Persistence of Native Trees in an Invaded Hawaiian Lowland Wet Forest: Experimental Evaluation of Light and Water Constraints[1]

Jodie R. Schulten,[2,6] *T. Colleen Cole*,[3] *Susan Cordell*,[4] *Keiko M. Publico*,[2] *Rebecca Ostertag*,[2] *Jaime E. Enoka*,[2] *and Jené D. Michaud*[5]

Abstract: Hawaiian lowland wet forests are heavily invaded and their restoration is most likely to be successful if native species selected for restoration have efficient resource-use traits. We evaluated growth, survival, and ecophysiological responses of four native and four invasive species in a greenhouse experiment that simulated reduced light and water conditions commonly found in invaded field conditions. Our results show that light is a more important limiting resource than water for all species. Specifically, values for photosynthesis, light compensation point, light saturation point, stomatal conductance, leaf mass per area, relative growth rate, and photosynthetic nitrogen use efficiency were all greater under high-light conditions than they were under low-light conditions. In contrast, water limitation negatively affected only stomatal conductance and $\delta^{13}C$. Our results also show that responses to light were species-specific rather than related to whether species were native or nonnative. We also tested restoration potential of top-performing native species under field conditions in a Hawaiian lowland wet forest by comparing relative growth and mortality rates in both invaded (low-light) plots and in plots from which invasive species had been removed (high-light conditions). Of the native species, *Myrsine lessertiana* and *Psychotria hawaiiensis* had highest survival and growth rates in low-light plots after 4 yr, and *Metrosideros polymorpha* showed 100% mortality under the same conditions. Under low light, *M. lessertiana* and *P. hawaiiensis* survived and grew at rates similar to those of invasive species in both field and greenhouse and thus represent suitable candidates for restoration in invaded Hawaiian lowland wet forests.

Biological invasions are recognized as a worldwide phenomenon and a major threat to native biodiversity, and are common worldwide. Invasions can adversely influence the structure and function of an ecosystem by changing species composition and seed dynamics (Holmes and Cowling 1997, Vitousek et al. 1997, Holl et al. 2000, D'Antonio and Kark 2002). Invasions can also alter light levels, microclimates, and nutrient cycling (Holl 1999, D'Antonio and Corbin 2003, Levine et al. 2003, Reinhart et al. 2006, Gomez-Aparicio and Canham 2008).

There are a variety of mechanisms by which invasive species are successful (Rejmánek and Richardson 1996, Pattison et al. 1998, Lloret et al. 2005). Some invasive species are characterized by prolific seed dispersal and seedling recruitment or vegetative reproduction, which allows them to expand into new and/or disturbed habitats (Rejmánek 2000). Other invaders exhibit faster growth,

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[2] Department of Biology, Tropical Conservation Biology and Environmental Sciences, University of Hawai'i at Hilo, Hilo, Hawai'i 96720.

[3] Three Mountain Alliance, Volcano, Hawai'i 96718.

[4] Institute of Pacific Islands Forestry, U.S. Department of Agriculture Forest Service, Hilo, Hawai'i 96720.

[5] Department of Geology, University of Hawai'i at Hilo, Hilo, Hawai'i 96720.

[6] Corresponding author (e-mail: schulten@hawaii.edu).

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faster photosynthetic rates, or greater phenotypic plasticity than natives (Williams et al. 1995, Pattison et al. 1998, Fogarty and Facelli 1999, Durand and Goldstein 2001). In addition, some invaders have the ability to use limiting resources at a time when native species cannot (Vitousek 1986, Harrington et al. 1989). However, although these traits appear to be characteristic of invasive species, recent reviews and meta–analyses of invasive species traits reveal that universal trends and the predictive power of trait-based approaches may not be forthcoming (Daehler 2003, Pyšek and Richardson 2007, Moles et al. 2008, van Kleunen et al. 2010).

The Hawaiian archipelago has been described as a showcase for invasions because over half of its flora is nonnative (Simberloff 1995, Denslow 2003). Invasion on these islands is especially prevalent at low elevations, where the original extent of native habitats is highly limited and the extent of native habitats has been greatly reduced by human activities. Lowland wet forests are currently found only in remnant fragments (predominantly on the islands of Hawai'i and Kaua'i (Price et al. 2007), and seedling regeneration of native species is uncommon (Zimmerman et al. 2008, Cordell et al. 2009). Because of their limited extent, fragmentation, and high degree of invasion, the management inputs and costs required to revert Hawaiian lowland forests to an all-native state are substantial and imply the use of hundreds of person-hours (Ostertag et al. 2009).

Because returning to an all-native state is no longer practically feasible, restoration efforts in the lowland wet forest type would be more successful by focusing on native species that can survive current invaded and altered conditions. Testing species traits in response to abiotic factors is useful in this context because ecological theory predicts that co-occurring native and invasive species should be similar in resource-use traits (Daehler 2003, Funk et al. 2008, van Kleunen et al. 2010). Hawaiian forests are typically characterized by more open canopies than their continental tropical counterparts, and most native Hawaiian forest species require high-light environments for germination and survival (Burton and Mueller-Dombois 1984, Drake 1993, Drake and Mueller-Dombois 1993). Unfortunately, the high-light conditions in Hawaiian lowland wet forests are also conducive for the establishment and growth of invasive species. For example, Pattison et al. (1998) found that invasive species in Hawai'i were able to capture and utilize light more efficiently than the natives, and their photosynthesis rates were significantly higher in high-light environments. Given that invasive species tend to be more light-use efficient than native species, restoration efforts in Hawai'i may need to target native species that survive and grow well under the heavily shaded conditions typical of invaded forest habitats.

Water is not commonly thought of as a limiting resource in wet forests; however, it may function as such under certain conditions in Hawaiian forests. Thin, well-drained soils on Hawai'i's very young lava substrates have very low available water capacities (Soil Survey Staff 2012). In addition, previous work (J.D.M., unpubl. data) has documented low soil water potentials in heavily invaded lowland wet forests under drought conditions. Low water potentials were likely the result of high transpiration associated with large nonnative biomass, and thus it is possible that drought conditions could reduce survival of native species, particularly seedlings and saplings.

In short, our motivation for understanding how species compete under limitations of light and water was to obtain information that could be used to design sustainable restoration treatments. Remaining native species, either in invaded environments in the field or in the seed bank, likely possess highly plastic traits that enable adaptation to limiting resources. In addition, if there are native species that are similar to nonnatives in terms of shade tolerance and efficient use of light and water, then they may be candidate species for restoration. Based on the role of light and water as potential limiting resources, the primary objective of this study was to experimentally determine the light and water conditions under which species of native Hawaiian trees with divergent life histories can survive and tolerate competition from invasive species. We mea-

sured a suite of ecophysiological traits on native and invasive species across a spectrum of life histories (e.g., pioneer to later successional) to test the following hypotheses: (1) light will be a more limiting resource than water for all species; (2) under high-light conditions, invasive species will outperform native species; and (3) seedling survival will decrease under low-water and low-light conditions.

MATERIALS AND METHODS

Study Site

The Keaukaha Military Reservation (KMR) encompasses 43.3 ha (107 acres) of fenced Hawaiian lowland wet forest adjacent to the Hilo International Airport, on the eastern coast of Hawai'i Island (19° 42.15′ N, 155° 2.240′ W). The site is located on a 750–1,500 yr old 'a'ā lava flow at 30 m elevation and receives an annual average rainfall of 3,280 mm (as recorded by the U.S. National Weather Service Hilo International Airport station). The soil has an available water capacity of less than 5.6 cm (Soil Survey Staff 2012). The vegetation is classified as lowland wet forest as defined by Price et al. (2007). Although the overstory at KMR is dominated by the native trees *Metrosideros polymorpha* ('ōhi'a) and *Diospyros sandwicensis* (lama), the understory is heavily invaded with little native recruitment (Zimmerman et al. 2008, Cordell et al. 2009). The most dominant invasive species at KMR include trees such as *Psidium cattleianum* (strawberry guava), *Macaranga mappa* (bingabing), and *Melastoma septemnervium* (melastoma), as well as the shrub *Clidemia hirta* (Koster's curse) (Zimmerman et al. 2008). The success of these invasive species has been attributed to a number of traits such as vegetative reproduction in *Melastoma* and *Psidium*, and high fecundity in *Clidemia*, a species that is able to produce hundreds of seeds per fruit (Wester and Wood 1977).

Species Selection

We chose species that are either common native components (*Metrosideros polymorpha*, *Psychotria hawaiiensis*, *Myrsine lessertiana*, *Pipturus albidus*) or highly successful nonnative invaders (*Clidemia hirta*, *Melastoma septemnervium*, *Cecropia obtusifolia*, *Macaranga mappa*) of lowland wet forests in Hawai'i. These species differ in their shade tolerance, sensitivity to disturbance, reproductive strategies, seed dispersal, and ability to resprout, providing a spectrum of species traits. Although *Diospyros sandwicensis* is a canopy dominant species in many lowland wet forests, we did not incorporate it into this study because seeds for this species are not commonly found at KMR. Nomenclature follows Wagner et al. (1999, 2012); hereinafter species are referred to by genus name.

Plant Preparation

Seedlings of *Cecropia*, *Clidemia*, *Macaranga*, *Melastoma*, and *Psychotria* were collected in February 2007 from KMR. *Myrsine*, *Metrosideros*, and *Pipturus* seedlings are limited at KMR and were grown from seeds collected in Hilo. Seedlings were allowed to acclimate in the pots and establish new leaves before the start of the experiment, and to ensure that plants had time to respond to the treatments we only measured leaves that had fully developed in the new treatment. Initial seedling heights ranged from 2.25 to 30.0 cm (averaging 14.8 cm). Once seedlings were established, they were transplanted into pots ranging from 15.24 cm (6 in.) diameter to 3.79 liters (1 gal.) with a 1:1 growing (Sunshine Mix, Sun Gro) and cinder media. One teaspoon (4.93 ml) of controlled release fertilizer (Nutricote, Florikan) (13-13-13) was applied once before repotting. Plants were managed for pests as necessary (Safer Soap, Pyrethrin, Neem oil, Marathon, and Avid).

Treatments

We determined leaf physiological traits on leaves that were fully developed in each treatment as well as growth and survival rates for native and nonnative species under experimental conditions in a greenhouse. We used a factorial design to assign light and water conditions to four experimental treatments: high light/high water, high light/low water, low light/high water, and low light/low water.

The treatments were set up by growing seedlings in two neighboring greenhouses at the U.S. Department of Agriculture Institute of Pacific Islands Forestry building in Hilo, Hawai'i, approximately 3 miles (4.83 km) from KMR. Each greenhouse was considered a block containing four treatments (one per each 244 cm by 122 cm greenhouse bench). Five individual seedlings of equal size of each species were randomly assigned to each bench, resulting in 40 plants per bench and 160 plants per block. Treatment benches were alternated across the block.

Low-light (shade) conditions were set at 1% transmittance, based on measurements at KMR (1%–5% transmittance in control plots [Wong 2006]). Low-light conditions were maintained via shade structures constructed from polyvinyl chloride and shade cloth surrounding plants on all sides. High-light treatments had no shade cloth, but the greenhouse did not provide true full-sun conditions, and plants in high-light treatments received approximately 50% transmittance. To simulate seasonal drought, we manipulated irrigation. High-water treatments received twice the amount of water relative to low-water treatments. A drip irrigation system was constructed and placed on a timer allowing the high-water treatments to receive a watering regime of 1 min, twice per day, every day. Low-water treatments received a watering regime of 1 min, twice per day, every other day. Although we cannot relate the water treatment to drought conditions explicitly, plants under the low-water treatment did show signs of water stress, and thus we feel that this watering regime does simulate the occasional drought conditions these forests experience.

Greenhouse Measurements

We measured the initial seedling height (as an experimental baseline) in February of 2007 and tagged the apical meristem to identify growth under treatment. Seedling height was remeasured in June 2007, and relative growth rates were calculated as cm cm^{-1} day^{-1}. Upon completion of trait data measurements, leaves were harvested and leaf area was determined using an area meter (LI-3100, LI-COR, Lincoln, Nebraska). The leaves were then dried at 70°C for 48 hr, and leaf mass per area was obtained by dividing dry leaf mass by area.

In addition to relative growth rate and leaf mass per area, we measured percentage survival and a suite of physiological parameters on leaves that matured during the course of the experiment (4 months). Physiological measurements included maximum rates of photosynthesis (A_{max}), light compensation point, and light saturation point derived from light response curves; water potential (ψ_p), photosynthetic nitrogen use efficiency, and foliar %C, %N, $\delta^{13}C$, and $\delta^{15}N$. Light response curves were generated from a single recently matured, fully expanded leaf per plant, using a Portable Photosynthesis System (LI-6400, LI-COR, Lincoln, Nebraska), for a total of 40 light response curves per species (assuming 0% mortality). Leaves were acclimated at a photosynthetic photo flux density of 1,500 μmol m^2 sec^{-1}, consistent ambient temperature, 65% relative humidity, 100.5 kPa of pressure, and a CO_2 reference value of 400 μmol mol^{-1}. Each leaf was exposed to a series of photosynthetic photo flux densities at 1,500, 1,000, 500, 200, 100, 75, 45, 30, 15, and 0 μmol m^{-2} sec^{-1}, and at each light level the photosynthetic rate was allowed to stabilize for 120–200 sec. In addition, three fully matured leaves were collected from three individuals per species per treatment and pooled for %C, %N, $\delta^{13}C$, and $\delta^{15}N$. Nutrient analyses were performed at the University of Hawai'i at Hilo Analytical Laboratory on samples ground with a Wiley mill. Isotopes were measured on a Thermo-Finnigan Delta V IRMS (Waltham, Massachusetts) attached to a Costech ECS 4010 CN Elemental Analyzer (Valencia, California). Photosynthetic photo flux density (PNUE) was then computed on an area basis, where

$$\text{PNUE} = \mu\text{mol}CO_2\, m^{-2}\, sec^{-1}\, molN^{-1}.$$

Planting

Greenhouse survival results were corroborated in the field by planting native seedlings in both high-light and low-light conditions. *Metrosideros*, *Myrsine*, and *Psychotria* were

planted in the field under both high-light and low-light conditions and monitored for relative growth rates and survivorship. Four Hawaiian lowland wet forest plots where all nonnative species were removed were used for the high-light plantings (removal), and four unmodified (control) plots were used for the low-light plantings. Light levels in the control plots averaged 2% light transmittance, and the removal plots averaged 31%; thus these conditions mimicked those of the greenhouse experiment. The 10 m by 10 m removal and control plots were established by a previous study (Cordell et al. 2009, Ostertag et al. 2009). Individuals of each species were randomly assigned to a plot so that each plot had 16 individuals per species (48 total plants per plot). The 10 m by 10 m plots were divided into 5 m by 5 m quadrats, and plants were planted at random 1 m by 1 m locations within each quadrat. Plants were watered at planting and did not receive water or fertilizer afterward. Relative growth and survival rates were monitored biannually for 2 yr and then annually for the following 2 yr.

Data Analysis

Photosyn Assistant (Dundee Scientific, Dundee, United Kingdom) was used to generate light response curves, based on assimilation and light levels, and to compute A_{max}, light compensation point, light saturation point, and stomatal conductance. Physiological and morphological traits were analyzed using a $2 \times 2 \times 7$ factorial three-way analysis of variance (ANOVA) with greenhouse (as a block), species, light treatment, and water treatment as main effects, and species and treatments as interactions (see Table 1). Low sample size of *Metrosideros* (high mortality in low-light treatments) created an unbalanced design, so we excluded this species from the factorial ANOVA but still present it graphically. Significance within treatment combinations was determined by post hoc Tukey's tests. Because many variables were highly correlated, a principal components analysis was performed on variables that were significantly different across species. All statistical analyses were performed using JMP v6.

TABLE 1

Results of Factorial ANOVA for Plants in the Greenhouse Experiment, Grown in Two Greenhouses (Block), under High and Low Light, and under Watering Daily or Every Other Day

Variable	Block	L	W	S	L × W	L × S	S × W	L × W × S
Physiological traits								
$Amax_{area}$	ns	<.0001	ns	<.0001	ns	<.0001	ns	ns
$Amax_{mass}$	ns	.0159	ns	.0141	ns	ns	ns	ns
Light compensation point	ns	<.0001	ns	.0096	ns	ns	ns	ns
Light saturation point	ns	<.0001	ns	.0083	ns	.0012	ns	ns
Water potential	ns	ns	ns	<.0001	ns	.0006	ns	ns
Conductance	ns	<0.0001	.0001	.0015	.0053	ns	ns	ns
Photosynthetic nitrogen use efficiency	ns	<.0001	ns	.033	ns	ns	ns	ns
N_{area}	ns	ns	ns	.0288	ns	.0397	ns	ns
N_{mass}	ns	<.0001	ns	<.0001	ns	<.0001	ns	ns
$\delta^{15}N$	<.0001	ns	ns	.0034	.0136	ns	ns	ns
$\delta^{13}C$	.0125	.0003	.0145	<.0001	ns	.0252	ns	ns
C:N	ns	.0111	ns	.0096	ns	ns	.0075	ns
Morphological traits								
Leaf mass per area	ns	.0078	ns	.0099	ns	ns	ns	ns
Relative growth rate	ns	<.0001	ns	<.0001	ns	<.0001	<.0001	.048

Note: Four native and four nonnative species were grown under these conditions, but analysis here does not consider the native *Metrosideros polymorpha* due to extreme unbalance in the design (high mortality in the low water treatment). Light, water, and species represented by L, W, and S, respectively. *P* values given if ≤.05, otherwise nonsignificant (ns).

RESULTS

Species responded more to the light treatment than to the water treatment. Light treatment had a significant effect on all measured variables except water potential and $\delta^{15}N$ (Table 1). In contrast, the water treatment only significantly affected stomatal conductance and $\delta^{13}C$. Most of the interactions between light and water were not significant (Table 1). We found a significant difference across all seven species for all leaf traits, which led to occasional significant interactions of species with light and species with water. However, because of the overwhelming influence of the factors of light and species, we focus on these main effects rather than the interaction terms. Due to its lack of effect, water was removed as a factor from the analyses to increase the power of Tukey's tests, and water is not graphically represented in the figures. We also do not emphasize the influence of the different greenhouses (block effect) because it was not significant for most variables (Table 1).

We hypothesized that in the high-light treatments the traits of invasive species would be consistent with higher performance and the traits of native species would be consistent with lower performance. Although this was often the case, for some traits (light compensation point, leaf mass per area, $\delta^{15}N$, and $\delta^{13}C$) there were no differences between native and nonnative species. For traits related to light use (such as A_{max} or light saturation point, which is a measure of light use efficiency), values were significantly higher in the high-light treatment across all species. When plants were grown in low light the light saturation point of all species did not differ between species (Figure 1). Rates of A_{max} in low light were species-specific and unrelated to species origin (native or nonnative). Although water availability did not appear to be a strong influence on species traits, there is some evidence that *Clidemia* and *Metrosideros* might be sensitive to water stress based on their water potential values under high-light conditions (Figure 2). Survival data confirm that these two species had higher mortality under low-water conditions (Table 2). A lack of a strong response in $\delta^{13}C$, a measure of integrated water use efficiency, also attests that water limitation is likely not a strong driver of plant traits and competitive interactions among species and species origins (Figure 2). However, some species exhibited plasticity levels (i.e., greater range in a given response variable [Feng et al. 2007]) in integrated water use efficiency response to the light treatment (Figure 2).

Leaf nitrogen values were similar across species in the high-light treatment but varied greatly across species in the low-light treatment. The species that had the highest nitrogen on a mass basis had lower values of nitrogen on an area basis, corresponding to their lower A_{max} in the low-light treatment (Figure 3). This is likely due to the tendency of plants to produce shade leaves that are adapted to maximize light acquisition (larger leaf area and less leaf mass). This trend was most noticeable in species that are pioneers in their native habitat (*Cecropia*, *Macaranga*, and *Pipturus*).

Across all species, both relative growth rates and leaf mass per area were greater in the high-light treatment than in the low-light treatment (Figure 4). In the low-light treatment, *Cecropia* and *Pipturus* had the lowest leaf mass per area. Similar to other traits, relative growth rate was individualistic and not related to species origin. In fact, native *Psychotria* had the highest relative growth rate in the low-light treatment, which is consistent with its relative success in heavily invaded and thus shaded environments.

In high-light conditions in the greenhouse, survival rates were high for nearly all species except *Clidemia*, which had moderate mortality under high light, regardless of water conditions (Table 2). Under low-light conditions, one invasive species (*Clidemia*) and two native species (*Metrosideros* and *Pipturus*) experienced high mortality. Six out of eight species experienced mortality under conditions of both low light and low water. *Metrosideros* did poorly under low light and very poorly under conditions of both low water and low light. *Pipturus* experienced moderate mortality under low light, regardless of water conditions. *Psychotria* faced some mortality under high light/high water and low light/low water.

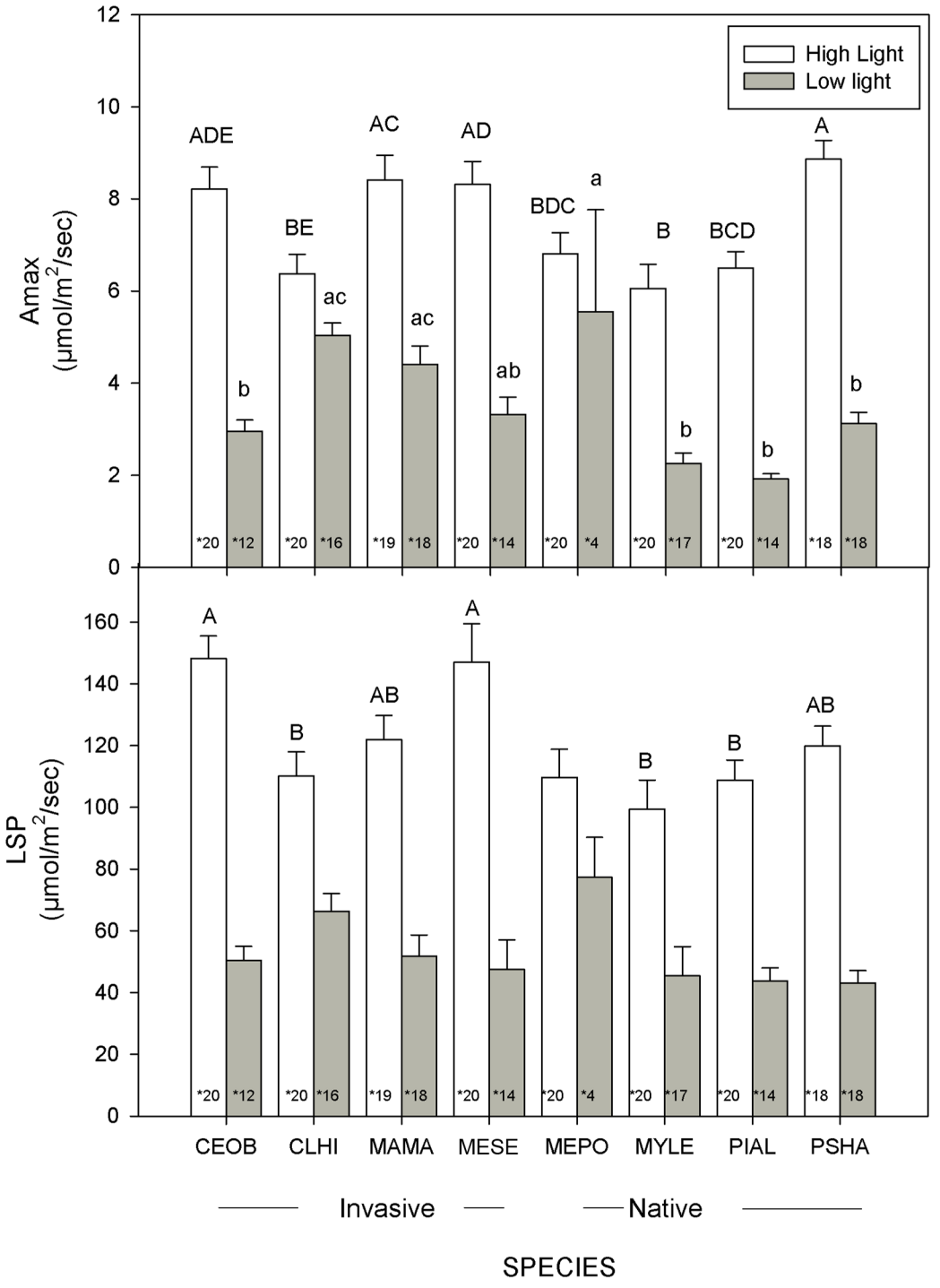

FIGURE 1. Maximum photosynthesis rates (A_{max}) and light saturation point (LSP) values for all species in low-light and high-light treatments. Error bars represent the standard error of the mean. Letters indicate significant differences between species, with upper-case and lower-case letters representing the species differences at high and low light, respectively. *Metrosideros polymorpha* was not included in the statistical analysis due to low sample size. Asterisked numbers represent sample size. CEOB, *Cecropia obtusifolia;* CLHI, *Clidemia hirta;* MAMA, *Macaranga mappa;* MESE, *Melastoma septemnervium;* MEPO, *Metrosideros polymorpha;* MYLE, *Myrsine lessertiana;* PIAL, *Pipturus albidus;* PSHA, *Psychotria hawaiiensis*.

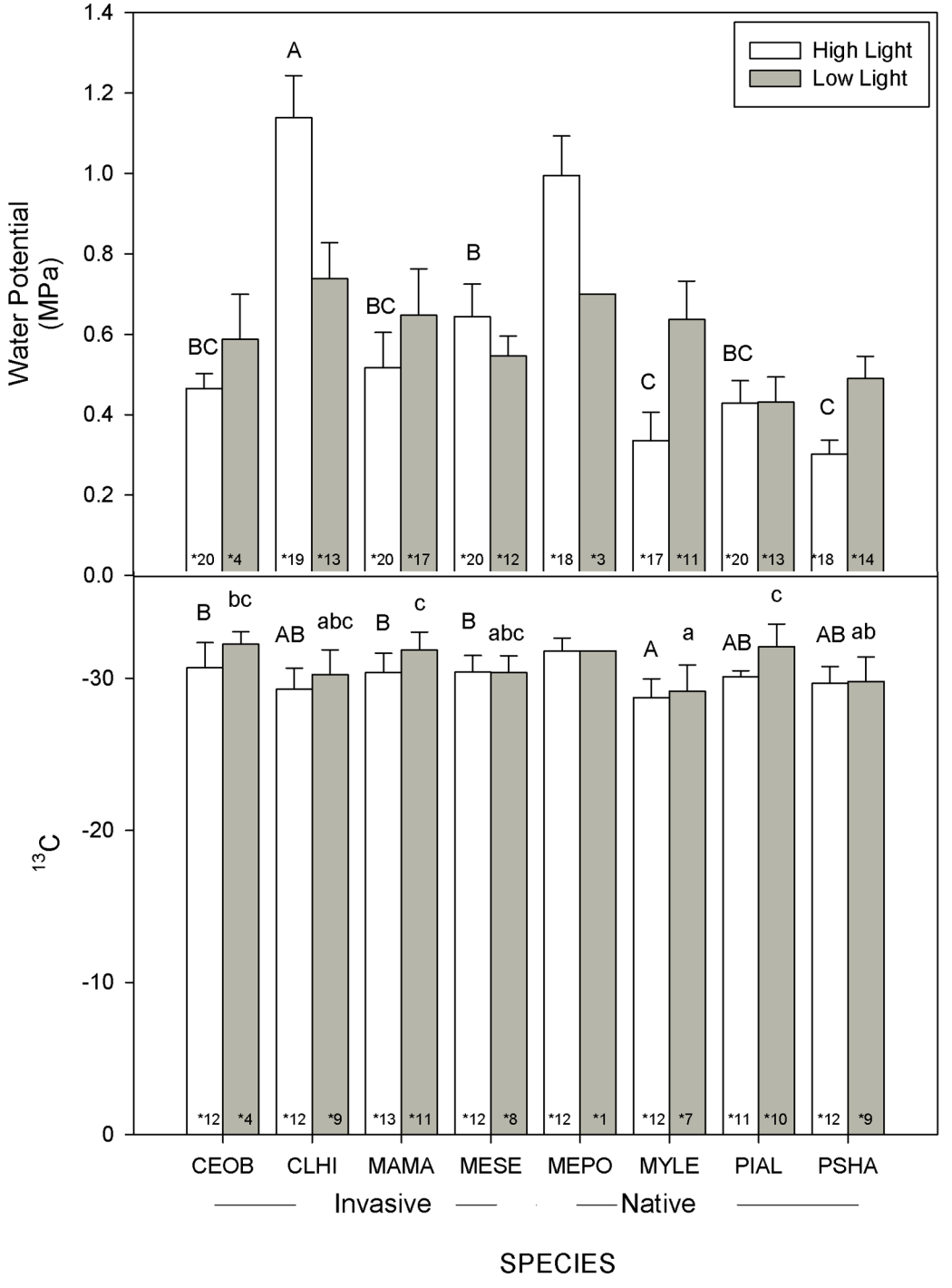

FIGURE 2. Water potential and δ^{13}C values for each species in low-light and high-light treatments. Error bars represent the standard error of the mean. Letters indicate significant differences between species, with upper-case and lower-case letters representing the species differences at high and low light, respectively. *Metrosideros polymorpha* was not included in the statistical analysis due to low sample size. Asterisked numbers represent sample size. CEOB, *Cecropia obtusifolia;* CLHI, *Clidemia hirta;* MAMA, *Macaranga mappa;* MESE, *Melastoma septemnervium;* MEPO, *Metrosideros polymorpha;* MYLE, *Myrsine lessertiana;* PIAL, *Pipturus albidus;* PSHA, *Psychotria hawaiiensis*.

TABLE 2

Species Percentage Survival by Greenhouse Treatment

Species	High Light		Low Light	
	High Water	Low Water	High Water	Low Water
Nonnative				
Cecropia obtustifolia	100%	100%	100%	100%
Clidemia hirta	100%	60%	100%	60%
Macaranga mappa	100%	100%	100%	90%
Melastoma septemnervium	100%	100%	90%	80%
Native				
Metrosideros polymorpha	90%	100%	40%	20%
Myrsine lessertiana	100%	100%	100%	100%
Pipturus albidus	100%	100%	60%	60%
Psychotria hawaiiensis	80%	100%	100%	80%

Contrasts between the greenhouse and outplants in the field offer insights into the applicability of our approach. Although mortality was always greater in the field, survival trends in low-light versus high-light conditions in the greenhouse and the field were similar (Figure 5). Both *Myrsine* and *Psychotria* had >75% survival in the field, suggesting their appropriateness for use in restoration treatments.

The principal components analysis (PCA) for high-light and low-light environments showed separation among species, but neither case presented clear separation between the native and invasive species. PCA results corroborated univariate analysis showing that variables related to light use and mortality were more important in separating species than water use variables. Under low-light conditions, PCA 1 was negatively associated with A_{max} and mortality, and positively associated with relative growth rate and %N; PCA 2 was mainly associated with $\delta^{13}C$ (Figure 6, Appendix). Under high-light conditions, PCA 1 was positively correlated with traits related to photosynthesis (A_{max}, %N, and light saturation point) and negatively associated with water potential. PCA 2 was positively associated with growth traits (relative growth rate, leaf mass per area) and negatively associated with water-use traits (water potential, $\delta^{13}C$) (Figure 6, Appendix).

Based on the trait results we categorized the potential of each native species for planting into lowland wet forests (Table 3). *Psychotria* has the highest probability of success due to its shade tolerance and plasticity to cope with both low-light and high-light conditions. *Metrosideros* was the worst-performing species due to poor growth and survival under low light, and limited plasticity.

DISCUSSION

The motivation for this study was to understand physiological, growth, and fitness traits relating to resource availability to develop tools for evaluating forest management and restoration strategies. Most of the literature takes a comparative approach between natives and nonnative invaders and generally concludes that: (1) invasive nonnative species have higher values of performance-related traits than native species (see meta–analysis by van Kleunen et al. 2010), and (2) in trait comparisons, successful invaders tend to fall into the fast-growth end of the global multi-leaf trait leaf economic spectrum (Leishman et al. 2007, van Kleunen et al. 2010). Other studies have concluded that fitness-related traits such as reproductive output are also associated with invasiveness (Daehler 2003, Pyšek and Richardson 2007, Mason et al. 2008). However, the pattern is

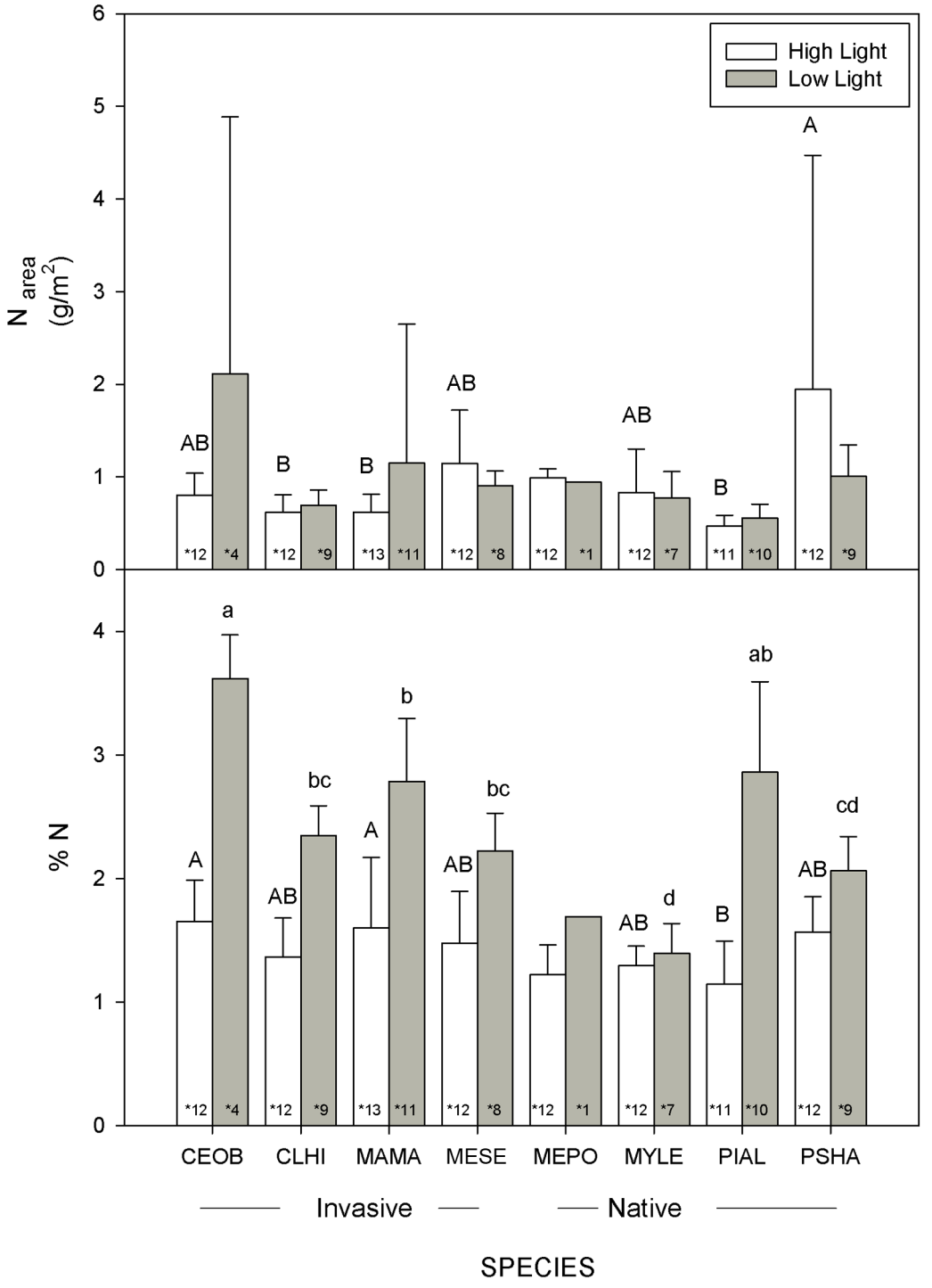

FIGURE 3. Foliar nitrogen per area (gN m^{-2}) and mass (%N or gN g^{-1}) values for each species in low-light and high-light treatments. Error bars represent the standard error of the mean, and letters indicate significant differences between species. *Metrosideros polymorpha* was not included in the statistical analysis due to low sample size. Asterisked numbers represent sample size. CEOB, *Cecropia obtusifolia;* CLHI, *Clidemia hirta;* MAMA, *Macaranga mappa;* MESE, *Melastoma septemnervium;* MEPO, *Metrosideros polymorpha;* MYLE, *Myrsine lessertiana;* PIAL, *Pipturus albidus;* PSHA, *Psychotria hawaiiensis*.

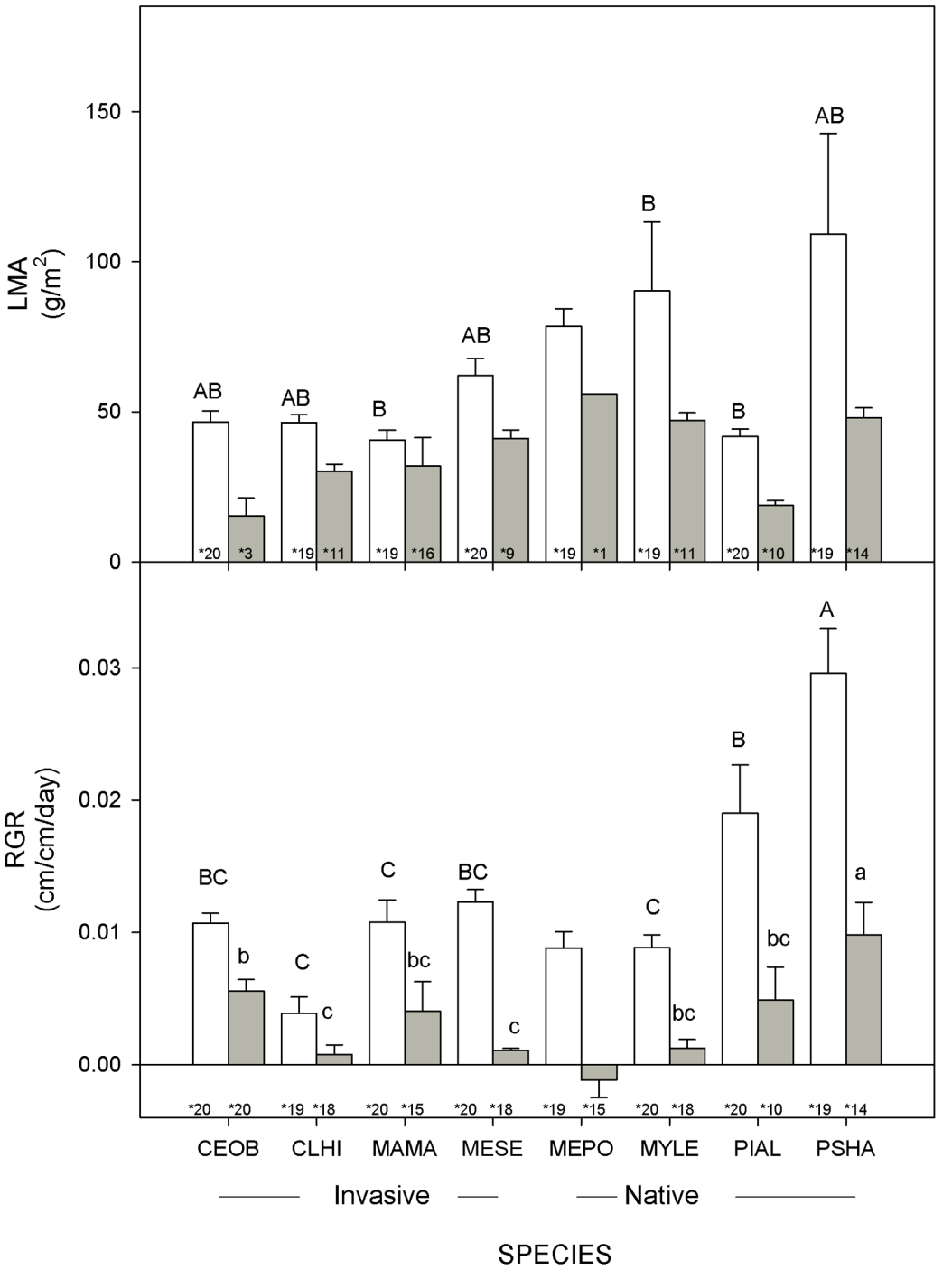

Figure 4. Leaf mass per area (LMA) and relative growth rate (RGR) values for each species in low-light and high-light treatments. Error bars represent the standard error of the mean, and letters indicate significant differences between species. *Metrosideros polymorpha* was not included in the statistical analysis due to low sample size. Asterisked numbers represent sample size. CEOB, *Cecropia obtusifolia;* CLHI, *Clidemia hirta;* MAMA, *Macaranga mappa;* MESE, *Melastoma septemnervium;* MEPO, *Metrosideros polymorpha;* MYLE, *Myrsine lessertiana;* PIAL, *Pipturus albidus;* PSHA, *Psychotria hawaiiensis*.

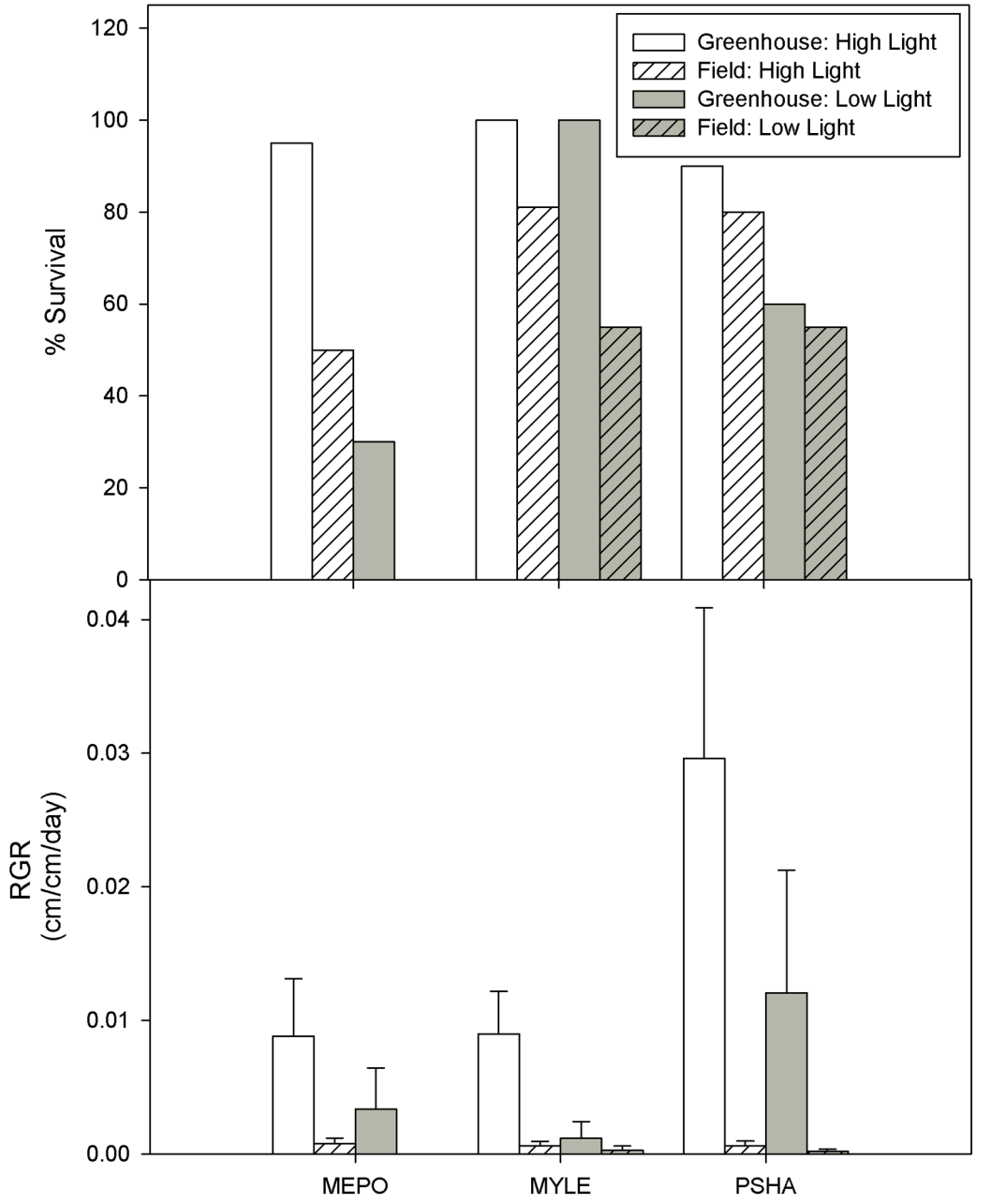

FIGURE 5. Comparison of percentage survival and relative growth rate (RGR) values in the greenhouse and outplanted in the field for the three native species in low-light and high-light treatments. Error bars represent the standard error of the mean. MEPO, *Metrosideros polymorpha;* MYLE, *Myrsine lessertiana;* PSHA, *Psychotria hawaiiensis*.

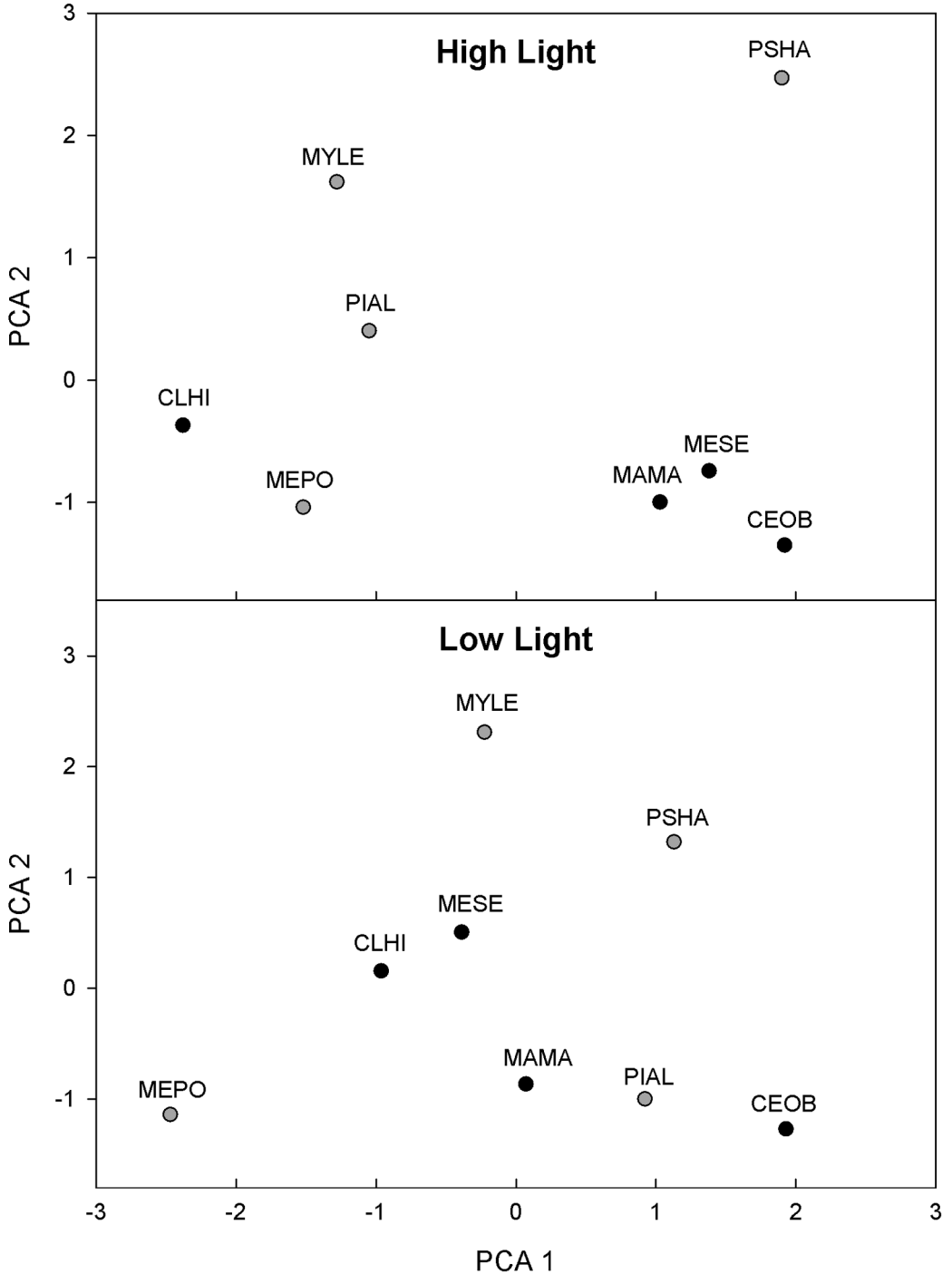

FIGURE 6. Principal components analysis of the eight species under the low-light and high-light treatments. Native species shown in gray and nonnative species in black. Under high-light conditions, PCA 1 explained 37.4% of the variation and PCA 2 explained 24.0%. Under low light, the first and second axes explained 37.4% and 34.4% of the variation, respectively. For factor loadings, see Appendix. CEOB, *Cecropia obtusifolia;* CLHI, *Clidemia hirta;* MAMA, *Macaranga mappa;* MESE, *Melastoma septemnervium;* MEPO, *Metrosideros polymorpha;* MYLE, *Myrsine lessertiana;* PIAL, *Pipturus albidus;* PSHA, *Psychotria hawaiiensis*.

TABLE 3

A Qualitative Assessment of Restoration Potential of the Four Native Species Used in This Experiment

Native Species	Survival	Plasticity	Growth
Metrosideros polymorpha	–	–	–
Myrsine lessertiana	++	+	+
Pipturus albidus	+	+	+
Psychotria hawaiiensis	++	+	++

Note: Plus and minuses refer to how well a species can perform under low light (approx. 1%), the predominant condition of invaded Hawaiian lowland wet forests. Survival is based on species persistence (ranging from 0 to100%), plasticity refers to flexibility in leaf traits under high versus low light (rank scale based on plasticity indices, ranging from 4.8% to 21.2%), and growth refers to the rate of increase in height (ranging from –0.0015 to 0.0350 $cm \cdot cm^{-1} \cdot day^{-1}$).

not always consistent and it is often unclear which traits confer invasiveness and which traits are merely correlated.

We focused on light and water for several reasons. In most tropical forests light is the greatest limiting resource, and thus many tropical species have evolved traits to either maximize growth in low-light environments or possess life history strategies to quickly take advantage of resources when they are not limiting (i.e., gap disturbance) (Denslow 1987, Clark and Clark 1992, Montgomery and Chazdon 1996, Denslow et al. 1998, Poorter 2002). In Hawaiian lowland wet forests, light availability is often up to five times higher than in most continental tropical forests (Pearcy 1983, McDaniel and Ostertag 2010). The percentage of light reaching the rain-forest floor in Hawai'i has been reported as between 1.9% and 10% (McDaniel and Ostertag 2010), in contrast to continental tropical forests in Central and South America, where this value is closer to 1%–2% (Chazdon and Fetcher 1984, Chazdon et al. 1988, Montgomery and Chazdon 2001) or less than 0.5% in Queensland, Australia (Björkman and Ludlow 1972). Consequently, Hawaiian native forest species may be less likely than other tropical species to have evolved competitive light acquisition strategies or plasticity. This puts them at a competitive disadvantage and may be one reason for the invasibility of Hawai'i's forests (Denslow and DeWalt 2008, Ostertag et al. 2009).

Although water is not usually considered to be a limiting factor in the humid tropics, the adverse effects of drought have been documented in several wet tropical forests (Engelbrecht et al. 2005, Engelbrecht et al. 2006, Newbery and Lingenfelder 2009). Monitoring of invaded plots at the KMR site has documented occasional episodes of reduced soil water potential during months of below-average rainfall (J.D.M., unpubl. data). Although the results of the greenhouse experiment clearly demonstrated that light was a more important resource than water for common Hawaiian lowland wet forest species, drought situations may exacerbate mortality of native seedlings in low-light environments.

Despite existing evidence that invasive species are able to outcompete natives in resource-rich environments (Burns 2004, Rickey and Anderson 2004, Funk and Vitousek 2007), our study did not assess the effects of nutrient limitation on plant growth or survival. Previous research at our KMR plots has shown that there are no significant differences in soil nutrients between control (invaded) and removal (noninvaded) plots (Ostertag et al. 2009). Although invasion has been documented to alter nutrient cycling in Hawaiian lowland wet forests (Mascaro et al. 2012), our study focused on limitation rather than alteration, and at this young and nutrient-limited site, it does not appear that nutrients are a more limiting resource than light or water.

We reasoned that remaining native species in invaded environments likely possess traits that confer fitness or adaptations to limiting light resources. Of the four native species evaluated in this study, *Psychotria* and *Myrsine* are suitable species choices for invaded Hawaiian lowland wet forest sites with little management. Based on its survival, plasticity, and growth, *Psychotria* is arguably the most versatile species (Table 3). Its high growth rate, persistence in the shade, and adaptability to changing light environments are likely linked to its relative commonness in lowland wet forests (relative abundance of nearly 11% [Zimmerman et al. 2008]) and its ability

to successfully regenerate in invaded, management-free forests (Mascaro 2011). *Myrsine*, despite being less common in the field than *Metrosideros* and *Psychotria* (relative abundance of under 1% [Mascaro et al. 2008, Zimmermann et al. 2008]), persists in heavily invaded lowland wet forests and had the overall highest survival in high-light and low-light environments. Given this high survival rate it may be that other factors are influencing its abundance in the field. This species is not often seen in a flowering or fruiting stage in lowland wet forests (J.R.S., pers. obs.).

Pipturus was examined because of its traits on the pioneer end of the spectrum (Buck 1982), and, although not as successful as *Psychotria* or *Myrsine*, it is capable of survival, growth, and trait plasticity in the low-light environment we tested. It may have been more prevalent in lowland wet forests in the past; it was the only native species represented in the seed bank in a previous lowland wet forest study (Cordell et al. 2009). We suggest that further testing should be done to determine if it is outcompeted by *Clidemia*, a shrub with similar morphology that is able to capture and utilize light in low-light environments in spite of its drought intolerance (Smith 1992, Baruch 2000). Although *Pipturus* is not as likely to be a successful species for restoration in invaded Hawaiian lowland wet forests, it could be a species of choice for restoration projects with ongoing management and accompanying higher light levels.

Despite its high relative abundance (over 40% [Zimmerman et al. 2008]) and its high photosynthetic performance under high-light conditions, *Metrosideros* is the least likely to survive and thrive in restoration projects, particularly under low-light and low-water conditions. This is consistent with its observed lack of regeneration in invaded forests and its very slow growth rates (Drake 1998, Cordell et al. 2009, Ostertag et al. 2009). However, this species has other typical pioneer traits such as a high seed output, high germination rates under high-light conditions (Drake 1998), and adaptation to nutrient-poor, rocky soils. We do not recommend this species for planting unless light levels are high and invasive species are actively managed, two situations uncommon in Hawaiian lowland wet forests. Although planting is unlikely to yield successful results, this species may colonize on its own in situations where light levels are high and seed sources are nearby (Cordell et al. 2009).

It should be noted, however, that our study neglected traits related to dispersal. For example, propagule pressure might be quite important in lowland wet forest systems due to proximity to habitation and other disturbances. The effects of propagule pressure may be magnified in cases where species also have vegetative reproduction (*Melastoma*, *Psidium*). Propagule pressure has been shown to overwhelm biotic resistance of native communities in some studies (Von Holle and Simberloff 2005, Eschtruth and Battles 2009; but see Catford et al. 2011, Nuñez et al. 2011, Roura-Pascual et al. 2011). Further study of the role and importance of propagule pressure in driving invasion in lowland wet forests in Hawai‘i is warranted.

We demonstrated that a trait-based approach can delineate species traits that confer success in an invaded environment. Although we do not know each species' initial pathway to successful establishment, the greenhouse and planting experiments clarified observed field patterns of abundance and lack of regeneration of native species. Based on our results, we can emphasize the utility of assessing species traits when considering restoration strategies. This information will be useful in selecting species with a higher probability of success for restoration of Hawaiian lowland wet forests.

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Appendix

Factor Loadings from Principal Components Analysis for High-Light and Low-Light Treatments

Variable	PC 1	PC 2
High light		
A_{max}	0.533	–0.054
Light saturation point	0.472	–0.317
Water potential	–0.345	–0.390
Relative growth rate	0.265	0.500
%N	0.477	–0.104
$\delta^{13}C$	0.110	–0.480
Mortality	–0.237	0.124
Leaf mass per area	0.089	0.488
Low light		
A_{max}	–0.51	–0.232
Relative growth rate	0.517	0.077
%N	0.488	–0.518
$\delta^{13}C$	0.095	–0.742
Mortality	–0.475	–0.348