, pairs of native and invasive species with the same life form, sharing the same habitat, elevation, and substrate. Ordination of species in a multivariate space was carried out with principal component analysis for all sampled populations.

Results

For all leaf measurements, source or geographic origin of the species did not interact significantly with life form, elevation, or substrate age. Taken as a group, the 34 native species (including one glabrous and one pubescent *M. polymorpha* population) and 30 invasive species differed significantly in 6 of 12 traits tested (Table 3). SLA, and N and P concentrations were higher for invasive species than native species (22.5, 30.5, and 37.5%, respectively). Leaf CC was higher for native species. Even though CC was only 3% higher on a mass basis (CC_{mass}), it was 36% higher on an area basis (CC_{area}) due to differences in SLA. Net CO_2 assimilation on an area basis (A_{area}) and mass basis (A_{mass}) were higher for invasive plants. Although not statistically significant, PNUE of invasive species was also higher than that of native plants (Table 3). Intrinsic water use efficiency (A/g_s) was $28.2 \mu\text{mol mol}^{-1}$ for natives and $37.6 \mu\text{mol}$

mol^{-1} for invasives. The higher A/g_s for the invasive species as a group was the result of their relatively high net CO_2 uptake rates.

In a more detailed analysis, native and invasive plants were subdivided with respect to life form, elevation, and substrate age. Consistent trends but fewer significant differences were observed than when considered globally. Taken either by life form, elevation, or substrate age, SLA, N concentration, and A were always higher for invasive plants, whereas CC was always higher in native plants (Figs. 1, 2 and 3). For example, leaf N was significantly higher in invasive species when herbs and trees were compared (Fig. 1). Leaf N was also significantly higher in invasive species at low and medium elevations (Fig. 2) and on old and recent lava substrate types (Fig. 3). Net CO_2 assimilation was significantly higher in invasive herbaceous species, but the differences were not significant for shrubs and trees (Fig. 1). Leaf P concentration exhibited the same trend as N concentration in all comparisons, and thus it was higher in the leaves of invasive species (data not shown).

Only five of the species studied had invasive and native representatives with similar life form; however, they never occurred together in the same study site (Table 4). The traits of the two pairs of native and invasive Fabaceae species followed the same pattern as the whole set of species: higher CC_{mass} and CC_{area} , but lower SLA and leaf N and P for the native species (Table 4). The comparison within the family Myrtaceae between one randomly selected population of the native *M. polymorpha* and two species of invasive *Psidium* was not significantly different regarding CC_{mass} but the re-

Table 3 Average specific leaf area (SLA), leaf N content on mass (N_{mass}) and area bases (N_{area}), leaf P and K contents, energy content (GE) on an ash-free basis, construction costs on mass (CC_{mass}) and area bases (CC_{area}), net CO_2 assimilation on area (A_{area}) and mass bases (A_{mass}), stomatal conductance (g_s), and photosynthetic nitrogen use efficiency (PNUE) of native and invasive species. All species and populations were included in the analysis. *P* indicates the level of significance of differences between native and invasive species under one-way ANOVA. Asterisks indicate statistically significant differences

Variable	Native	Invasive	<i>P</i>
SLA ($\text{cm}^{-2} \text{g}^{-1}$)	122.06	167.58	0.005*
N_{mass} (%)	1.36	2.09	0.0001*
N_{area} (g m^{-2})	1.33	1.38	0.715
P (%)	0.080	0.141	0.0001*
K (%)	0.864	0.911	0.810
GE (kJ g^{-1})	20.65	20.33	0.137
CC_{mass} (glucose eq. g^{-1})	1.394	1.342	0.026*
CC_{area} (glucose eq. m^{-2})	164.17	96.77	0.0001*
A_{area} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	6.91	9.65	0.061
A_{mass} ($\mu\text{mol g}^{-1} \text{s}^{-1}$)	0.067	0.150	0.002*
g_s ($\text{mmol m}^{-2} \text{s}^{-1}$)	0.278	0.252	0.625
PNUE ($\mu\text{mol g}^{-1} \text{N s}^{-1}$)	4.98	7.01	0.137

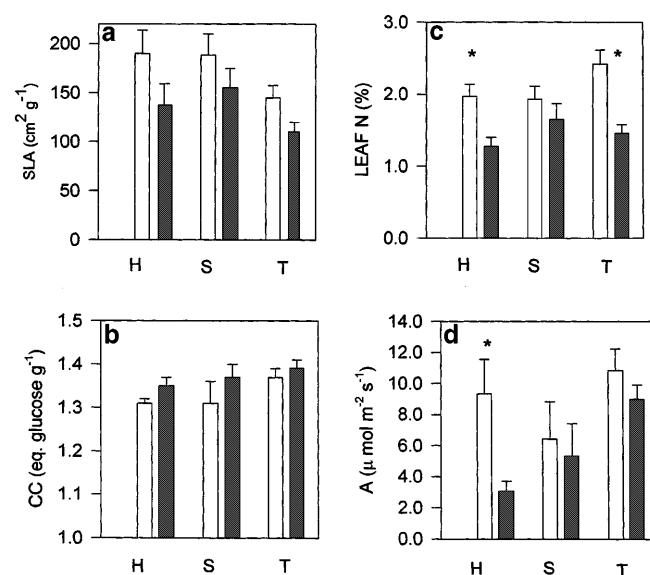


Fig. 1 Specific leaf area (SLA) (a), leaf construction cost (CC on a mass basis) (b), leaf N concentration (c), and net CO_2 assimilation (A) (d) of native (shaded bars) and invasive (open bars) species. Both groups of species were subdivided according to life form: herb (H), shrub (S), and tree (T). Bars are the mean \pm 1 SD. Asterisks denote ANOVAs with statistically significant differences at $P < 0.05$ between native and invasive species

mainder of the traits exhibited the same pattern as the whole set of species (Table 4). The native and invasive species of the other two families, Poaceae and Rosaceae,

did not conform to the patterns seen when comparing all species (Table 4). When comparing native and invasive ecologically equivalent species, all traits, except CC_{mass}

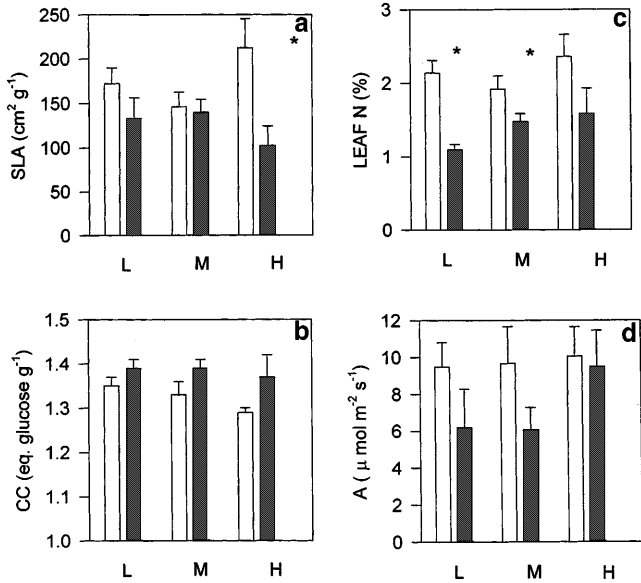


Fig. 2 Specific leaf area (SLA) (a), leaf construction cost (CC on a mass basis) (b), leaf N concentration (c), and net CO₂ assimilation (A) (d) of native (shaded bars) and invasive (open bars) species from low (L), medium (M), and high (H) elevations. Bars are the mean ± 1 SD. Statistics as in Fig. 1

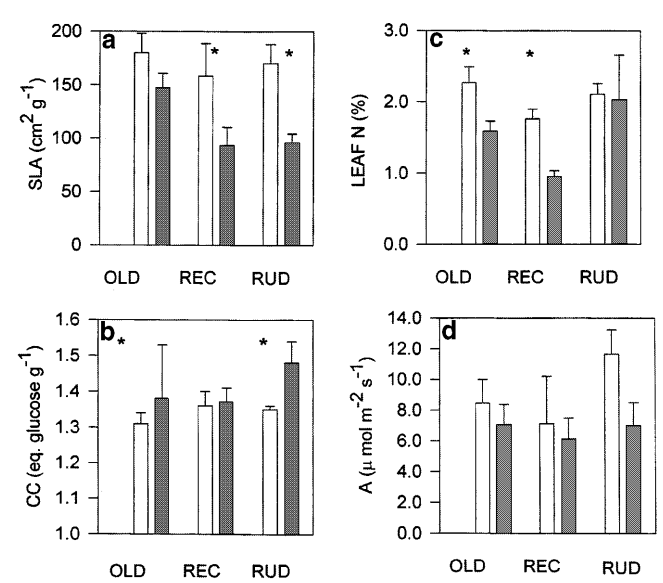


Fig. 3 Specific leaf area (SLA) (a), leaf construction cost (CC on a mass basis) (b), leaf N concentration (c), and net CO₂ assimilation (A) (d) of native (shaded bars) and invasive (open bars) species from old (OLD), young (REC), and ruderal (RUD) substrates. Bars are the mean ± 1 SD. Statistics as in Fig. 1

Table 4 Comparisons between native (N) and invasive (I) species by taxonomic family and by ecological equivalents, which have similar life form and share habitat, life form and elevation. Symbols and units as in Tables 1 and 3

	Life form and elevation	CC_{mass}	CC_{area}	SLA	N_{mass}	P concentration
By family						
Fabaceae						
<i>Acacia koa</i> (N)	T, MED	1.55	176.4	87.9	2.66	0.08
<i>Sophora chrysophylla</i> (N)	T, HIGH	1.41	161.9	87.1	2.89	0.15
<i>Albizia chinensis</i> (I)	T, LOW	1.42	87.9	161.5	2.87	0.12
<i>Leucaena leucocephala</i> (I)	T, LOW	1.37	64.8	211.46	3.95	0.13
Myrtaceae						
<i>Metrosideros polymorpha</i> (N)	T, LOW	1.44	242.1	59.5	0.87	0.06
<i>Psidium cattleianum</i> (I)	T, LOW	1.36	170.6	79.7	1.15	0.09
<i>Psidium guajava</i> (I)	T, LOW	1.45	172.8	83.9	1.71	0.16
Poaceae						
<i>Heteropogon contortus</i> (N)	H, LOW	1.21	54.9	221.26	1.18	0.11
<i>Pennisetum setaceum</i> (I)	H, LOW	1.17	140.9	83.4	1.21	0.06
<i>Melinis minutiflora</i> (I)	H, LOW	1.39	54.3	256.0	2.46	0.32
<i>Andropogon virginicus</i> (I)	H, LOW	1.43	115.5	123.87	1.33	0.10
Rosaceae						
<i>Rubus hawaiiensis</i> (N)	S, HIGH	1.31	48.2	273.1	2.95	0.22
<i>Rubus argutus</i> (I)	S, MED	1.34	71.8	187.4	1.76	0.08
By ecological equivalents						
<i>Metrosideros polymorpha</i> (N)	T, LOW	1.49	208.2	71.6	0.77	0.06
<i>Spathodea campanulata</i> (I)	T, LOW	1.44	60.8	236.7	2.48	0.20
<i>Miconia calvescens</i> (I)	T, LOW	1.30	93.9	138.4	1.90	0.17
<i>Metrosideros polymorpha</i> (N)	T, MED	1.61	337.2	49.2	0.77	0.02
<i>Myrica faya</i> (I)	T, MED	1.45	154.9	93.9	1.75	0.04
<i>Rhus sandwicensis</i> (N)	T, MED	1.37	66.2	207.5	1.40	0.08
<i>Trema orientalis</i> (I)	T, MED	1.29	82.8	159.6	2.93	0.19
<i>Psychotria</i> sp. (N)	S, LOW	1.36	95.89	142.6	1.31	0.08
<i>Melastoma candidum</i> (I)	S, LOW	1.13	41.6	273.0	1.83	0.12
<i>Heteropogon contortus</i> (N)	H, LOW	1.21	54.9	221.26	1.18	0.11
<i>Pennisetum setaceum</i> (I)	H, LOW	1.17	140.9	83.4	1.21	0.06
<i>Machaerina mariscoides</i> (N)	H, MED	1.33	298.8	44.6	0.69	0.02
<i>Arundina graminifolia</i> (I)	H, MED	1.42	124.9	114.4	1.61	0.08

of the *M. mariscoides* (native) and *Arundina graminifolia* (invasive) herbs, followed the same pattern as the whole data set with native species having higher CC_{mass} and CC_{area} but lower SLA and leaf N and P than invasive species (Table 4).

Despite the range of temperature and humidity conditions under which A was measured, A_{mass} per unit leaf N of invasive species tended to be higher than that of native species (Fig. 4). Net CO_2 assimilation increased with increasing leaf N, particularly for invasive species, in which it increased from about 0.05 to approximately $0.25 \mu\text{mol g}^{-1} \text{s}^{-1}$ with a 2% increase in leaf N. Both groups of plants show a trend of decreasing CC with increasing SLA (Fig. 5), suggesting that thinner leaves cost less to produce per unit mass. However, no signifi-

cant differences between native and invasive plants were observed. The ordination of the species by principal component analysis, using SLA, leaf N and P concentrations, and CC_{area} as orthogonal variables for the multivariate analysis, distinguished different groups of native and invasive species (Fig. 6), consistent with the previous univariate analyses. Non-indigenous invasive species were grouped on the lefthand side of the ordination and were associated with high SLA, whereas native species tended to be grouped on the righthand and upper side of the ordination and were associated with high CC and relatively low leaf N and P concentrations.

Discussion

SLA, foliar nutrients, and photosynthesis

SLA, leaf N and P, and A were clearly related to the origin or source of the species. SLA was 22.5% lower for native than for invasive species, and also lower for most of the comparisons between ecologically equivalent native and invasive species. SLA is a plant trait that appears to be extremely important in the regulation and control of plant functions such as carbon assimilation and carbon allocation (Lambers and Poorter 1992; Reich et al. 1997). By having leaves with a high SLA, invasive plants can produce larger assimilatory surfaces for a given amount of carbon fixed. Although not statistically significant, A_{area} was 24% higher for invasive than for native plants. Due to differences in SLA, the photosynthetic differences between native and invasive

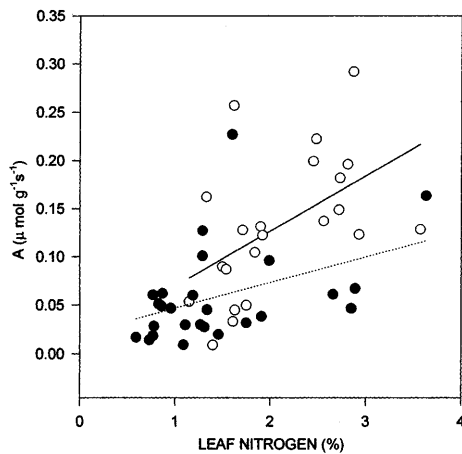


Fig. 4 Relationship between leaf N concentration and net CO_2 assimilation (A) both expressed in mass units. *Open circles* and the *continuous line* represent invasive species ($A = 0.119 + 0.057N$; $r^2 = 0.265$). *Filled circles* and the *dotted line* represent native species ($A = 0.020 + 0.026N$; $r^2 = 0.175$)

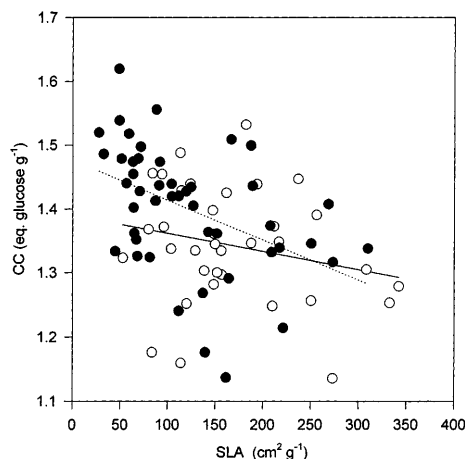


Fig. 5 Relationship between specific leaf area (SLA) and leaf construction cost (CC_{mass}). Symbols and lines as in Fig. 4. Regression equation for invasive species: $CC_{\text{mass}} = 1.394 - 3.242\text{SLA}$; $r^2 = 0.064$. Regression equation for native species: $CC_{\text{mass}} = 1.477 - 6.381\text{SLA}$; $r^2 = 0.199$

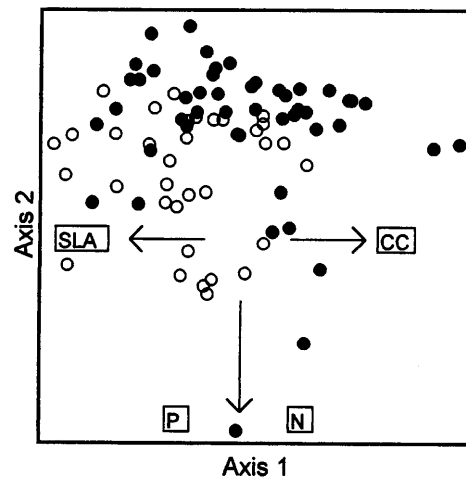


Fig. 6 First two axes of principal component analysis of the effects of leaf construction cost (CC), specific leaf area (SLA), and leaf N and P content on the ordination of all populations of native (*filled circles*) and invasive (*open circles*) species. The *arrows* indicate increasing effect of the variables considered on the ordination. CC and SLA were strongly correlated with the ordination along axis 1 ($r^2 = 0.91$ and -0.93 , respectively). Leaf N and P concentrations were strongly correlated with the ordination along axis 2 ($r^2 = -0.75$ for both variables)

species increased significantly when net CO₂ assimilation was expressed on a mass basis. Few studies have compared net CO₂ assimilation rates between native and invasive tropical plants. In three such studies, invasive species showed higher *A* (Baruch et al. 1985; Williams and Black 1993; Pattison et al. 1998). In this study, *A* of invasive plants was also higher for invasive species with different life forms and elevations. The higher *A* was likely a result of higher leaf N and higher SLA. The relationships between *A*, N, and SLA were similar to the interspecific relationships among leaf structure and function described by Reich et al. (1997). They found that potential carbon gain increased in similar proportion with increasing leaf nitrogen concentration and increasing SLA for 280 plant species from different ecosystems. This universal response also included leaf life span and growth rates, two variables not measured in the present study. In addition they found that variation in leaf traits among species was related strongly to whole-plant properties. Species of high SLA and *A*_{max} had high relative growth rates. Our results suggest that variation in leaf traits is highly constrained, with invasive and native species falling in different set points of a more general tradeoff surface. Thus, we should also expect that invasive species, having high SLA, N concentration, and *A*_{max}, will have higher growth rates than native species.

Leaf nutrient concentration was higher for invasive species in general and also in species-specific comparisons between native and invasive plants. In particular, N was nearly always significantly higher for invasive species regardless of whether the comparison with natives was done according to life form, elevation, or substrate type. Considered in isolation, this would make invasive species less efficient in nutrient use than native species because nitrogen use efficiency generally is inversely correlated to foliar N (Chapin 1991). On the other hand, the substantially higher *A* of invasive species compensated for the increase in foliar N resulting in a PNUE that was 15% higher for the invasive species. This may promote carbon assimilation and enhance the growth potential of invasive species (Field and Mooney 1986).

Cost of construction

Leaf energy content (GE) was in the range reported for many vascular species (Larcher 1980). Herbs had the lowest GE, and GE tended to be higher in shrubs and trees. Ecological theory predicts that synthesis costs should respond to resource availability and should be reflected by short- or long-term gains in either growth, defense, or reproduction (Orians and Solbrig 1977; Chapin 1980; Mooney and Gulmon 1982; Bloom et al. 1985). In general, low leaf CC has been associated with plants with high relative growth rates (Lambers and Poorter 1992; Poorter and Villar 1997). In this study, leaf CCs were lower for invasive than native species. Furthermore, when several pairs of ecologically equiv-

alent native and invasive species from the same elevation and substrate were compared, native plants exhibited higher leaf CC_{mass} and CC_{area} in 80% of the comparisons (Table 4). Although the difference in CC_{mass} between native and invasive plants was small, it could lead to substantial differences in growth rate (Poorter and Villar 1997). The lower leaf CC of invasive species suggest that these species utilized carbon resources more efficiently than native species by investing less energy per unit of leaf produced. Similar results were observed when native and introduced grasses were compared in a Neotropical savanna (Baruch and Gómez 1996). The difference in CC between native and invasive species was magnified when considered on an area basis, reflecting the differences in SLA discussed above. The effect of SLA on CC is evident as dense leaves contain more sclerenchyma tissue with a proportionally higher contribution of cellulosic components that are relatively energy rich (Griffin 1994; Poorter 1994). Invasive species had lower CC despite higher N leaf concentration. It is possible that N concentration contributed relatively little to CC because NH₃ is the main source of N for plants in tropical soils, and costs less to incorporate than NO₃ (Williams et al. 1987; Poorter and Villar 1997).

Phylogenetically related and ecologically equivalent species

The families with most invasive species on the Mauna Loa environmental matrix are the woody Melastomataceae, Myrtaceae, and Fabaceae and the mostly herbaceous Poaceae, Asteraceae, and Zingiberaceae. The Poaceae, Asteraceae and Fabaceae are large families and the Myrtaceae are over-represented among natural-area invaders (Daehler 1998). It has been argued that ecological comparisons are more meaningful for phylogenetically related species (Harvey and Purvis 1991). Comparison between closely related species should be made between traits that are functionally important to their success in a given specific habitats (Noble 1988). The comparison across species ignores patterns of phylogenetic relatedness, which may constrain variation in species morphology and physiology. Furthermore, closely related species are likely to have more traits in common and more overlapping resource requirements than more distantly related species (Goldberg 1987). In this study, however, few genera or families had species in both native and invasive groups. Only *Rubus* was represented with a native and an invasive species and their comparison did not conform to our predictions. The taxonomic comparisons showed ambiguous results mainly due to the paucity of species in the same family and marked differences in life form and habitat of the pairs of species under comparison. Also, traits not measured here, such as leaf area ratio, root/shoot ratio, and reproductive behavior, may contribute to the success of invasive species, as shown in other studies (Williams and Black 1993; Pattison et al. 1998).

Another powerful method to assess the traits that contribute to the invasiveness of non-indigenous species is comparison between ecologically similar, sympatric invasive and native taxa (Mack 1996). Contrasts between ecologically equivalent native and invasive species growing under similar environmental conditions yielded results that were consistent with our predictions. We consider this type of comparison ecologically meaningful in our study as the native and invasive species co-occurred in the same habitat and are probably utilizing the same resources. The comparison between the ecologically equivalent grasses *Heteropogon contortus* (native) and *Pennisetum setaceum* (invasive) from the lowland dry site in the island of Oahu showed that although CC_{mass} was higher, N was lower, and SLA was higher in the native grass. However, other traits such as A and leaf area ratio (not measured here) were higher in the invasive grass *P. setaceum* and may have contributed to its higher competitive potential (Williams and Black 1993). It is also possible that the arid environment where these two grasses co-occurred had imposed a different set of selective pressures than those present in the humid slopes of Mauna Loa. If an invasive species is to be successful in seasonally dry environments, it should be able to adapt by adjusting its physiological activity to the reduced level of available resources in order to avoid damage and survive until the next favorable growing season. In this case, phenotypic plasticity, rather than overall resource utilization efficiency, may be a more important predictor of invasive ability in seasonal environments.

Results from a recent study with six invasive and five native Hawaiian rainforest species indicated that the former had significantly higher growth rates (Pattison et al. 1998). These were a consequence of higher photosynthetic capacities, lower respiratory costs and higher leaf area ratio (the ratio of total leaf area and biomass per plant). In their study, dark respiration was used to estimate leaf costs rather than the cost of construction, as used in the current study. The results were nevertheless similar in that the invasive species were able to attain higher photosynthetic rates at a lower cost than native species. Their study included two congeneric species, one native and one non-indigenous invasive. Because of its experimental nature, Pattison et al. (1998) were able to evaluate the relative ability of invasive and native plants to adjust their physiology and carbon allocation patterns to changes in light levels. They found that physiological plasticity was an important component in the success of invasive species.

Conclusion

A possible ultimate explanation for the difference between invasive and native species in general, and particularly on oceanic islands, is that native species have undergone less selective pressure to compete for limiting resources than invasive plants. Arguments have arisen

against the idea that competition for resources is stronger on mainland than on island ecosystems unless resource availability is empirically determined to be higher in island than in mainland ecosystems (Simberloff 1995). Even though species diversity is relatively low and the flora is disharmonic in isolated island ecosystems (Carlquist 1974), additional empirical studies are necessary to functionally link species diversity, resource availability, competitive ability, and invasibility of non-indigenous species. Our results indicate clear differences in leaf traits between native and invasive plants across several diverse life forms and environments. By virtue of their higher SLA, CC, and A , invasive plants can apparently capture resources more efficiently (use more resources at a lower carbon cost) than native species. These leaf traits of invasive species may promote not only a more efficient use of resources but may potentially also result in higher growth rates compared to native species, consistent with the rapid spread of the invasive species in isolated oceanic islands, particularly in environments where seasonal water deficits are not pronounced.

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