ARE SYMBIOTIC NITROGEN FIXATION STRATEGIES TIED TO INVASIVENESS FOR NON-NATIVE WOODY LEGUMES IN HAWAI‘I?

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAI‘I AT HILO IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

TROPICAL CONSERVATION BIOLOGY & ENVIRONMENTAL SCIENCE

MAY 2020

By

Angalee S. Kirby

Thesis Committee:

Rebecca Ostertag
Jennifer Funk
Jonathan Price

Keywords: isotopic tracer, HPWRA, obligate strategy, facultative strategy, N-fixation regulation

Acknowledgments

This research was funded in large part by the National Science Foundation award number DEB-1457650 awarded to Jennifer Funk of Chapman University, California, USA. Additional funding was provided by Rebecca Ostertag. Laboratory tests were conducted by the University of California Davis Stable Isotope Facility, California, USA. Laboratory support and instruction were provided by the University of Hawaiʻi at Hilo Analytical Lab, Hawaiʻi, USA, which is supported in part by the National Science Foundation award number EPS-0903833. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

Throughout the course of this research I received assistance from many individuals, including my graduate committee Rebecca Ostertag, Jennifer Funk, and Jonathan Price. Further assistance was provided by Molly Murphy with the Big Island Invasive Species Committee, Chuck Chimera with the Hawaiʻi Invasive Species Council, Joanna Norton, Aileen Yeh, and Elizabeth Stacy. I am grateful to each of these groups and individuals for their contributions to this research.

Abstract

A diversity of strategies is used by symbiotic nitrogen-fixing plants, each well suited for specific environmental conditions. Little is known about whether fixation strategies are related to invasiveness when these species are introduced to new environments. Weed risk assessment scores were used as an index for invasiveness for eight non-native N-fixing tree species in Hawaiʻi. In a shade house experiment using an isotopic tracer, I show that these eight species (four high risk and four low risk for invasiveness in Hawaiʻi) varied in their growth, allocation, and N-fixing traits, in response to three levels of nitrogen fertilization and could be grouped into three distinct fixation strategies: one obligate, four facultative, and three over-regulating facultative. Strategies are associated with the trait plasticity of each species, but do not appear related to risk assessments for invasiveness in Hawaiʻi. Over-regulating facultative fixers had the highest trait plasticity and were able to regulate symbiotic nitrogen fixation with the greatest magnitude, while the obligate fixer had low trait plasticity and did not regulate fixation. This implies that species identity is a more likely predictor of N fixation strategy, and thus how a species will respond to varying nutrient conditions, than weed risk assessment scores.

Table of contents

List of tables

List of figures

Introduction

Nitrogen (N) is often the limiting factor for primary production in terrestrial ecosystems (Vitousek et al. 2002). The atmosphere contains an abundant pool of stable gas dinitrogen (N_2), a form that is not biologically useful (Sprent and Sprent 1990; Vitousek 1990). Atmospheric N becomes available for biological processes once it has been reduced to ammonia (NH_3) (Mylona et al. 1995), a process that demands a significant amount of energy (Sprent and Sprent 1990; Vitousek et al. 2002). Some soil bacteria, through symbioses with certain plants' roots (Mylona et al. 1995) provide one of the most efficient systems for reducing, or fixing, atmospheric N needed in the biosphere.

Symbiotic N-fixing systems between bacteria and plants have been studied in depth and the basic components are well understood. N-fixing soil bacteria infect the roots of compatible plants to create a N-fixing site, generally nodules. The plant and bacteria cooperate to reduce (fix) N gas from the atmosphere into biologically useful compounds for the plant. The relationship between N-fixing bacteria and host plants is mutualistic in nature: bacteria provide reduced N for the plant; the plant provides reduced carbon (C) and other metabolic elements for bacteria (Udvardi and Poole 2013). This is costly for the plant, but having access to fixed N results in a strong competitive advantage under conditions of low soil N availability (Houlton et al. 2008; Udvardi and Poole 2013).

Some plants can regulate the amount of N derived from fixation depending on what is available in the soil and what the plant needs. Fundamentally, symbiotic N-fixing plant species use either an obligate or facultative fixation strategy, resulting in different amounts and rates of N fixation (Hartwig 1998; Hedin et al. 2009; Menge et al. 2009; Menge and Hedin 2009; Barron et al. 2011; Drake 2011; Batterman et al. 2013). Obligate fixation occurs at a constant rate per plant biomass unit, independent of the amount of available soil N; whereas facultative fixation adjusts the rate per plant biomass unit with changes in the amount of available soil N to meet the plant's needs (Hartwig 1998; Hedin et al. 2009; Menge et al. 2009). In this respect, obligate fixers devote energy and resources to fixing atmospheric N, where facultative fixers that regulate fixation are able to allocate energy and resources to growth if there is adequate available N in the soil (Pearson and Vitousek 2001; Houlton et al. 2008; Menge et al. 2015), a trade-off that may result in a competitive advantage for facultative N-fixers.

Invasive plant species are non-native species that naturalize and increase rapidly outside their home range (Richardson et al. 2000; Daehler 2003). Invasives have been observed having greater physiological performance, increased growth rates, greater leaf areas, and higher fitness compared to non-invasive alien species (van Kleunen et al. 2010), and lower construction costs (Daehler 2003) compared to natives. These traits allow invasive plants to outcompete natives and non-invasive species, particularly in areas with high resource availability (e.g., disturbed environments) (Davis et al. 2000).

Trait plasticity is another important characteristic of invasive plant species. Plasticity gives a species the ability to adapt to a variety of environmental conditions while maintaining or increasing fitness, a characteristic that allows a species to colonize and invade ecosystems outside their native ranges. Meta-analyses have concluded that invasive plant species have higher trait plasticity than non-invasive plant species (Richards et al. 2006; Davidson et al. 2011). Even in low nutrient environments, invasives demonstrate higher trait plasticity than natives that evolved in those conditions (Funk 2008).

Many studies have attempted to identify the mechanisms for invasiveness, focusing on differences and plasticity in traits contributing to physiology, growth rates, and allocation of resources (van Kleunen et al. 2010). Studies have tied the ability to fix N with invasion (Castro-Díez et al. 2014), but these studies typically focus on plants that are known to be aggressive invaders. There are many non-native N-fixers that do not become invasive. It is possible that invasive N-fixers have more efficient fixation strategies than non-invasive N-fixers. If fixation is well regulated (i.e., facultative strategy), N-fixers can limit their investment in N fixation and allocate more resources to growth. It is possible that the strategy used for N fixation rather than the ability to fix N explains the differential success of invasive N-fixing species. If so, exploring fixation strategies among invasive and non-invasive plant species is an important step to understanding invasion and forest dynamics. The relationship between N-fixation strategy and invasibility has yet to be thoroughly investigated.

Invading N-fixers have the potential to disrupt ecosystem processes (Vitousek 1990), and many invasive plant species are symbiotic N-fixers (Daehler 2003, Castro-Díez et al. 2014). Invasives can assist other non-native plant species to successfully invade (Hughes et al. 2014; August-Schmidt et al. 2015), often with devastating consequences for native forests and ecosystems. By contributing more biologically available N to soils (Vitousek et al. 1987), altering forest structure and the amount and quality of litter (Hughes and Denslow 2005), and contributing to elevated enzyme activities in soils (Allison et al. 2006), positive feedbacks between N-fixers and biogeochemical processes can alter outcomes for developing and existing ecosystems.

In Hawaiʻi, N-fixing invasive plants have been shown to transform ecosystems (Vitousek et al. 1987; Allison et al. 2006). For example, the invasive symbiotic N-fixing tree *Morella faya* has altered forest development on young volcanic substrate by increasing inputs of biologically available N with substantial impacts on N cycling in these N-limited habitats where no native symbiotic nitrogen fixers are present (Vitousek et al. 1987). Other studies have shown increases in forest gas emission (nitrous oxide, a harmful greenhouse gas) after successful invasion of *M. faya* into native forest habitats (Hall and Asner 2007). Increased quality and quantity of litterfall are a result of invasion by a N-fixing canopy tree, *Falcataria moluccana*, another aggressive invader. In lowland forest areas on young volcanic substrates invasion by *F. moluccana* corresponds to changes in soil microbial community composition and elevated production rates of soil enzymes, increasing nutrient cycling rates (Allison et al. 2006).

Hawaiʻi has been subject to plant invasion for roughly two and a half centuries. Prior to human inundation, the islands' flora included approximately two thousand seven hundred native plant species (Negata 1985). The Polynesian settlers that arrived first to the islands brought approximately thirty plant species with them (Nagata 1985). It wasn't until the late 18th century, when European settlers arrived, that a majority of plant introductions began (Negata 1985). Since then, over five thousand plant species have been introduced to Hawaiʻi (Negata 1985). Over a thousand plants that have been introduced to the islands have naturalized (Wagner et al. 1999), which is close to half the plants on the islands (Simberloff 2013). This is not surprising given the level of isolation the island chain is under, which has allowed the evolution of endemic species suited to specific environments and poorly adapted to frequent environmental disturbance that recent humans have invoked (Vitousek et al. 1987). Hawaiʻi lacks and is in need of regulations and enforcement to prevent alien plants from being introduced (Plant Industry Division 2017), including improved risk assessment based on traits.

Hawai‘i has adopted a risk assessment system based on the Australian and New Zealand Weed Risk Assessment system (Daehler et al. 2004) called the Hawai‘i Pacific Weed Risk Assessment (HPWRA, https://sites.google.com/site/weedriskassessment/home). To date, 2,069 species have been evaluated using this system. The assessment renders a numeric risk score that considers factors such as species history of invasiveness outside its native range, favorable environmental conditions in the new location, life history events such as persistence, reproduction and dispersal, as well as the ability to fix N (Daehler et al. 2004). Plant scores range from -12 to 28. Plants are evaluated as either High Risk (HR, generally scores >6), Low Risk (LR, generally scores ≤6), or Evaluate (E, generally scores close to 6). However, the assessment for N fixation is simply a question of whether or not the plant can fix N and does not consider the strategy used for N fixation which, as hypothesized above, may differentiate invasive and non-invasive N-fixers. Thus, N-fixation strategy may correlate with the level of risk the plant poses on a new environment. Little, if any, research has been dedicated to determining N-fixation strategies for either HR or LR plants. Filling this gap in research may contribute to a more informative assessment system for plants being introduced to Hawai‘i.

My research seeks to answer the following questions: Do growth rates, allocation traits, and N-fixation traits vary among non-native N-fixing woody plant species that have a range of assessment scores using the HPWRA? To what extent do growth rates, allocation traits, and N fixation traits change with N addition? Can N-fixation strategies be detected? Are the strategies correlated with HPWRA scores? Do species groupings in trait space reflect N-fixation strategies? To guide this study, I used the modeling approach developed by Menge et al. (2015) to identify fixation strategies. I conducted a shade house experiment examining eight N-fixing species with a range of HPWRA scores (-2 to 14) under low, medium, and high N conditions using an isotopic N tracer to assess N fixation. I expected that HR species would have greater growth rates than LR risk species. I further hypothesized that HR species would have decreased N fixation rates and nodule density with N addition, evidence that would support a facultative strategy. I also hypothesized that LR species would have little or no change in N-fixing rates, slightly increased growth, and little or no change in nodule density with N addition, evidence that would support an obligate strategy. Because trait plasticity is characteristic of invasive species, I hypothesized that HR species would have greater trait plasticity than LR species. Thus, I expected a positive association between facultative fixation and trait plasticity across species.

Methods

In order to determine the strategy of N fixation in plant species, several aspects of the plant need to be assessed: growth rates under varying nutrient conditions, biomass N, biomass allocation, and the percent of N derived from fixation (%N_{dfa}) (Menge et al. 2015). Greenhouse studies allow for environmental factors, such as temperature, light, and precipitation, to remain constant. With these factors constant we can isolate N-fixing plants' responses to N availability by providing N-limited and N-saturated conditions while keeping other nutrients constant and in adequate supply. Whether N is derived from the soil or fixed (atmospheric) can be determined by using an isotopic tracer administered through fertilizer treatments followed by isotope ratio mass spectrometry (Burris et al. 1943). Facultative strategy users either downregulate fixation so that N supply meets the N demand of the plant, or regulate so that N supply is greater (under-regulate) or less (over-regulate) than the N demand. Obligate strategy users cannot regulate fixation, and fix at a constant rate relative to biomass regardless of soil N availability.

Experimental Design

In a shade house experiment, eight N-fixing tree species within the family Fabaceae were grown (Table 1), all of which have been evaluated using the HPWRA. One non-fixing reference species from Fabaceae was grown under the same conditions for comparison. Figure 1 demonstrates the distribution of numeric scores for every plant that has been screened using the HPWRA, as well as the distributions of each evaluation level: HR (white), LR (black), and E (gray). The median score is four. Scores and evaluations are derived from the 49 questions on the HPWRA followed by interviews of experts with personal field experience for each plant (Daehler et al. 2004). Four HR and four LR species were selected for experimentation, and a HR non-fixer. Species within the E category were not studied, to avoid confusion. The non-fixing reference species, *Senna siamea* (HR), was grown simultaneously under the same conditions. Data from *S. siamea* were used to calculate % N_{dfa} in fixing plants. A LR non-fixing species was attempted, but due to high mortality was not considered for comparison in analyses. Three levels of N addition were given for each species, beginning with 16 replicates each (12 for *E. variegata*).

Study Species, seed and soil collection, and growing conditions

Study species were N-fixing tropical tree species chosen based on their weed risk assessment scores (Table 1). Hereafter study species will be referred to by abbreviations: *Erythrina variegata* (ERVA), *Sesbania grandiflora* (SEGR), *Pterocarpus indicus* (PTIN), *Samanea saman* (SASA), *Albizia lebbeck* (ALLE), *Falcataria moluccana* (FAMO), *Acacia confusa* (ACCO), and *Pithecellobium dulce* (PIDU). *Senna siamea* (SESI) was the non-fixing species used for comparison.

TABLE 1. Nitrogen-fixing study species (family Fabaceae) chosen based on a range of HPWRA scores. Scores greater than six denote high risk of invasion.

Species	**HPWRA Score**
Low Risk	
Erythrina variegata Lam.	-2
Sesbania grandiflora (L.) Pers.	2
Pterocarpus indicus Willd.	4
Samanea saman (Jacq.) Merr.	4
High Risk	
Albizia lebbeck (L.) Benth.	7
Falcataria moluccana (Miq.) Barneby & J.W. Grimes	8
Acacia confusa Merr.	10
Senna siamea (Lam.) H.S. Irwin & Barneby *	10
Pithecellobium dulce (Roxb.) Benth.	14

*Non-fixing reference species grown at the same time, under the same conditions.

Seeds were collected in the field on Hawai‘i Island, except for ERVA and SEGR which were purchased from online vendors. Seeds (10-60) of each species were dried at 70º C and weighed to run composite samples for % N to quantify % N in the seeds. Seeds (≈100 per species) were scarified in hot water, imbibed for 10-24 hours, and germinated on trays according to the needs of each species. Seedlings were planted in a 1:1:1 mixture of perlite (Pahroc Giant #2, Wilkin Mining & Trucking, Inc. Caliente, NV, USA), vermiculite (#2 coarse, Therm-O-Rock West, Inc. Chandler, AZ, USA), and volcanic cinder (naturally occurring on Hawai‘i Island, sterilized) in 4”x4”x14” sapling pots (Stuewe & Sons, Inc. Tangent, OR, USA). While N content of the soil media was not measured, I assumed that initial levels were quite low.

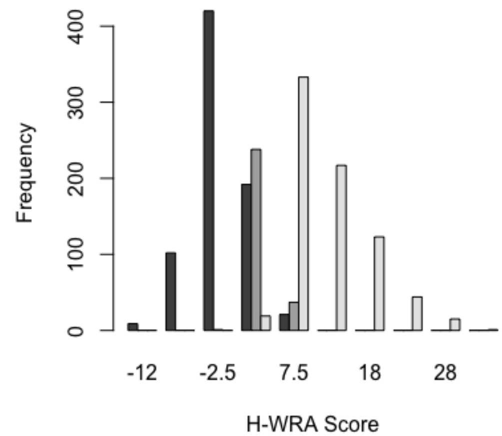


FIGURE 1. Distributions of numeric risk scores for HR plants in white (n=751), LR plants in black (n=744), and E plants in gray (n=276) evaluated using the HPWRA.

Seedlings were inoculated with a small quantity of crushed nodules and rhizosphere soil slurry collected beneath naturally occurring trees for each species (Menge et al. 2015). Soil was collected from near the roots of the mature tree unless seedlings were present, in which case entire seedlings were collected for their root nodules. All seeds, soil, and seedling samples were placed in Ziploc bags, stored in a cooler for transport, then stored in a refrigerator until germination. When possible, seedlings were grown ahead of time for nodule harvest to ensure experimental seedlings were exposed to their proper symbionts (Sprent and Sprent 1990).

Plants were watered adequately with overhead sprinkler irrigation depending on seasonal needs (three to six times daily). Saplings grew for approximately four months after first fertilization treatment. Plants were randomly arranged in three blocks per species and rotated around the shade house by block every two weeks to account for variation in light. All plants were grown between January 2018 and November 2019 in Keaʻau, Hawaiʻi (19.55733º N, -154.97638º W). Average daily temperature was 72.5ºF (22.5ºC). Light measurements were taken at three locations inside and two locations outside the shade house, three times per day, every few weeks. Light inside the shade house averaged 73% of light outside the shade house.

Fertilization

Each plant received a standard Hoagland N-free fertilizer corresponding to 0.252 g P m^{-2} y^{-1} for phosphorus, a level that should make plant growth limited by non-nitrogen soil nutrients at high N levels. Three levels of nitrogen addition were used for each species: 0.3 g N m^{-2} y^{-1}, 6 g N m^{-2} y^{-1}, and 20 g N m^{-2} y^{-1} (low, medium, and high, respectively). Low N addition imitates a N-limited environment similar to young substrates in Hawai'i (Vitousek and Sanford 1986), medium N addition imitates a N non-limited environment similar to old substrates (Vitousek and Sanford 1986), and high N addition imitates a N-saturated environment (Menge et al. 2015). Labelled ^{15}N fertilizer (Cambridge Isotope Labs, Tewksbury, MA, USA) was added with a 7 atom %, making it distinguishable from atmospheric N (0.359-0.377 atom %). Fertilizers were added every other week by micropipette (Menge et al. 2015) beginning when true leaves had emerged and were open.

Growth Measurements

Final growth measurements were taken for each plant. Measurements included: leaf count, height (cm), and stem diameter at base (mm). All components of the plants were harvested after approximately four months of growth (Menge et al. 2015). Leaf area (cm^2) was measured on fresh leaves using a LI 3100 Area Meter (Licor, Inc. Lincoln, NE). Root nodules, roots, stems, and leaves were dried separately at 70ºC and weighed. Because plants were grown for different periods of time (115-132 days), measurements for height, stem diameter, total biomass, nodule biomass, root biomass, stem biomass, leaf biomass, and leaf area were converted to growth rates to account for variation in growth periods ($\text{growth rate} = \frac{\text{biomass measure}}{\text{growth period}} \times 365$). Samples were then pooled (per individual) for % N and ^{15}N analysis. Plant biomass is an indicator of the effects of N-limitation on plant productivity; root nodule mass is a measure of structural allocation to N fixation; % N_{dfa} indicates how much N has been fixed over the lifetime of the plant.

Quantifying Nitrogen Fixation

The percentage of fixed N (% N_{dfa}) was quantified by comparing ^{15}N enrichment in plant tissues to atmospheric N_2, and between study species and reference plants. Non-fixing plant values were used as a baseline for comparison. Plant tissues were ground, and whole plant subsamples were analyzed at the UC Davis Stable Isotope Facility (Davis, CA, USA) using a PDZ Europa ANCA-GSL elemental analyser coupled with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Isotopic values were converted to atom % and standard atmospheric ^{15}N value was subtracted to give atom % excess (AE). Tissue ^{15}N values of individuals were averaged per species and treatment before calculating % N_{dfa} using the following equation (Yelenik et al. 2013):

$$\% N_{dfa} = \frac{^{15}N\ AE_{non\text{-}fixer} - {}^{15}N_{fixer}}{^{15}N\ AE_{non\text{-}fixer}} \times 100$$

Statistics and Analyses

To investigate differences in species means for growth rates, allocation traits, and N-fixation traits, linear models (two-way ANOVAs) were performed on two factors, species and N treatments, followed by Tukey's honest significant difference (HSD) post hoc comparison test. Each reponse variable was analyzed separately for individual species. Main response variables include: biomass growth rate and leaf area growth rate to represent growth; SLA and root-to-shoot ratio to represent resource allocation; and nodule density, % N in tissue, and % N_{dfa} to represent N fixation traits. Height, stem diameter, total biomass, root-to-shoot ratio, and leaf area data were log transformed to achieve normality. Untransformed data are represented in figures. FAMO and SESI are missing data for leaf biomass and are excluded from statistical tests for leaf biomass and SLA.

To determine fixation strategies for each species, biomass N, nodule density, and % N_{dfa} were plotted against N addition treatments for qualitative evaluation. Biomass N for fixers was plotted with biomass N for the non-fixer SESI, whose values were used for soil end members in % N_{dfa} calculations. Strategies were determined based on the shape of the plots compared to suggested models from Menge et al. (2015).

To investigate traits and trait plasticity, a principal components analysis (PCA) was conducted on all response variable means (biomass, height, stem diameter, and leaf area growth rates, root-to-shoot ratio, nodule density, % N in tissue, % N_{dfa}) to explore species grouping in trait space. To investigate if trait plasticity correlated with N-fixation ability, plasticity indices were calculated using the coefficients of variation (Schulten et al. 2014) for several uncorrelated functional traits (biomass, height, stem diameter, leaf area, root-to-shoot ratio, % N in tissue). A second PCA was run and the resulting PC 1 scores were regressed with N-fixation trait means for HN treatment per species. Statistical analyses were performed using RStudio1.2.5033 (RStudio 2015) and PRIMER v6 (Clarke and Gorley 2006).

Results

All growth measurements, allocation traits, and N-fixation traits were found to have statistically significant differences among species (Table 2). ERVA had the highest biomass growth rate (g yr^{-1}), leaf area growth rate (cm^2 yr^{-1}) , and % N_{dfa}. SEGR had the lowest nodule density (mg g^{-1}), % N in tissue, and % N_{dfa}. While SASA had the lowest biomass and leaf area growth rates, it had the highest specific leaf area (SLA, cm^2 g^{-1}), nodule density, % N in tissue, and was among the highest root-to-shoot ratio and % N_{dfa}. ALLE had the lowest SLA and the highest root-to-shoot ratio. ACCO had the lowest root-to-shoot ratio and was among the highest % N_{dfa}. PTIN, FAMO, and PIDU were intermediates among growth, allocation, and N-fixation traits (Figures 2-4). The non-fixing species, SESI, did not nodulate and did not fix any N.

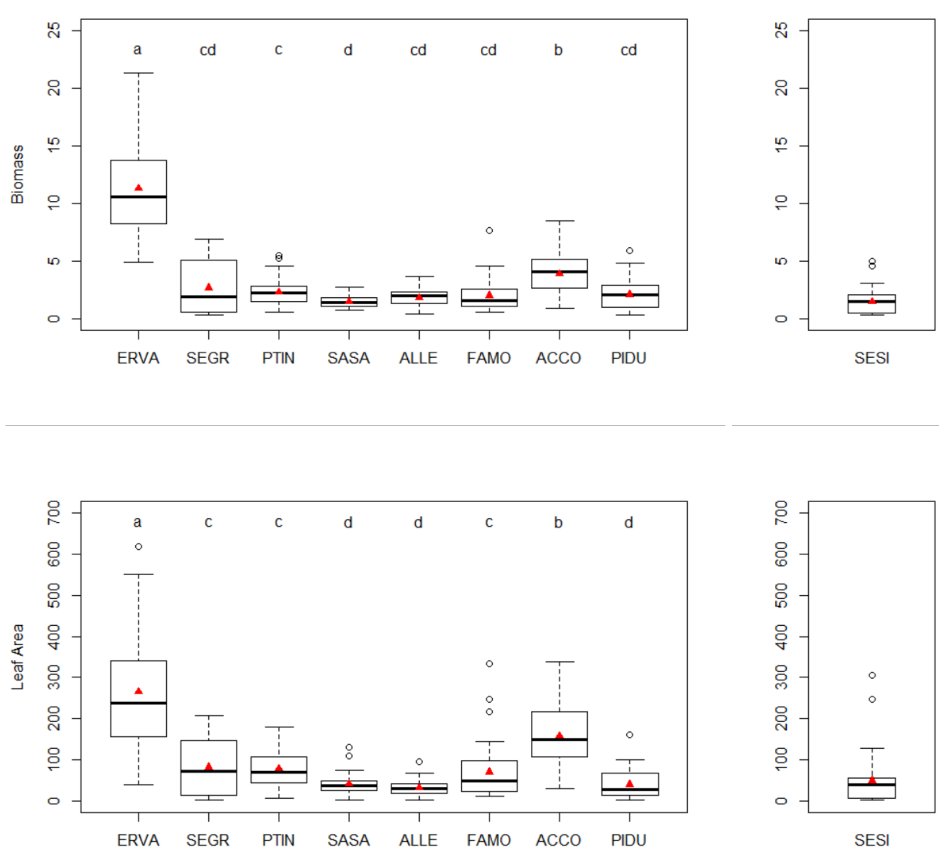


FIGURE 2. Growth rates for each species ordered from left to right by HPWRA score (low to high), separated by N-fixers (left) and non-fixer SESI (right). Biomass is measured in g yr^{-1}, leaf area is measured in cm^2 yr^{-1}. Means are represented by solid red triangles, medians are thick black midlines of each box, edges of boxes show the upper and lower quartiles, whiskers show the highest and lowest values excluding outliers, outliers are represented by black circles, and letters indicate significant differences ($p<0.05$, $\alpha=0.05$) among species.

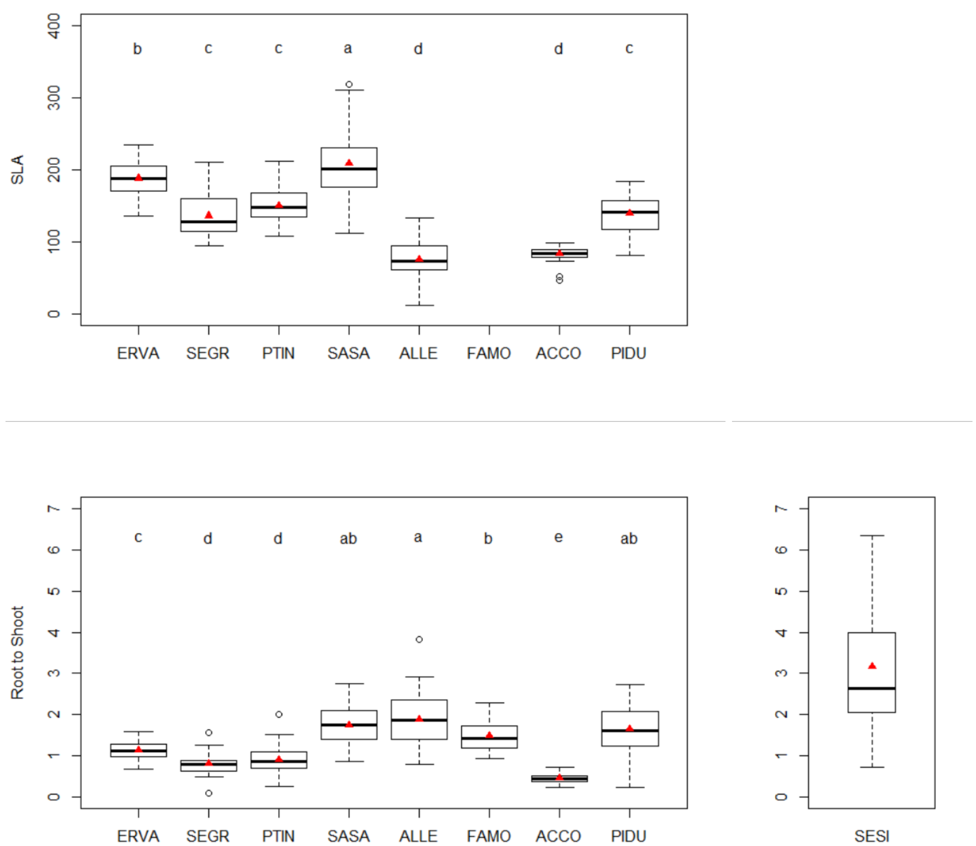


FIGURE 3. Allocation traits for each species ordered from left to right by HPWRA score (low to high), separated by N-fixers (left) and non-fixer SESI (right). Specific leaf area (SLA) is measured in $cm^2 g^{-1}$, root-to-shoot is a biomass ratio. Means are represented by solid red triangles, medians are thick black midlines of each box, edges of boxes show the upper and lower quartiles, whiskers show the highest and lowest values excluding outliers, outliers are represented by black circles, and letters indicate significant differences ($p<0.05$, $\alpha=0.05$) among species. Data are missing for FAMO and SESI for SLA.

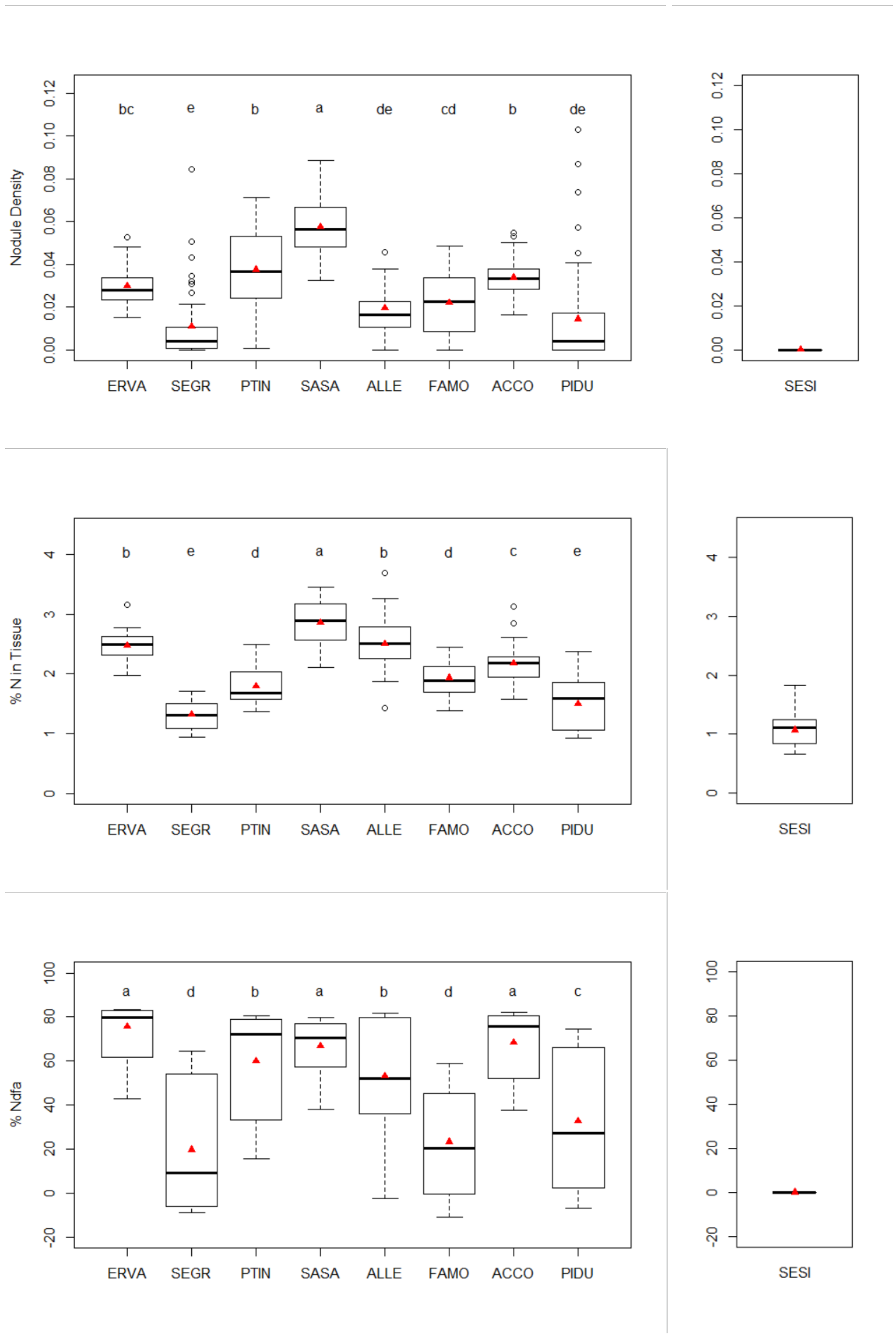


FIGURE 4. N fixation traits for each species ordered from left to right by HPWRA score (low to high), separated by N-fixers (left) and non-fixer SESI (right). Nodule density is represented as g nodules to g biomass, % N in tissue is total N (including N from soil and N from fixation), % N_{dfa} is percent of N derived from fixation. Means are represented by solid red triangles, medians are thick black midlines of each box, edges of boxes show the upper and lower quartiles, whiskers show the highest and lowest values, and letters indicate significant differences ($p<0.05$, $\alpha=0.05$) among species.

Growth measurements, allocation traits and N-fixation traits were affected by N addition treatments as well (Table 2). Statistically significant differences in means for all response variables were found except SLA. No significant difference was found between low and medium treatments for % N in tissue (Figure 5).

TABLE 2. Results of two-way ANOVAs for N-fixers by factors species and N treatment

Variable	Species			N			Species x N		
	P value	F value	Df	P value	F value	Df	P value	F value	Df
Growth rates									
biomass	<0.001	100.131	7	<0.001	74.034	2	<0.001	19.183	14
height	<0.001	118.493	7	<0.001	93.831	2	<0.001	17.136	14
stem diameter	<0.001	437.243	7	<0.001	53.087	2	<0.001	11.533	14
nodule biomass	<0.001	164.854	7	<0.001	7.913	2	<0.001	4.741	14
root biomass	<0.001	140.900	7	<0.001	10.075	2	<0.001	4.123	14
stem biomass	<0.001	166.658	6	<0.001	17.215	2	<0.001	4.768	12
leaf biomass	<0.001	106.041	6	<0.001	32.237	2	<0.001	7.674	12
leaf area	<0.001	65.508	7	<0.001	56.058	2	<0.001	11.312	14
Allocation traits									
SLA	<0.001	138.901	6	0.638	0.449	2	<0.001	2.574	12
root-to-shoot ratio	<0.001	115.691	7	<0.001	18.346	2	0.022	1.935	14
N-fixation traits									
nodule density	<0.001	68.498	7	<0.001	44.129	2	<0.001	3.467	14
% N in tissue	<0.001	90.573	7	<0.001	11.452	2	<0.001	4.344	14
% N_{dfa}	<0.001	199.227	7	<0.001	640.994	2	<0.001	14.307	14

F. moluccana is not included in statistical tests for stem biomass, leaf biomass, or specific leaf area due to missing data. *S. siamea* is a non-fixer and was not included in statistical tests. P-values, F-values, and degrees of freedom given with α=0.05.

Strong evidence for interaction effects of the two factors (species and N treatments) was found for all response variables except root-to-shoot ratio (Table 2). SEGR, FAMO, ACCO, and PIDU had statistically significant increases in means with N addition for biomass and leaf area growth rates, while SASA had statistically significant decreases (Figure 6). SEGR and PIDU had statistically significant differences in means across N treatments for SLA. SEGR had highest mean SLA with medium N addition, while PIDU had lowest mean SLA with medium N addition (Figure 7). ERVA, SEGR, FAMO, and PIDU had statistically significant decreases in means across N treatments for root-to-shoot ratio, although PIDU increased with medium N addition (Figure 7). ERVA, PTIN, ALLE, FAMO, ACCO, and PIDU had statistically significant decreases in means across N treatments for nodule density, although ACCO increased with medium N addition (Figure 8). ERVA, SEGR, SASA, FAMO, and PIDU had statistically significant differences in means across N treatments for % N in tissue, ERVA and SEGR had variable responses while SASA, FAMO, and PIDU increased with N addition (Figure 8). All species had statistically significant decreases in means across N treatments for % N_{dfa} (Figure 8).

Fixation strategies were determined for each species as either facultative, over-regulating facultative, or obligate. SASA was determined to be the only obligate strategy user. Biomass growth rates for SASA decreased with N addition, therefore biomass N (mg N in tissue)

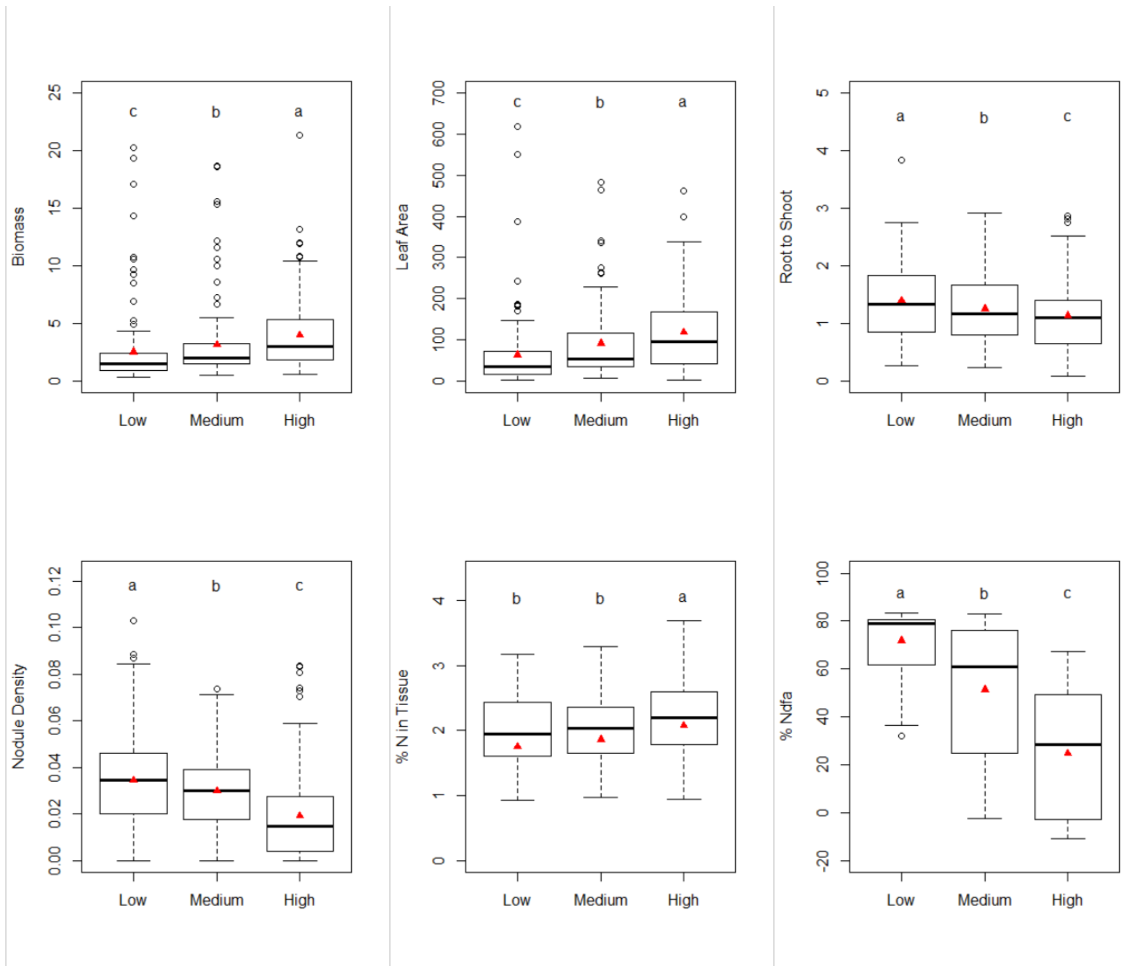
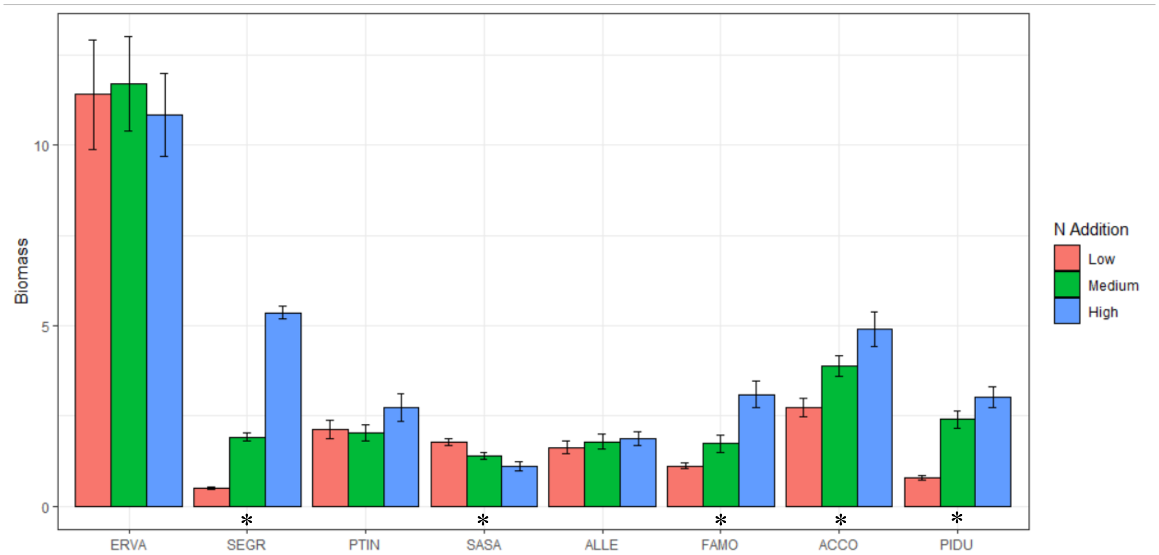


FIGURE 5. Growth measurements, allocation traits, and N fixation traits distributions for N addition treatments that were found to have statistically significant difference in means. Means are represented by solid red triangles, medians are thick black midlines of each box, edges of boxes show the upper and lower quartiles, whiskers show the highest and lowest values excluding outliers, outliers are represented by black circles, and letters indicate significant differences ($p<0.05$, $\alpha=0.05$) between species. No statistically significant differences were found among treatment means for SLA.



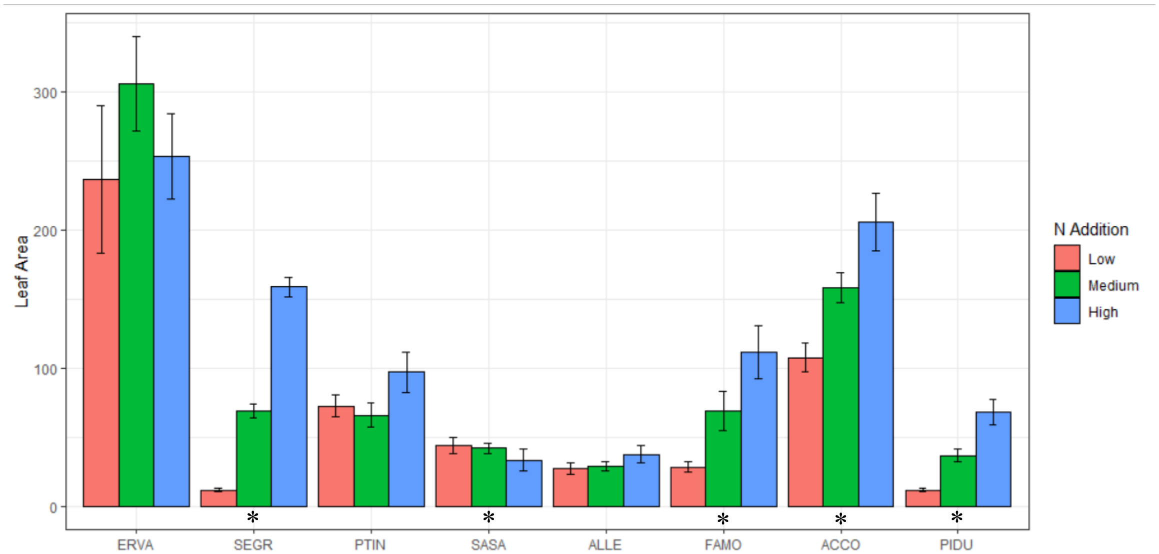


FIGURE 6. The effect of N addition on growth rates among species ordered from left to right by HPWRA score (low to high). SEGR, SASA, FAMO, ACCO, and PIDU had statistically significant differences across N addition for biomass and leaf area growth rates, represented by the asterisk above species names. Bars are means (± 1 SE) of responses to N treatments low (red), medium (green), and high (blue) ($p<0.05$, $\alpha=0.05$).

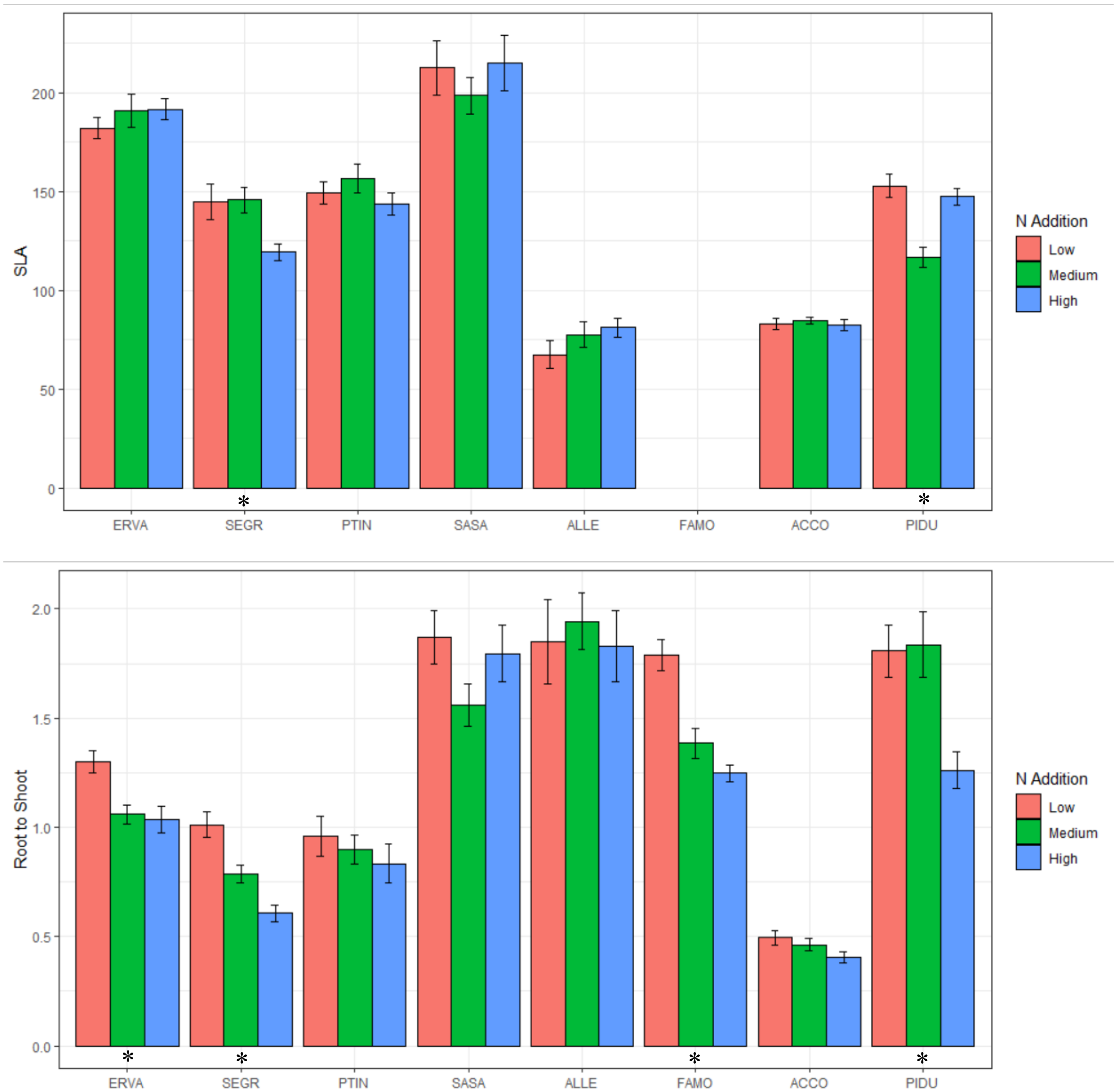


FIGURE 7. The effect of N addition on allocation traits among species ordered from left to right by HPWRA score (low to high). Significant differences in means are represented by an asterisk above species names. SEGR and PIDU had statistically significant differences in means across N treatments for SLA. ERVA, SEGR, FAMO, and PIDU had statistically significant differences ($p<0.05$, $\alpha=0.05$) in means across N treatments for root-to-shoot ratio. Bars are means (± 1 SE) of responses to N treatments low (red), medium (green), and high (blue) ($p<0.05$, $\alpha=0.05$).

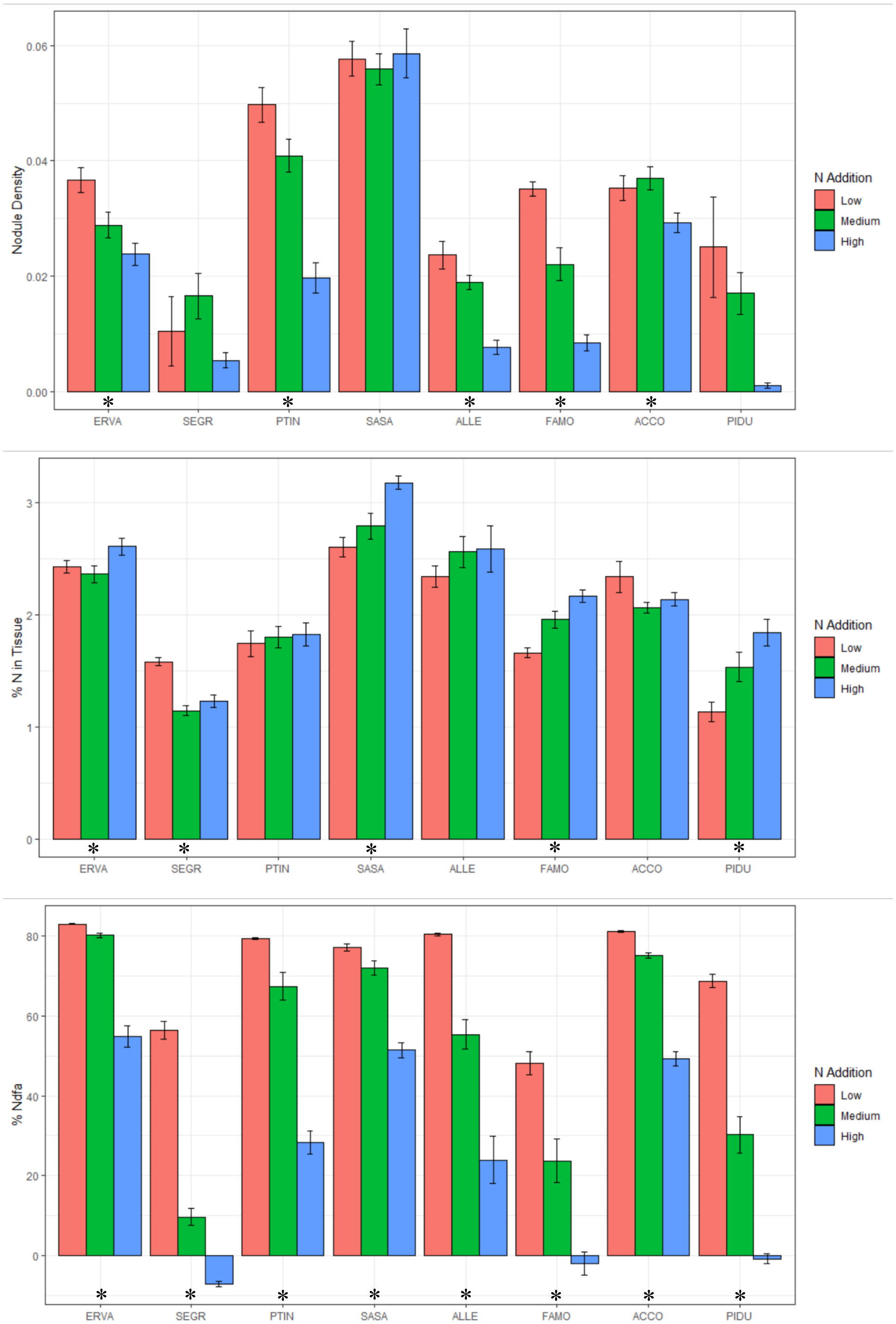


FIGURE 8. The effect of N addition on N fixation traits among species ordered from left to right by HPWRA score (low to high). Significant differences in means are represented by an asterisk above species names. ERVA, PTIN, ALLE, FAMO, ACCO, and PIDU had statistically significant differences in means across N treatments for nodule density. ERVA, SEGR, SASA, FAMO, and PIDU had statistically significant differences in means across N treatments for % N in tissue, and all had statistically significant differences in means across N treatments for % N_{dfa}. Bars are means (± 1 SE) of responses to N treatments low (red), medium (green), and high (blue) ($p<0.05$, $\alpha=0.05$).

decreased as well. However, nodule density remained consistent while % N_{dfa} decreased with N addition (Figure 9). A facultative strategy was determined for each of the other species. With an increase in biomass N across N treatments, the other seven species regulated nodule growth (decreased nodule density) and N fixation (decreased % N_{dfa}) to some extent (Figure 9). SEGR, FAMO, and PIDU regulated fixation with the highest magnitude leaving them N limited at the high N treatment (Figure 9), appearing to be over-regulating.

A PCA on all species traits showed species grouping by growth rates and N-fixation traits. (Figure 10). PC1 was strongly associated with growth (driven by biomass, height, stem diameter, and leaf area growth rates, and root-to-shoot ratio), explaining 49% of the variation among species groups. PC2 was strongly associated with N-fixation traits (driven by nodule density, % N in tissue, and % N_{dfa}), explaining 32% of the variation. Together these two axes explained over 80% of the variation among species groups. SASA had high measures of nodule density, % N in tissue, and % N_{dfa}, across all three N treatments, showing that it had little or no ability to regulate fixation under varying nutrient conditions. SASA was intermediate for growth overall, a potential trade-off for contributing so much energy to fixation. ERVA had the most aggressive growth, but intermediate for N-fixation traits. SEGR, FAMO, and PIDU had low measures of nodule density and % N_{dfa} at the highest N treatment. Growth for these species was low compared to other species, possibly due to N limitation. ERVA, PTIN, ALLE, and ACCO were moderate in their N-fixation traits compared to other species and varied in growth compared to each other.

Regression analyses between trait plasticity and N-fixation traits resulted in a clear association. PC score 1 explained 75.2% of the variation and was used as the plasticity index for each species. An increase in plasticity was associated with an increase in fixation regulation via reduction in nodule biomass (r^2=0.49, $F_{1,6}$=8.69, p>0.05) and reduction in % N_{dfa} (r^2=0.89, $F_{1,6}$=32.19, p>0.01) (Figure 11). SASA had low trait plasticity and did not show any capacity to regulate N fixation. SEGR, FAMO, and PIDU had the most trait plasticity and were able to regulate their N fixation with the greatest magnitude.

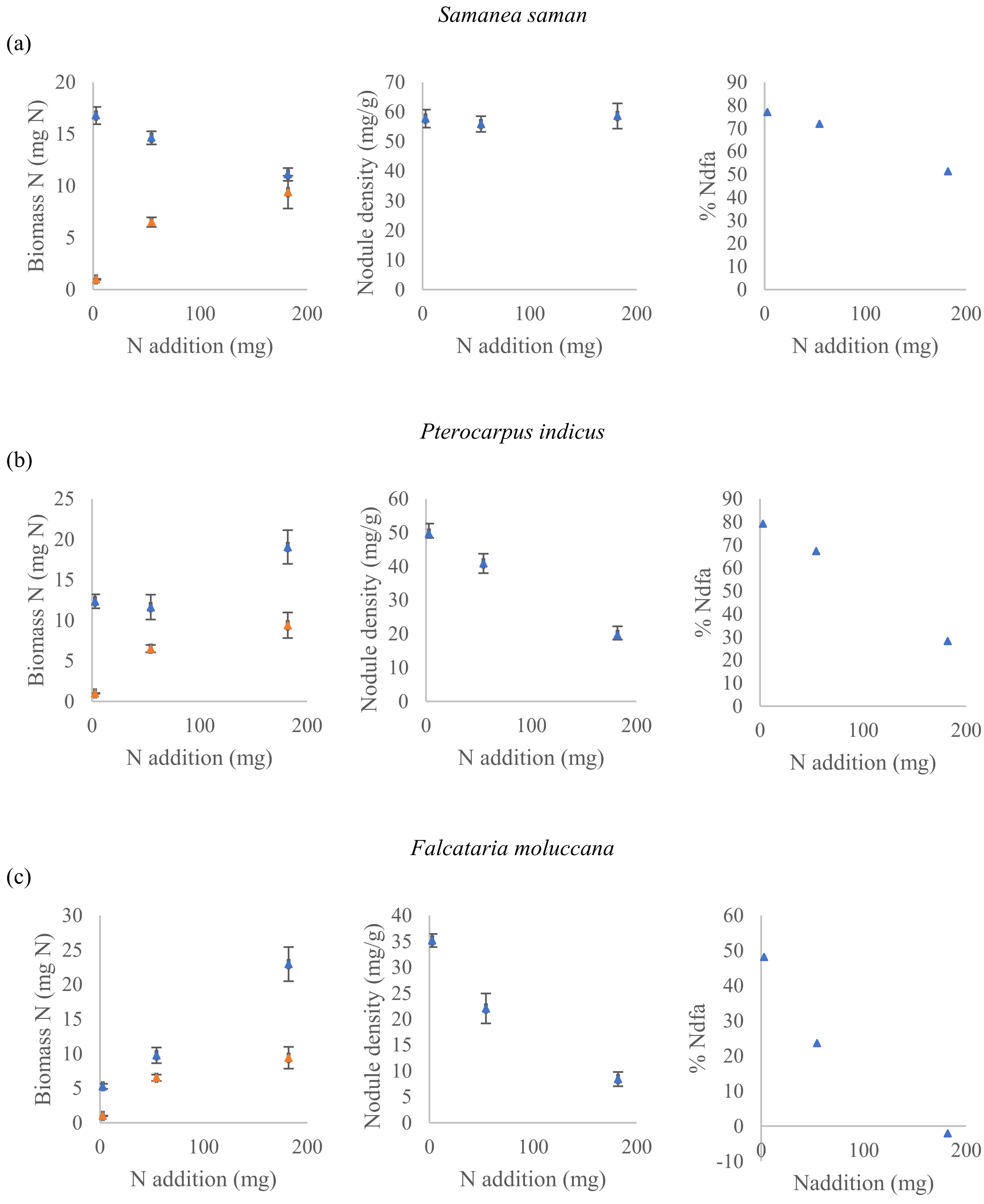


FIGURE 9. N fixation traits plotted against N addition treatments for obligate (a), facultative (b and c), and over-regulation (c). Blue triangles represent means (± 1 SE) for N-fixing species, orange triangles represent means (± 1 SE) for the non-fixer SESI. The obligate fixation strategy was determined for SASA (a), facultative for several other species (b, only PTIN shown here), and facultative over-regulation for SEGR, FAMO, and PIDU (c, only FAMO shown here). Note the difference in scale on y-axes.

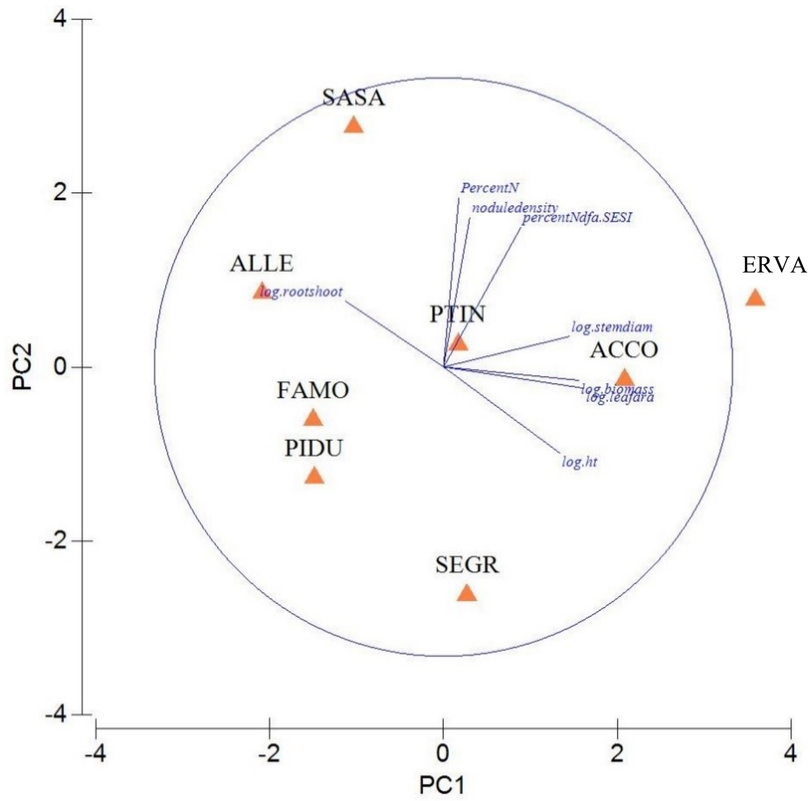
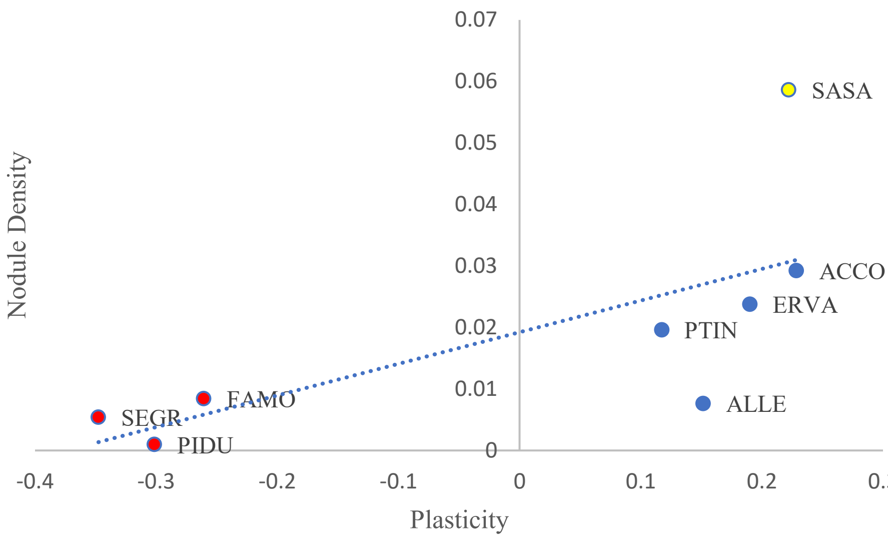


FIGURE 10. Principal components analysis with species means for growth (biomass, height, stem diameter, and leaf area growth rates), allocation (root-to-shoot ratio), and N fixation (nodule density, % N in tissue, and % N_{dfa}). Separation of species along PC1 was driven by growth and allocation traits, PC2 was driven by N-fixation traits.

(a)



(b)

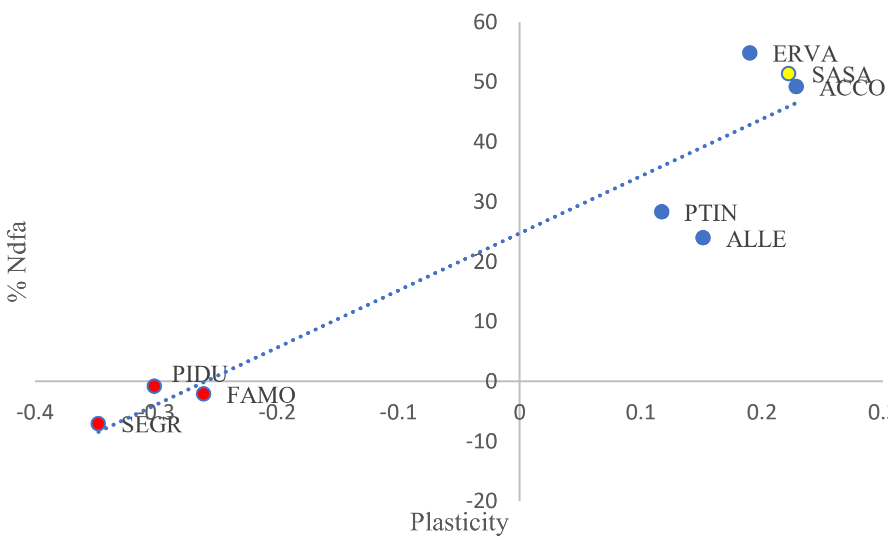


FIGURE 11. Plasticity indices (PC score 1) regressed with species means with HN treatment for nodule density (a) and % N_{dfa} (b). Facultative strategy is represented by blue dots, over regulation strategy is represented by red dots, obligate strategy is represented by yellow dots. A lower plasticity index means greater plasticity. Plasticity indices were found to be positively related to nodule density (r^2=0.49, $F_{1,6}$=8.69, p>0.05) and % N_{dfa} (r^2=0.89, $F_{1,6}$=32.19, p>0.01).

Discussion

Using an isotopic tracer, my study revealed that the eight N-fixing species varied in their growth, allocation, and N-fixing traits, and could be grouped into three distinct fixation strategies: one species, SASA (LR), used the obligate strategy; three species, SEGR (LR), FAMO (HR), and PIDU (HR), used over regulation; and four species, ERVA (LR), PTIN (LR), ALLE (HR), and ACCO (HR), used a facultative strategy. Strategies appear to be associated with the trait plasticity of each species, but do not appear related to HPWRA scores. The results of this experiment support the idea that many Fabaceae species are facultative fixers (Barron et al. 2001; Pearson and Vitousek 2001; Menge et al. 2015) and that the obligate strategy may be rare.

One LR species, SASA, demonstrated an obligate strategy where it did not show the ability to adjust fixation (i.e., reduce nodule density and % N_{dfa}) even when more soil N was available (Figure 9). SASA is native to northern South America, has naturalized throughout the tropics, but is only considered invasive in Fiji and Vanuatu (Staples and Elevitch 2006). Obligate fixers tend to do poorly in tropical ecosystems, which are typically not N limited, because the investment of resources into long-lasting nodules that fix N at a constant rate is too costly to compete with coexisting non-fixers (Menge et al. 2009). However, young volcanic substrates in Hawaiʻi are N limited (Vitousek and Sanford 1986) and may provide a habitat suitable for colonization of symbiotic N-fixing species using the obligate strategy. Obligate fixers can do well in tropical ecosystems during early succession if N availability is low, but after enriching the soil via fixation and litterfall they will likely be outcompeted by non-fixers (Menge et al. 2014). In N-rich environments, comparable to the oldest substrates in Hawaiʻi (Vitousek and Sanford 1986), obligate fixers likely over-fix, leading to N losses (via tissue turnover), and loss of their competitive advantage.

Conversely, facultative strategy users downregulate fixation depending on soil N availability to meet the needs of the plant. With higher N availability, facultative fixers will decrease resource expenditures to fixation and allocate them to growth resulting in changes in biomass, leaf area, and root-to-shoot ratio (Pearson and Vitousek 2001). Within the facultative strategy, there can be three strategy distinctions: over regulation, so that with increased soil N availability fixation is downregulated so much that less N is fixed than is needed to meet the plant's demand (making it N limited); under regulation, where increased regulation occurs with increased soil N availability, but regulated to the point that fixed N is greater than the needs of the plant; and incomplete down regulation, in which there is some down regulation, but fixation rate will stay constant in all soil conditions (Menge et al. 2015). These changes were found in each of the other experimental species (aside from SASA) to varying degrees (Figures 6, 7, and 8). ERVA, PTIN, ALLE, and ACCO reduced fixation with N addition, and were determined to be facultative fixers. ERVA is a LR species indigenous to the tropics of the Old World, likely originating in India to Malaysia. It has been cultivated throughout the tropics and is not considered to be invasive due to unsuccessful dispersal of large seeds (Whistler and Elevitch 2006). ERVA is susceptible to gall wasp infestation causing defoliation and stem degradation from gall formation. ERVA did fall prey to infestation for this experiment and would likely need to be reevaluated under more protective growing conditions to conclusively determine the fixation strategy used. PTIN is a LR species native to Southeast and East Asia, and the northern and southwest Pacific region. It has been cultivated and naturalized in Central and South America, Africa, Asia, the Caribbean, and several Pacific islands (CABI 2020). PTIN is not likely to invade intact native plant communities (Thomson 2006) but has been shown to be invasive outside its native range as it is highly adaptable to different conditions and a pioneer in disturbed areas (CABI 2020). PTIN and ALLE responded to N addition the same way across all variables with similar magnitude for this experiment. ALLE is a HR species native to tropical Asia and Australia, introduced and naturalized in many parts of the tropics where it invades natural environments (Global Invasive Species Database 2020), and is considered highly invasive in the Bahamas and Caribbean region (CABI 2020) and throughout the tropics (US Forest Service 2020). ACCO is a HR species native to Taiwan and the northern Philippines. Its biology and management have not been widely studied, but due to its invasive nature in Hawaiʻi, it is not recommended for introduction to new islands (CABI 2020).

Over regulation was clearly observed in SEGR (LR), FAMO (HR), and PIDU (HR) based on their negative values for % N_{dfa} with high N treatment (Figure 8). SEGR is native to South and Southeast Asian countries and has been cultivated throughout the tropics. It is reported to be invasive on many Pacific islands, the Philippines, and the Chagos in the Indian Ocean but is evaluated as low risk in Hawaiʻi (CABI 2020). FAMO is native to the Moluccas and has been introduced throughout the tropics. It is invasive in natural forests on Pacific islands and Indian

Ocean islands and is banned from import (of any whole or plant parts) in French Polynesia (CABI 2020). PIDU is native to Central America and has been introduced throughout the tropics and subtropics. It is a highly invasive species due to its adaptability to different environments and its rapid germination rate (CABI 2020). Two things stand out with respect to fixation patterns for these three species: First, % N_{dfa} does not drop below zero, either there is fixation (a positive %) or there is not (0 %). Second, implementing an over regulation strategy means that the plant down regulates fixation to the extent of becoming N limited, which would inhibit growth. However, SEGR, FAMO, and PIDU all had increased growth rates and shoot allocation with N addition (Figures 6 and 7). These behaviors lead me to believe that using a representative non-fixer (SESI) for the soil end-member of % N_{dfa} calculations is not the best method. In Menge et al. (2015), these data were derived by inoculating half the individuals per species with bacterial symbionts and withholding inoculum from the other half. The individuals without symbionts did not nodulate or fix any N, so these sets of data were compared to find % N_{dfa}. With this method, more precise calculations could be performed.

Under regulation may have been observed in PTIN and ALLE because although they had no change in growth rates and shoot allocation (Figures 6 and 7), they did have significant decreases in nodule density and % N_{dfa} with N addition (Figure 8). This implies that there was some regulation occurring, but perhaps not enough to maintain tissue and increase growth. Using the experimental method described above (Menge et al. 2015) would be more conclusive.

In a review and synthesis, Richards et al. (2006) acknowledge that greater trait plasticity generally implies that a species can sustain fitness in unfavorable conditions, and/or increase fitness when conditions are more favorable, and that invaders tend to have greater plasticity in fitness traits in response to environments that correspond with the plastic traits. I found that there was a positive correlation between trait plasticity in response to N addition and the ability to regulate N fixation (Figure 11). SASA had the least trait plasticity and was determined to be using the obligate fixation strategy. This implies that SASA has little capacity to adapt to changing or new environments and would not likely be an aggressive invader, but may have more success colonizing younger substrates based on its fixation strategy. On the other hand, SEGR, FAMO, and PIDU had the most trait plasticity and down regulated fixation with the greatest magnitude. This implies that these three species do have the capacity to adapt to changing environments and would very likely be aggressive invaders since they are able to capitalize in varying nutrient conditions (Daehler 2003). Being N fixers, we would expect the species in this experiment to be invasive if their N-fixation traits were the most plastic and the environment was N poor. In other words, they would utilize a perfectly facultative fixation strategy, allowing them to coexist with natives adapted to the N-poor local environment and outcompete them through resource conservation and allocation, similar to what was observed by Funk and Vitousek (2007) in their investigation of resource-use efficiency and plant invasion in Hawaiʻi. FAMO and PIDU both appear to fall into this specific situation: they were found to have high trait plasticity, utilized an efficient facultative fixation strategy, and have successfully invaded (coexisted and outcompeted natives) N-poor and N-rich environments in Hawaiʻi.

Under regulation may have been used by PTIN and ALLE, but could not be conclusively determined. Although I did determine a diversity of fixation strategies in plants with a wide range of HPWRA scores, I did not find an association between fixation strategies and risk; thus, this particular hypothesis was not supported. Several reasons may contribute to this finding. First, the HPWRA is not a continuous scale from lowest risk scores to highest risk scores, and does not consider interactions between plant functional traits. Rather, it asks a series of "yes" or "no" questions about the plant's life-history traits, native geographic and climate range, and history of invasiveness outside its native range and generates an additive score (Daehler et al. 2004). Answers to the questions are derived from scientific literature and experts in the field. Assessment scores using this system should ultimately be considered a prediction of whether an introduced plant is likely to become invasive in Hawaiʻi, rather than as a scale for how invasive a species is likely to become if introduced. Second, there is only one question on the HPWRA that asks whether or not a species can fix N. N fixation itself does not determine whether or not a species will be invasive, but the strategy used for fixation may carry more weight than just one "yes" or "no" answer.

Perhaps N-fixation strategy in conjunction with other invasive traits contribute to invasiveness in Hawaiʻi. However, in comparing HPWRA datasheets for each species (Appendices A-I) there is no clear pattern between responses and N-fixation strategies. In other words, the three over-regulating facultative fixers (SEGR, FAMO, and PIDU) in this study do not share a set of HPWRA responses that is set apart from the rest of the species' responses.

Many responses are the same, for example: are they suited to tropical climates? Yes; have they naturalized beyond their native ranges? Yes; do they tolerate a wide range of soil conditions? Yes. The responses that do vary among these three species, for example: does it form dense thickets? SEGR no, FAMO no, PIDU yes; are propagules adapted to wind dispersal? SEGR no, FAMO yes, PIDU no, etc., do not show a pattern. In addition, the remaining five species in this experiment typically had the same answer as the common answer for the above questions.

My findings suggest that species identity and N addition had strong effects on growth and fixation traits, which is consistent with other recent studies (Batterman et al. 2013, Wurzburger and Hedin 2015). Trait plasticity allows species to adapt to changing environments and was shown to be highest in those species that were able to regulate fixation with the greatest magnitude. In tropical forests, different N-fixing tree species fix N at different developmental stages (age) and at different rates, implementing mostly facultative strategies (Batterman et al. 2013). Fixation strategies are inherent in and vary across individual species, and fixation occurs in response to growth and resource availability (Wurzburger and Hedin 2015). This is the first study, to my knowledge, to seek to determine N-fixation strategies for invasive and non-invasive non-native plants intending to answer the question of whether fixation strategy is related to invasiveness. Only eight species were observed for this study and it is unclear whether fixation strategies contribute to invasiveness. More studies are needed to conclusively answer this question. My results suggest that fixation strategies are associated with trait plasticity, a known characteristic of invasive species, but are not associated with weed risk assessment scores using the HPWRA.

Appendix A.

	Australian/New Zealand Weed Risk Assessment adapted for Hawai'i. Research directed by C. Daehler (UH Botany) with funding from the Kaulunani Urban Forestry Program and US Forest Service				
University of Hawai'i at Manoa BOTANY	***Erythrina variegata (E. indica);coral tree***		**Answer**	**Source**	**Notes**
1.01	Is the species highly domesticated?	y=-3, n=0	n		no evidence
1.02	Has the species become naturalized where grown?	y=-1, n=-1	n		no evidence
1.03	Does the species have weedy races?	y=-1, n=-1	n		no evidence
2.01	Species suited to tropical or subtropical climate(s) (0-low; 1-ir	See Appen	2	(1)CAB	natural
2.02	Quality of climate match data (0-low; 1-intermediate; 2-high)		2		
2.03	Broad climate suitability (environmental versatility)	y=1, n=0		(1)CAB	is primarily a
2.04	Native or naturalized in regions with tropical or subtropical clir	y=1, n=0	y	CAB	natural
2.05	Does the species have a history of repeated introductions ou	?=-1, n=0	y	CAB	countries
3.01	Naturalized beyond native range y = 1*multiplier (see Append 2), n= (		n		no evidence
3.02	Garden/amenity/disturbance weed y = 1*mu	n=0	n		no evidence
3.03	Agricultural/forestry/horticultural weed y = 2*n	n=0	n		no evidence
3.04	Environmental weed y = 2*mu	n=0	n		no evidence
3.05	Congeneric weed y = 1*m	n=0	y	G.	control of
4.01	Produces spines, thorns or burrs	y=1, n=0		(1)CAB	variety]
4.02	Allelopathic	y=1, n=0	n	CAB	is a suitable
4.03	Parasitic	y=1, n=0	n		no evidence
4.04	Unpalatable to grazing animals	y=1, n=-1	n	(1)USD	Browse
4.05	Toxic to animals	y=1, n=0	n		no evidence
4.06	Host for recognized pests and pathogens	y=1, n=0	y	(1)CAB	(1)"E.
4.07	Causes allergies or is otherwise toxic to humans	y=1, n=0	n	(1)CAB	and leaves
4.08	Creates a fire hazard in natural ecosystems	y=1, n=0	n		no evidence
4.09	Is a shade tolerant plant at some stage of its life cycle	y=1, n=0	n	USDA,	Tolerance:
4.1	Tolerates a wide range of soil conditions (or limestone conditi	y=1, n=0	y	(1)CAB	physiography
4.11	Climbing or smothering growth habit	y=1, n=0	n	CAB	erect tree
4.12	Forms dense thickets	y=1, n=0	n	CAB	types: coastal
5.01	Aquatic	y=5, n=0	n	CAB	terrestrial
5.02	Grass	y=1, n=0	n	CAB	Fabaceae
5.03	Nitrogen fixing woody plant	y=1, n=0	y	CAB	form nodules
5.04	Geophyte (herbaceous with underground storage organs -- b	y=1, n=0	n	CAB	tree
6.01	Evidence of substantial reproductive failure in native habitat	y=1, n=0	n		no evidence
6.02	Produces viable seed.	y=1, n=-1	y	CAB	by seeds is
6.03	Hybridizes naturally	y=1, n=-1			no evidence
6.04	Self-compatible or apomictic	y=1, n=-1			no evidence
6.05	Requires specialist pollinators	y=-1, n=0	y	Wesley,	effect on
6.06	Reproduction by vegetative fragmentation	y=1, n=-1	n		no evidence
6.07	Minimum generative time (years) 1 year = 1, 2 or 3 y	See left	4	ww.flori	flower in as
7.01	Propagules likely to be dispersed unintentionally (plants growi	y=1, n=-1	n		no evidence
7.02	Propagules dispersed intentionally by people	y=1, n=-1	y	CAB	countries
7.03	Propagules likely to disperse as a produce contaminant	y=1, n=-1	n		no evidence
7.04	Propagules adapted to wind dispersal	y=1, n=-1	n		no evidence
7.05	Propagules water dispersed	y=1, n=-1		S.	seeds do not
7.06	Propagules bird dispersed	y=1, n=-1	n	s.ifas.ufl	characteristic
7.07	Propagules dispersed by other animals (externally)	y=1, n=-1	n	s.ifas.ufl	characteristic
7.08	Propagules survive passage through the gut	y=1, n=-1			no evidence
8.01	Prolific seed production (>1000/m2)	y=1, n=-1	n	H. D.	activities of
8.02	Evidence that a persistent propagule bank is formed (>1 yr)	y=1, n=-1	y	http://w	scarification to
8.03	Well controlled by herbicides	y=-1, n=1			no evidence
8.04	Tolerates, or benefits from, mutilation, cultivation, or fire	y=1, n=-1	y	CAB	may be
8.05	Effective natural enemies present locally (e.g. introduced bioc	y=-1, n=1			no evidence
	Total score:		-2		

Appendix B.

University of Hawai'i at Manoa BOTANY	Australian/New Zealand Weed Risk Assessment adapted for Hawai'i. Research directed by C. Daehler (UH Botany) with funding from the Kaulunani Urban Forestry Program and US Forest Service				
	***Sesbania grandiflora* (agati)**		**Answe**	**Source**	**Notes**
1.01	Is the species highly domesticated?	y=-3, n=0	n	Did not	
1.02	Has the species become naturalized where grown?	y=-1, n=-1	y	1)Com	Wagner,W.
1.03	Does the species have weedy races?	y=-1, n=-1	n	Did find	
2.01	Species suited to tropical or subtropical climate(s) (0-low; 1-ir	See Appen	2	Specie	Bose, T. K.,
2.02	Quality of climate match data (0-low; 1-intermediate; 2-high)		1	There	Evans, D. O.
2.03	Broad climate suitability (environmental versatility)	y=1, n=0	n	'S.	REFERENC
2.04	Native or naturalized in regions with tropical or subtropical clir	y=1, n=0	y	There	Evans, D. O.
2.05	Does the species have a history of repeated introductions ou	?=-1, n=0	y	It has	CAB
3.01	Naturalized beyond native range y = 1*multiplier (see Append 2), n= (		y	1)Com	Wagner,W.
3.02	Garden/amenity/disturbance weed y = 1*mu	n=0	n	No	
3.03	Agricultural/forestry/horticultural weed y = 2*m	n=0	n	1) 'A	Holm, L.,
3.04	Environmental weed y = 2*mu	n=0	n	No	
3.05	Congeneric weed y = 1*m	n=0	y	(1)	Lorenzi H. J.
4.01	Produces spines, thorns or burrs	y=1, n=0	n	It does	In gardens
4.02	Allelopathic	y=1, n=0	n	Did not	
4.03	Parasitic	y=1, n=0	n	No	
4.04	Unpalatable to grazing animals	y=1, n=-1	n	Cattle	Gupta, R. K.
4.05	Toxic to animals	y=1, n=0	n	Did not	
4.06	Host for recognized pests and pathogens	y=1, n=0	n	Did not	http://nt.ars-
4.07	Causes allergies or is otherwise toxic to humans	y=1, n=0	n	Leaves,	Bose, T. K.,
4.08	Creates a fire hazard in natural ecosystems	y=1, n=0	n	Fire	http://plants.
4.09	Is a shade tolerant plant at some stage of its life cycle	y=1, n=0	n	It is a	CAB
4.1	Tolerates a wide range of soil conditions (or limestone conditi	y=1, n=0	y	It can	CAB
4.11	Climbing or smothering growth habit	y=1, n=0	n	The	
4.12	Forms dense thickets	y=1, n=0	n	The	
5.01	Aquatic	y=5, n=0	n		
5.02	Grass	y=1, n=0	n		
5.03	Nitrogen fixing woody plant	y=1, n=0	y	It is an	CAB
5.04	Geophyte (herbaceous with underground storage organs -- b	y=1, n=0	n		
6.01	Evidence of substantial reproductive failure in native habitat	y=1, n=0	n	The	
6.02	Produces viable seed.	y=1, n=-1	y	Did not	
6.03	Hybridizes naturally	y=1, n=-1		No	
6.04	Self-compatible or apomictic	y=1, n=-1		Did not	
6.05	Requires specialist pollinators	y=-1, n=0		No	
6.06	Reproduction by vegetative fragmentation	y=1, n=-1	n	Propag	http://www.h
6.07	Minimum generative time (years) 1 year = 1, 2 or 3 y	See left	2	Floweri	Bose, T. K.,
7.01	Propagules likely to be dispersed unintentionally (plants growi	y=1, n=-1	n	The	
7.02	Propagules dispersed intentionally by people	y=1, n=-1	y	Comm	http://www.h
7.03	Propagules likely to disperse as a produce contaminant	y=1, n=-1	n	It is a	
7.04	Propagules adapted to wind dispersal	y=1, n=-1	n	The	http://www.wi
7.05	Propagules water dispersed	y=1, n=-1		It is a	
7.06	Propagules bird dispersed	y=1, n=-1	n	No	
7.07	Propagules dispersed by other animals (externally)	y=1, n=-1	n	Probabl	
7.08	Propagules survive passage through the gut	y=1, n=-1		Conflict	
8.01	Prolific seed production (>1000/m2)	y=1, n=-1		The	http://www.wi
8.02	Evidence that a persistent propagule bank is formed (>1 yr)	y=1, n=-1	y	Germin	http://www.a
8.03	Well controlled by herbicides	y=-1, n=1		No	
8.04	Tolerates, or benefits from, mutilation, cultivation, or fire	y=1, n=-1	n	(1)	(1) Ella, A.,
8.05	Effective natural enemies present locally (e.g. introduced bioc	y=-1, n=1		No	
	Total score:		2		

Appendix C.

University of Hawai'i at Manoa BOTANY	Australian/New Zealand Weed Risk Assessment adapted for Hawai'i. Research directed by C. Daehler (UH Botany) with funding from the Kaulunani Urban Forestry Program and US Forest Service				
	Pterocarpus indicus; (red sandalwood, Burmese rose		**Answer**	**Notes**	**Source**
1.01	Is the species highly domesticated?	y=-3, n=0	n	No	
1.02	Has the species become naturalized where grown?	y=-1, n=-1	y	(1)	(1)http://www
1.03	Does the species have weedy races?	y=-1, n=-1	n	No	
2.01	Species suited to tropical or subtropical climate(s) (0-low; 1-ir	See Appen	2	P.	CAB
2.02	Quality of climate match data (0-low; 1-intermediate; 2-high)		2	P.	CAB
2.03	Broad climate suitability (environmental versatility)	y=1, n=0			(1)CAB
2.04	Native or naturalized in regions with tropical or subtropical clir	y=1, n=0	y	P.	CAB
2.05	Does the species have a history of repeated introductions ou	?=-1, n=0	y	P.	CAB
3.01	Naturalized beyond native range y = 1*multiplier (see Append 2), n= (		y	(1)	(1)http://www
3.02	Garden/amenity/disturbance weed y = 1*mu	n=0	n	No	
3.03	Agricultural/forestry/horticultural weed y = 2*n	n=0	n	No	
3.04	Environmental weed y = 2*mu	n=0		AB:	Swarbrick,
3.05	Congeneric weed y = 1*m	n=0	n	No	
4.01	Produces spines, thorns or burrs	y=1, n=0	n	No	
4.02	Allelopathic	y=1, n=0	n	No	
4.03	Parasitic	y=1, n=0	n	No	
4.04	Unpalatable to grazing animals	y=1, n=-1	n	(1)Char	(1)http://216.
4.05	Toxic to animals	y=1, n=0	n	No	
4.06	Host for recognized pests and pathogens	y=1, n=0	y	(1)P.	(1)CAB
4.07	Causes allergies or is otherwise toxic to humans	y=1, n=0	n	No	
4.08	Creates a fire hazard in natural ecosystems	y=1, n=0	n	(1)Usu	(1)CAB
4.09	Is a shade tolerant plant at some stage of its life cycle	y=1, n=0		(1) 'P.	(1)CAB
4.1	Tolerates a wide range of soil conditions (or limestone conditi	y=1, n=0	n	(1)Soil	(!)CAB
4.11	Climbing or smothering growth habit	y=1, n=0	n	Perenni	http://www.il
4.12	Forms dense thickets	y=1, n=0	n	No	
5.01	Aquatic	y=5, n=0	n	No	
5.02	Grass	y=1, n=0	n	Fabace	
5.03	Nitrogen fixing woody plant	y=1, n=0	y	Ability	CAB
5.04	Geophyte (herbaceous with underground storage organs -- t	y=1, n=0	n	No	
6.01	Evidence of substantial reproductive failure in native habitat	y=1, n=0	n	'In the	CAB
6.02	Produces viable seed.	y=1, n=-1	y	(1)It	(1)CAB
6.03	Hybridizes naturally	y=1, n=-1		No	
6.04	Self-compatible or apomictic	y=1, n=-1	y	'AB: "A	ET: The
6.05	Requires specialist pollinators	y=-1, n=0	n	AB:	Escobin, R.
6.06	Reproduction by vegetative fragmentation	y=1, n=-1	n	No	
6.07	Minimum generative time (years) 1 year = 1, 2 or 3 y	See left	4	the	http://www.wi
7.01	Propagules likely to be dispersed unintentionally (plants growi	y=1, n=-1	n	Probabl	
7.02	Propagules dispersed intentionally by people	y=1, n=-1	y		CAB
7.03	Propagules likely to disperse as a produce contaminant	y=1, n=-1	n	Probabl	
7.04	Propagules adapted to wind dispersal	y=1, n=-1	y	(1)	(1)Bose, T K,
7.05	Propagules water dispersed	y=1, n=-1	y	(1)	(1)Bose, T K,
7.06	Propagules bird dispersed	y=1, n=-1	n		
7.07	Propagules dispersed by other animals (externally)	y=1, n=-1	n	Probabl	
7.08	Propagules survive passage through the gut	y=1, n=-1		Probabl	
8.01	Prolific seed production (>1000/m2)	y=1, n=-1	n	few	(1)Bose, T K,
8.02	Evidence that a persistent propagule bank is formed (>1 yr)	y=1, n=-1		(1) AB:	ET: The
8.03	Well controlled by herbicides	y=-1, n=1	n	No	
8.04	Tolerates, or benefits from, mutilation, cultivation, or fire	y=1, n=-1	y	(1)	(1)CAB
8.05	Effective natural enemies present locally (e.g. introduced bioc	y=-1, n=1		Don't	
	Total score:		4		

Appendix D.

University of Hawai'i at Manoa BOTANY	Australian/New Zealand Weed Risk Assessment adapted for Hawai'i. Research directed by C. Daehler (UH Botany) with funding from the Kaulunani Urban Forestry Program and US Forest Service				
	Samanea saman (Albizia saman)		**Answei**	**Source**	**Notes**
1.01	Is the species highly domesticated?	y=-3, n=0	N		Did not find
1.02	Has the species become naturalized where grown?	y=-1, n=-1	Y	Wagner	'...in Hawaii
1.03	Does the species have weedy races?	y=-1, n=-1	N		Did not find
2.01	Species suited to tropical or subtropical climate(s) (0-low; 1-ir	See Appen	2	Durr-P-	'Samanea
2.02	Quality of climate match data (0-low; 1-intermediate; 2-high)		2	CAB	
2.03	Broad climate suitability (environmental versatility)	y=1, n=0	Y	CAB	Altitude
2.04	Native or naturalized in regions with tropical or subtropical clir	y=1, n=0	Y	Wagner	'...in Hawaii
2.05	Does the species have a history of repeated introductions ou	?=-1, n=0	Y	CAB	Introduced in
3.01	Naturalized beyond native range y = 1*multiplier (see Append 2), n= (		Y	Wagner	'Native to
3.02	Garden/amenity/disturbance weed y = 1*mu	n=0	N		Did not find
3.03	Agricultural/forestry/horticultural weed y = 2*m	n=0	N		Did not find
3.04	Environmental weed y = 2*mu	n=0	N		This plant
3.05	Congeneric weed y = 1*m	n=0			There is no
4.01	Produces spines, thorns or burrs	y=1, n=0	N	Wagner	The species
4.02	Allelopathic	y=1, n=0	N	Magnu	'Especially
4.03	Parasitic	y=1, n=0	N		Did not find
4.04	Unpalatable to grazing animals	y=1, n=-1	N	Durr-P-	'The tree
4.05	Toxic to animals	y=1, n=0	Y	(1)	(2) 'This is a
4.06	Host for recognized pests and pathogens	y=1, n=0	n	The	http://nt.ars-
4.07	Causes allergies or is otherwise toxic to humans	y=1, n=0	N	CAB	The sticky
4.08	Creates a fire hazard in natural ecosystems	y=1, n=0	N		no evidence
4.09	Is a shade tolerant plant at some stage of its life cycle	y=1, n=0	N	http://w	Seedlings
4.1	Tolerates a wide range of soil conditions (or limestone conditi	y=1, n=0	y	CAB	grows well
4.11	Climbing or smothering growth habit	y=1, n=0	N	Wagner	The species
4.12	Forms dense thickets	y=1, n=0	N	canopy	Did not find
5.01	Aquatic	y=5, n=0	N		
5.02	Grass	y=1, n=0	N		
5.03	Nitrogen fixing woody plant	y=1, n=0	Y	CAB	A tree
5.04	Geophyte (herbaceous with underground storage organs -- b	y=1, n=0	N	0	
6.01	Evidence of substantial reproductive failure in native habitat	y=1, n=0	N		Did not find
6.02	Produces viable seed.	y=1, n=-1	Y		Did not find
6.03	Hybridizes naturally	y=1, n=-1	N		No
6.04	Self-compatible or apomictic	y=1, n=-1			No
6.05	Requires specialist pollinators	y=-1, n=0	N	Janzen,	'The
6.06	Reproduction by vegetative fragmentation	y=1, n=-1	N	http://w	monkey-pod
6.07	Minimum generative time (years) 1 year = 1, 2 or 3 y	See left	4		No
7.01	Propagules likely to be dispersed unintentionally (plants growi	y=1, n=-1	N	Wagner	Although this
7.02	Propagules dispersed intentionally by people	y=1, n=-1	y		Widely
7.03	Propagules likely to disperse as a produce contaminant	y=1, n=-1	n		Seed are
7.04	Propagules adapted to wind dispersal	y=1, n=-1	N		
7.05	Propagules water dispersed	y=1, n=-1	N		
7.06	Propagules bird dispersed	y=1, n=-1	Y	Janzen,	'Peccaries
7.07	Propagules dispersed by other animals (externally)	y=1, n=-1	N	Janzen,	'A few are
7.08	Propagules survive passage through the gut	y=1, n=-1	Y	(1)	(1) 'Grazing
8.01	Prolific seed production (>1000/m2)	y=1, n=-1		http://w	pod contains
8.02	Evidence that a persistent propagule bank is formed (>1 yr)	y=1, n=-1	Y	Janzen,	According to
8.03	Well controlled by herbicides	y=-1, n=1	y	http://w	The species
8.04	Tolerates, or benefits from, mutilation, cultivation, or fire	y=1, n=-1			No
8.05	Effective natural enemies present locally (e.g. introduced bioc	y=-1, n=1		Biologi	Did not find
	Total score:		4		

Appendix E.

	Australian/New Zealand Weed Risk Assessment adapted for Hawai'i. Research directed by C. Daehler (UH Botany) with funding from the Kaulunani Urban Forestry Program and US Forest Service ***Albizia lebbeck***		**Answe r**	**Source**	**Notes**
1.01	Is the species highly domesticated?	y=-3, n=0	N		Did not find
1.02	Has the species become naturalized where grown?	y=-1, n=-1	Y	Steento	...originally
1.03	Does the species have weedy races?	y=-1, n=-1	N		Did not find
2.01	Species suited to tropical or subtropical climate(s) (0-low; 1-ir	See Appen	2	McCan	Distribution:
2.02	Quality of climate match data (0-low; 1-intermediate; 2-high)		2	Hockin	has wide
2.03	Broad climate suitability (environmental versatility)	y=1, n=0	Y	Hockin	has wide
2.04	Native or naturalized in regions with tropical or subtropical clir	y=1, n=0	Y	McCan	Distribution:
2.05	Does the species have a history of repeated introductions ou	?=-1, n=0	Y	FC	
3.01	Naturalized beyond native range y = 1*multiplier (see Append 2), n= (		Y	Steento	...originally
3.02	Garden/amenity/disturbance weed y = 1*mu	n=0	N		Not
3.03	Agricultural/forestry/horticultural weed y = 2*m	n=0	N		Did not find
3.04	Environmental weed y = 2*mu	n=0	y	Univers	invading
3.05	Congeneric weed y = 1*m	n=0	Y	Lorenzi,	Albizzia
4.01	Produces spines, thorns or burrs	y=1, n=0	N	Saldan	Unarmed
4.02	Allelopathic	y=1, n=0	N	Lowry	Did not find
4.03	Parasitic	y=1, n=0	N		Did not find
4.04	Unpalatable to grazing animals	y=1, n=-1	N	Lowry	seedlings
4.05	Toxic to animals	y=1, n=0	N	Lowry	Leaves of
4.06	Host for recognized pests and pathogens	y=1, n=0	N	NOT	
4.07	Causes allergies or is otherwise toxic to humans	y=1, n=0	N	Tripathi	This plant is
4.08	Creates a fire hazard in natural ecosystems	y=1, n=0	N	Gupta	No direct
4.09	Is a shade tolerant plant at some stage of its life cycle	y=1, n=0	Y	Gupta	Though a
4.1	Tolerates a wide range of soil conditions (or limestone conditi	y=1, n=0	Y	Hockin	grows on
4.11	Climbing or smothering growth habit	y=1, n=0	N	(1)Nels	(1)'Deciduou
4.12	Forms dense thickets	y=1, n=0	N		Did not find
5.01	Aquatic	y=5, n=0	N		
5.02	Grass	y=1, n=0	N		
5.03	Nitrogen fixing woody plant	y=1, n=0	Y	Kadiata	A. lebbeck is
5.04	Geophyte (herbaceous with underground storage organs -- b	y=1, n=0	N		
6.01	Evidence of substantial reproductive failure in native habitat	y=1, n=0	N		No reference
6.02	Produces viable seed.	y=1, n=-1	Y		No reference
6.03	Hybridizes naturally	y=1, n=-1	N		No reference
6.04	Self-compatible or apomictic	y=1, n=-1			No
6.05	Requires specialist pollinators	y=-1, n=0	N	Lowry	Flowers are
6.06	Reproduction by vegetative fragmentation	y=1, n=-1	N	Gupta	The tree can
6.07	Minimum generative time (years) 1 year = 1, 2 or 3 y	See left	4	Dr.	
7.01	Propagules likely to be dispersed unintentionally (plants growi	y=1, n=-1	n	Gupta	Grown as
7.02	Propagules dispersed intentionally by people	y=1, n=-1	Y	Grown	
7.03	Propagules likely to disperse as a produce contaminant	y=1, n=-1	N		
7.04	Propagules adapted to wind dispersal	y=1, n=-1	N	Gravity	Seeds 4-12,
7.05	Propagules water dispersed	y=1, n=-1	N		
7.06	Propagules bird dispersed	y=1, n=-1	N		
7.07	Propagules dispersed by other animals (externally)	y=1, n=-1	N		The seeds
7.08	Propagules survive passage through the gut	y=1, n=-1	Y	Lowry	Some seed
8.01	Prolific seed production (>1000/m2)	y=1, n=-1	n	Hockin	BORDERLIN
8.02	Evidence that a persistent propagule bank is formed (>1 yr)	y=1, n=-1	y		Hard
8.03	Well controlled by herbicides	y=-1, n=1			No reference
8.04	Tolerates, or benefits from, mutilation, cultivation, or fire	y=1, n=-1	Y	Gupta	It sprouts
8.05	Effective natural enemies present locally (e.g. introduced bioc	y=-1, n=1			unknown
	Total score:		7		

Appendix F.

Australian/New Zealand Weed Risk Assessment adapted for Hawai'i.
Research directed by C. Daehler (UH Botany) with funding from the
Kaulunani Urban Forestry Program and US Forest Service

University of Hawai'i at Manoa BOTANY

	Falcataria moluccana [synonym: Albizia falcataria an		**Answer**	**Notes**	**Source**
1.01	Is the species highly domesticated?	y=-3, n=0	n	No	
1.02	Has the species become naturalized where grown?	y=-1, n=-1	y	Naturali	Wagner,W.
1.03	Does the species have weedy races?	y=-1, n=-1	n	No	
2.01	Species suited to tropical or subtropical climate(s) (0-low; 1-ir	See Appen	2	It is	CAB
2.02	Quality of climate match data (0-low; 1-intermediate; 2-high)		2		
2.03	Broad climate suitability (environmental versatility)	y=1, n=0	y	Approxi	CAB
2.04	Native or naturalized in regions with tropical or subtropical clir	y=1, n=0	y	A	http://www.h
2.05	Does the species have a history of repeated introductions ou	?=-1, n=0	y	The	CAB
3.01	Naturalized beyond native range y = 1*multiplier (see Append 2), n= (		y	A	http://www.h
3.02	Garden/amenity/disturbance weed y = 1*mu	n=0	n	No	
3.03	Agricultural/forestry/horticultural weed y = 2*m	n=0	n	No	
3.04	Environmental weed y = 2*mu	n=0	y	(1)A	(1)Motooka,
3.05	Congeneric weed y = 1*m	n=0	y	No	
4.01	Produces spines, thorns or burrs	y=1, n=0	n	No	Wagner,W.
4.02	Allelopathic	y=1, n=0	n	No	
4.03	Parasitic	y=1, n=0	n	No	
4.04	Unpalatable to grazing animals	y=1, n=-1	n	Freque	http://www.h
4.05	Toxic to animals	y=1, n=0	n	The	CAB
4.06	Host for recognized pests and pathogens	y=1, n=0	n	(1)Inse	(1)CAB
4.07	Causes allergies or is otherwise toxic to humans	y=1, n=0	n	No	
4.08	Creates a fire hazard in natural ecosystems	y=1, n=0		It is not	http://www.b
4.09	Is a shade tolerant plant at some stage of its life cycle	y=1, n=0	n	P.	CAB
4.1	Tolerates a wide range of soil conditions (or limestone conditi	y=1, n=0	y	Tree	http://www.h
4.11	Climbing or smothering growth habit	y=1, n=0	n	It is not	
4.12	Forms dense thickets	y=1, n=0	n	No	
5.01	Aquatic	y=5, n=0	n		
5.02	Grass	y=1, n=0	n		
5.03	Nitrogen fixing woody plant	y=1, n=0	y	Large	CAB
5.04	Geophyte (herbaceous with underground storage organs -- b	y=1, n=0	n		
6.01	Evidence of substantial reproductive failure in native habitat	y=1, n=0	n	No	
6.02	Produces viable seed.	y=1, n=-1	y	Germin	http://www.p
6.03	Hybridizes naturally	y=1, n=-1		No	
6.04	Self-compatible or apomictic	y=1, n=-1		No	
6.05	Requires specialist pollinators	y=-1, n=0	n	Probabl	
6.06	Reproduction by vegetative fragmentation	y=1, n=-1	n	No	
6.07	Minimum generative time (years) 1 year = 1, 2 or 3 y	See left		No	
7.01	Propagules likely to be dispersed unintentionally (plants growi	y=1, n=-1	n	Seeds	
7.02	Propagules dispersed intentionally by people	y=1, n=-1	y	frequen	http://www.wi
7.03	Propagules likely to disperse as a produce contaminant	y=1, n=-1	n	Seeds	
7.04	Propagules adapted to wind dispersal	y=1, n=-1	y	This	http://www.p
7.05	Propagules water dispersed	y=1, n=-1	n		
7.06	Propagules bird dispersed	y=1, n=-1	n		
7.07	Propagules dispersed by other animals (externally)	y=1, n=-1	n		
7.08	Propagules survive passage through the gut	y=1, n=-1		No	
8.01	Prolific seed production (>1000/m2)	y=1, n=-1	n	Pods 9-	Wagner,W.
8.02	Evidence that a persistent propagule bank is formed (>1 yr)	y=1, n=-1	y	Can be	http://www.wi
8.03	Well controlled by herbicides	y=-1, n=1	y	"falcata	http://www.wi
8.04	Tolerates, or benefits from, mutilation, cultivation, or fire	y=1, n=-1	y	regener	CAB
8.05	Effective natural enemies present locally (e.g. introduced bioc	y=-1, n=1		Don't	
	Total score:		8		

Appendix G.

Australian/New Zealand Weed Risk Assessment adapted for Hawai'i.
Research directed by C. Daehler (UH Botany) with funding from the Kaulunani Urban Forestry Program and US Forest Service

University of Hawai'i at Manoa BOTANY

	Acacia confusa		Answe	Source	Notes	
1.01	Is the species highly domesticated?	y=-3, n=0	N		Did not find	
1.02	Has the species become naturalized where grown?	y=-1, n=-1	Y	Wagner	'...in Hawaii	641
1.03	Does the species have weedy races?	y=-1, n=-1	N		Did not find	
2.01	Species suited to tropical or subtropical climate(s) (0-low; 1-ir	See Appen	2	http://w	A native of	
2.02	Quality of climate match data (0-low; 1-intermediate; 2-high)		2			
2.03	Broad climate suitability (environmental versatility)	y=1, n=0	N	(1) CAB	INDICATE	
2.04	Native or naturalized in regions with tropical or subtropical clir	y=1, n=0	Y	Wagner	'Native to	641
2.05	Does the species have a history of repeated introductions ou	?=-1, n=0	Y	http://w	Micronesia:	
3.01	Naturalized beyond native range y = 1*multiplier (see Append 2), n= (		Y	Wagner	'...in Hawaii	641
3.02	Garden/amenity/disturbance weed y = 1*mu	n=0	N		Did not find	
3.03	Agricultural/forestry/horticultural weed y = 2*n	n=0	N		Did not find	
3.04	Environmental weed y = 2*mu	n=0	Y	(1)Smit	(1)Consider	183
3.05	Congeneric weed y = 1*m	n=0	Y	Weed	Acacia	466
4.01	Produces spines, thorns or burrs	y=1, n=0	N	Wagner	Species	641
4.02	Allelopathic	y=1, n=0	Y	Journal-	Aqueous	abstract
4.03	Parasitic	y=1, n=0	N		Did not find	
4.04	Unpalatable to grazing animals	y=1, n=-1	Y	http://w	NOT	
4.05	Toxic to animals	y=1, n=0		http://w	All parts of	
4.06	Host for recognized pests and pathogens	y=1, n=0	N	http://nt.	Acacia	
4.07	Causes allergies or is otherwise toxic to humans	y=1, n=0	N		Did not find	
4.08	Creates a fire hazard in natural ecosystems	y=1, n=0	N	Smith,	'The plant is	183
4.09	Is a shade tolerant plant at some stage of its life cycle	y=1, n=0			No	
4.1	Tolerates a wide range of soil conditions (or limestone conditi	y=1, n=0	Y	CAB	'It grows	
4.11	Climbing or smothering growth habit	y=1, n=0	N	Wagner	It is a tree	641
4.12	Forms dense thickets	y=1, n=0		Tuniso		507
5.01	Aquatic	y=5, n=0	N		Fabaceae	
5.02	Grass	y=1, n=0	N		Fabaceae	
5.03	Nitrogen fixing woody plant	y=1, n=0	Y	CAB	It is a	641
5.04	Geophyte (herbaceous with underground storage organs -- b	y=1, n=0	N		Fabaceae	
6.01	Evidence of substantial reproductive failure in native habitat	y=1, n=0	N		No evidence	
6.02	Produces viable seed.	y=1, n=-1	y		Grown from	
6.03	Hybridizes naturally	y=1, n=-1			No	
6.04	Self-compatible or apomictic	y=1, n=-1			No	
6.05	Requires specialist pollinators	y=-1, n=0	N	http://w	flowers are	
6.06	Reproduction by vegetative fragmentation	y=1, n=-1	N	http://w	No evidence	
6.07	Minimum generative time (years) 1 year = 1, 2 or 3 y	See left			No	
7.01	Propagules likely to be dispersed unintentionally (plants growi	y=1, n=-1	N	Wagner	The	641
7.02	Propagules dispersed intentionally by people	y=1, n=-1	Y	CAB	The species	
7.03	Propagules likely to disperse as a produce contaminant	y=1, n=-1	N	http://w	Seed size is	
7.04	Propagules adapted to wind dispersal	y=1, n=-1	N	Smith,	' The small	183
7.05	Propagules water dispersed	y=1, n=-1	N		No evidence	
7.06	Propagules bird dispersed	y=1, n=-1	N		No evidence	
7.07	Propagules dispersed by other animals (externally)	y=1, n=-1	N	Wagner	The seeds	641
7.08	Propagules survive passage through the gut	y=1, n=-1			No evidence	
8.01	Prolific seed production (>1000/m2)	y=1, n=-1	N	http://w	On	
8.02	Evidence that a persistent propagule bank is formed (>1 yr)	y=1, n=-1	Y	http://w	Seeds	
8.03	Well controlled by herbicides	y=-1, n=1		(1)Tuni	(1)The	514
8.04	Tolerates, or benefits from, mutilation, cultivation, or fire	y=1, n=-1	Y	Smith,	'Aerial	183
8.05	Effective natural enemies present locally (e.g. introduced bioc	y=-1, n=1	N		Has spread	
	Total score:		10			

Appendix H.

Australian/New Zealand Weed Risk Assessment adapted for Hawai'i.
Research directed by C. Daehler (UH Botany) with funding from the
Kaulunani Urban Forestry Program and US Forest Service

University of Hawai'i at Manoa BOTANY

	Cassia siamea (Senna siamea); Siamese cassia		Answer	Source	Notes
1.01	Is the species highly domesticated?	y=-3, n=0	n		no evidence
1.02	Has the species become naturalized where grown?	y=-1, n=-1	y	CAB	been
1.03	Does the species have weedy races?	y=-1, n=-1	n		no evidence
2.01	Species suited to tropical or subtropical climate(s) (0-low; 1-ir	See Appen	2	CAB	natural
2.02	Quality of climate match data (0-low; 1-intermediate; 2-high)		2		
2.03	Broad climate suitability (environmental versatility)	y=1, n=0	y	(1)CAB	S. siamea is
2.04	Native or naturalized in regions with tropical or subtropical clir	y=1, n=0	y	CAB	natural
2.05	Does the species have a history of repeated introductions ou	?=-1, n=0	y	CAB	introductions
3.01	Naturalized beyond native range y = 1*multiplier (see Append 2), n= (		y	CAB	been
3.02	Garden/amenity/disturbance weed y = 1*mu	n=0	n		no evidence
3.03	Agricultural/forestry/horticultural weed y = 2*m	n=0	n		no evidence
3.04	Environmental weed y = 2*mu	n=0	n		no evidence
3.05	Congeneric weed y = 1*m	n=0	y	Noxiou	5 Senna
4.01	Produces spines, thorns or burrs	y=1, n=0	n		of these traits
4.02	Allelopathic	y=1, n=0	y	Prawoto	Research on
4.03	Parasitic	y=1, n=0	n		no evidence
4.04	Unpalatable to grazing animals	y=1, n=-1	n	yake, H.	(Cassia
4.05	Toxic to animals	y=1, n=0	y	(1)CAB	leaves, pods
4.06	Host for recognized pests and pathogens	y=1, n=0	n	(1) CAB	S. siamea is
4.07	Causes allergies or is otherwise toxic to humans	y=1, n=0		CAB	wood
4.08	Creates a fire hazard in natural ecosystems	y=1, n=0	n	ww.win	because it is a
4.09	Is a shade tolerant plant at some stage of its life cycle	y=1, n=0	n	CAB	strong light
4.1	Tolerates a wide range of soil conditions (or limestone conditi	y=1, n=0	y	(1)CAB	not exacting in
4.11	Climbing or smothering growth habit	y=1, n=0	n	CAB	medium-size
4.12	Forms dense thickets	y=1, n=0	n		no evidence
5.01	Aquatic	y=5, n=0	n		terrestrial
5.02	Grass	y=1, n=0	n		Fabaceae
5.03	Nitrogen fixing woody plant	y=1, n=0	n	(1)CAB	well accepted
5.04	Geophyte (herbaceous with underground storage organs -- b	y=1, n=0	n		tree
6.01	Evidence of substantial reproductive failure in native habitat	y=1, n=0	n	CAB	records of ex
6.02	Produces viable seed.	y=1, n=-1	y	CAB	plant
6.03	Hybridizes naturally	y=1, n=-1			no evidence
6.04	Self-compatible or apomictic	y=1, n=-1			no evidence
6.05	Requires specialist pollinators	y=-1, n=0	n	ww.bar	[Picture of
6.06	Reproduction by vegetative fragmentation	y=1, n=-1	n		no evidence
6.07	Minimum generative time (years) 1 year = 1, 2 or 3 y	See left	2	6.239.57	fruiting begin
7.01	Propagules likely to be dispersed unintentionally (plants growi	y=1, n=-1	n		no evidence
7.02	Propagules dispersed intentionally by people	y=1, n=-1	y	CAB	introductions
7.03	Propagules likely to disperse as a produce contaminant	y=1, n=-1	n		no evidence
7.04	Propagules adapted to wind dispersal	y=1, n=-1	n	ww.dfs	[indehiscent
7.05	Propagules water dispersed	y=1, n=-1	n		no evidence
7.06	Propagules bird dispersed	y=1, n=-1	n		no evidence
7.07	Propagules dispersed by other animals (externally)	y=1, n=-1	n		no evidence
7.08	Propagules survive passage through the gut	y=1, n=-1	y	ww.win	eaten by
8.01	Prolific seed production (>1000/m2)	y=1, n=-1	n	CAB	between
8.02	Evidence that a persistent propagule bank is formed (>1 yr)	y=1, n=-1	y	(1) CAB	seeds are
8.03	Well controlled by herbicides	y=-1, n=1			no evidence
8.04	Tolerates, or benefits from, mutilation, cultivation, or fire	y=1, n=-1	y	ww.win	Plantations
8.05	Effective natural enemies present locally (e.g. introduced bioc	y=-1, n=1		Sheet,	pest or
	Total score:		5		

Keywords: High Risk, Naturalized, Weedy Tree, Allelopathic, Coppices

Family: *Fabaceae*

Taxon: *Senna siamea*

Synonym: *Cassia siamea Lam. (basionym)*

Common Name: Siamese cassia
Siamese senna
Thai cassia
Thailand shower
Thailand shower

Questionaire :	current 20090513	**Assessor:** Assessor	**Designation:** H(HPWRA)
Status:	Assessor Approved	**Data Entry Person:** Assessor	**WRA Score** 10

101	Is the species highly domesticated?	y=-3, n=0	n
102	Has the species become naturalized where grown?	y=1, n=-1	
103	Does the species have weedy races?	y=1, n=-1	
201	Species suited to tropical or subtropical climate(s) - If island is primarily wet habitat, then substitute "wet tropical" for "tropical or subtropical"	(0-low; 1-intermediate; 2-high) (See Appendix 2)	High
202	Quality of climate match data	(0-low; 1-intermediate; 2-high) (See Appendix 2)	High
203	Broad climate suitability (environmental versatility)	y=1, n=0	y
204	Native or naturalized in regions with tropical or subtropical climates	y=1, n=0	y
205	Does the species have a history of repeated introductions outside its natural range?	y=-2, ?=-1, n=0	y
301	Naturalized beyond native range	y = 1*multiplier (see Appendix 2), n= question 205	y
302	Garden/amenity/disturbance weed	n=0, y = 1*multiplier (see Appendix 2)	y
303	Agricultural/forestry/horticultural weed	n=0, y = 2*multiplier (see Appendix 2)	n
304	Environmental weed	n=0, y = 2*multiplier (see Appendix 2)	
305	Congeneric weed	n=0, y = 1*multiplier (see Appendix 2)	y
401	Produces spines, thorns or burrs	y=1, n=0	n
402	Allelopathic	y=1, n=0	y
403	Parasitic	y=1, n=0	n
404	Unpalatable to grazing animals	y=1, n=-1	n
405	Toxic to animals	y=1, n=0	y
406	Host for recognized pests and pathogens	y=1, n=0	
407	Causes allergies or is otherwise toxic to humans	y=1, n=0	
408	Creates a fire hazard in natural ecosystems	y=1, n=0	n
409	Is a shade tolerant plant at some stage of its life cycle	y=1, n=0	n

410	Tolerates a wide range of soil conditions (or limestone conditions if not a volcanic island)	y=1, n=0	y
411	Climbing or smothering growth habit	y=1, n=0	n
412	Forms dense thickets	y=1, n=0	y
501	Aquatic	y=5, n=0	n
502	Grass	y=1, n=0	n
503	Nitrogen fixing woody plant	y=1, n=0	n
504	Geophyte (herbaceous with underground storage organs -- bulbs, corms, or tubers)	y=1, n=0	n
601	Evidence of substantial reproductive failure in native habitat	y=1, n=0	n
602	Produces viable seed	y=1, n=-1	y
603	Hybridizes naturally	y=1, n=-1	
604	Self-compatible or apomictic	y=1, n=-1	
605	Requires specialist pollinators	y=-1, n=0	n
606	Reproduction by vegetative fragmentation	y=1, n=-1	n
607	Minimum generative time (years)	1 year = 1, 2 or 3 years = 0, 4+ years = -1	2
701	Propagules likely to be dispersed unintentionally (plants growing in heavily trafficked areas)	y=1, n=-1	n
702	Propagules dispersed intentionally by people	y=1, n=-1	y
703	Propagules likely to disperse as a produce contaminant	y=1, n=-1	n
704	Propagules adapted to wind dispersal	y=1, n=-1	n
705	Propagules water dispersed	y=1, n=-1	y
706	Propagules bird dispersed	y=1, n=-1	n
707	Propagules dispersed by other animals (externally)	y=1, n=-1	n
708	Propagules survive passage through the gut	y=1, n=-1	y
801	Prolific seed production (>1000/m2)	y=1, n=-1	n
802	Evidence that a persistent propagule bank is formed (>1 yr)	y=1, n=-1	y
803	Well controlled by herbicides	y=-1, n=1	
804	Tolerates, or benefits from, mutilation, cultivation, or fire	y=1, n=-1	y
805	Effective natural enemies present locally (e.g. introduced biocontrol agents)	y=-1, n=1	
		Designation: H(HPWRA)	**WRA Score 10**

Appendix I.

Australian/New Zealand Weed Risk Assessment adapted for Hawai'i.
Research directed by C. Daehler (UH Botany) with funding from the
Kaulunani Urban Forestry Program and US Forest Service

University of Hawai'i at Manoa BOTANY

	***Pithecellobium dulce* (Roxb.) Benth.; *Inga dulcis*, Mir**		**Answe r**	**Notes**	**Source**
1.01	Is the species highly domesticated?	y=-3, n=0	n	variegat	International,
1.02	Has the species become naturalized where grown?	y=-1, n=-1	y	Pithecell	H.H. &
1.03	Does the species have weedy races?	y=-1, n=-1	y	Although	http://www.af
2.01	Species suited to tropical or subtropical climate(s) (0-low; 1-ir	See Appen	2	NORTHE	National
2.02	Quality of climate match data (0-low; 1-intermediate; 2-high)		2		National
2.03	Broad climate suitability (environmental versatility)	y=1, n=0	y	nd the	International,
2.04	Native or naturalized in regions with tropical or subtropical clir	y=1, n=0	y	Pithecell	National
2.05	Does the species have a history of repeated introductions ou	?=-1, n=0	y	of	International,
3.01	Naturalized beyond native range y = 1*multiplier (see Append 2), n= (		y	Pithecell	H.H. &
3.02	Garden/amenity/disturbance weed y = 1*mu	n=0	y	reputatio	inrock.org/fore
3.03	Agricultural/forestry/horticultural weed y = 2*m	n=0	y	thorny,	International,
3.04	Environmental weed y = 2*mu	n=0		major	T. Hart, R.
3.05	Congeneric weed y = 1*m	n=0	y	other	fa.gov.au/cont
4.01	Produces spines, thorns or burrs	y=1, n=0	y	or small	H.H. &
4.02	Allelopathic	y=1, n=0		"Laborat	(1998)
4.03	Parasitic	y=1, n=0	n	evidenc	
4.04	Unpalatable to grazing animals	y=1, n=-1	n	a good	H.H. &
4.05	Toxic to animals	y=1, n=0	n	seed oil	H.H. &
4.06	Host for recognized pests and pathogens	y=1, n=0	n	study	Irianto, R. S. B.
4.07	Causes allergies or is otherwise toxic to humans	y=1, n=0	y	irritating	International,
4.08	Creates a fire hazard in natural ecosystems	y=1, n=0	n	plant is	abase.com/go/
4.09	Is a shade tolerant plant at some stage of its life cycle	y=1, n=0	n	is a	International,
4.1	Tolerates a wide range of soil conditions (or limestone conditi	y=1, n=0	y	physiogr	International,
4.11	Climbing or smothering growth habit	y=1, n=0	n	small	H.H. &
4.12	Forms dense thickets	y=1, n=0	y	sown	fa.gov.au/cont
5.01	Aquatic	y=5, n=0	n	native	International,
5.02	Grass	y=1, n=0	n	Mimosac	
5.03	Nitrogen fixing woody plant	y=1, n=0	y	fixing	International,
5.04	Geophyte (herbaceous with underground storage organs -- b	y=1, n=0	n	tree	
6.01	Evidence of substantial reproductive failure in native habitat	y=1, n=0	n	thorny,	International,
6.02	Produces viable seed.	y=1, n=-1	y	obium	H.H. &
6.03	Hybridizes naturally	y=1, n=-1		evidenc	
6.04	Self-compatible or apomictic	y=1, n=-1		evidenc	
6.05	Requires specialist pollinators	y=-1, n=0	n	s are	International,
6.06	Reproduction by vegetative fragmentation	y=1, n=-1	y	es	International,
6.07	Minimum generative time (years) 1 year = 1, 2 or 3 y	See left	4	start to	International,
7.01	Propagules likely to be dispersed unintentionally (plants growi	y=1, n=-1	n	East	H.H. &
7.02	Propagules dispersed intentionally by people	y=1, n=-1	y	East	H.H. &
7.03	Propagules likely to disperse as a produce contaminant	y=1, n=-1	n	fruits	
7.04	Propagules adapted to wind dispersal	y=1, n=-1	n	fruits	
7.05	Propagules water dispersed	y=1, n=-1		found	International,
7.06	Propagules bird dispersed	y=1, n=-1	y	are	International,
7.07	Propagules dispersed by other animals (externally)	y=1, n=-1		be	
7.08	Propagules survive passage through the gut	y=1, n=-1		dulce	International,
8.01	Prolific seed production (>1000/m2)	y=1, n=-1	n	fruits	International,
8.02	Evidence that a persistent propagule bank is formed (>1 yr)	y=1, n=-1	n	h seeds	International,
8.03	Well controlled by herbicides	y=-1, n=1	y	: Larger	ear.org/pier/sp
8.04	Tolerates, or benefits from, mutilation, cultivation, or fire	y=1, n=-1	y	ices	International,
8.05	Effective natural enemies present locally (e.g. introduced bioc	y=-1, n=1		Hawaii	International,
	Total score:		14		

References

Allison, S. D., C. Nielson, and R. F. Hughes. 2006. Elevated enzyme activities in soils under the invasive nitrogen-fixing tree *Falcataria moluccana*. Soil Biology & Biochemistry 38:1537–1544.

August-Schmidt, E. M., G. Haro, A. Bontrager, and C. M. D'Antonio. 2015. Preferential associations of invasive *Lantana camara* (Verbenaceae) in a seasonally dry Hawaiian woodland. Pacific Science 69:385–397.

Barron, A. R., D. W. Purves, and L. O. Hedin. 2011. Facultative nitrogen fixation by canopy legumes in a lowland tropical forest. Oecologia 16:511–520.

Batterman, S. A., L. O. Hedin, M. van Breugel, J. Ransijn, D. J. Craven, and J. S. Hall. 2013. Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. Nature 502:224–229.

Burris, R. H., F. J. Eppling, H. B. Wahlin, and P. W. Wilson. 1943. Detection of nitrogen fixation with isotopic nitrogen. The Journal of Biological Chemistry 148:349–357.

CABI, 2020. Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Castro-Díez, P., O. Godoy, A. Alonso, A. Gallardo, and A. Saldaña. 2014. What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. Ecology Letters 17:1–12.

Clarke, K.R. and Gorley, R.N. (2006) PRIMER v6: User Manual/Tutorial (Plymouth Routines in Multivariate Ecological Research). PRIMER-E, Plymouth.

Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: Implications. Annual Review of Ecology and Evolution Systematics 34:183–211.

Daehler, C. C., J. S. Denslow, S. Ansari, and H.-C. Kuo. 2004. A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific Islands. Conservation Biology 18:360–368.

Davidson, A. M., M. Jennions, and A. B. Nicotra. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters 14:419–431.

Davis, M. A., J.P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528-534.

Drake, D. C. 2011. Invasive legumes fix N_2 at high rates in riparian areas of an N-saturated, agricultural catchment. Journal of Ecology 99:515–523.

Funk, J. L. 2008. Differences in plasticity between invasive and native plants from a low resource environment. Journal of Ecology 96:1162–1173.

Funk, J. L., and P. M. Vitousek. 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature 446:1079–1081.

Global Invasive Species Database (2020) Species profile: *Albizia lebbeck*. Downloaded from http://www.iucngisd.org/gisd/species.php?sc=1293 on 02-04-2020.

Hall, S. J., and G. P. Asner. 2007. Biological invasion alters regional nitrogen-oxide emissions from tropical rainforests. Global Change Biology 13:2143–2160.

Hartwig, U. A. 1998. The regulation of symbiotic N_2 fixation: a conceptual model of N feedback from the ecosystem to the gene expression level. Perspectives in Plant Ecology 1:92–120.
Hedin, L. O., J. Brookshire, D. N. L. Menge, and A. R. Barron. 2009. The nitrogen paradox in tropical forest ecosystems. Annual Review of Ecology, Evolution, and Systematics 20:613–635.
Houlton, B. Z., Y.-P. Wang, P. M. Vitousek, and C. B. Field. 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. Nature 454:327–331.
Hughes, R. F., G. P. Asner, J. Mascaro, A. Uowolo, and J. Baldwin. 2014. Carbon storage landscapes of lowland Hawaii: the role of native and invasive species through space and time. Ecological Applications 24:716–731.
Hughes, R. F., and J. S. Denslow. 2005. Invasion by a N_2-fixing tree alters function and structure in wet lowland forests of Hawaii. Ecological Applications 15:1615–1628.
Menge, D. N. L., and L. O. Hedin. 2009. Nitrogen fixation in different biogeochemical niches along a 120000-year chronosequence in New Zealand. Ecology 90:2190–2201.
Menge, D. N. L., S. A. Levin, and L. O. Hedin. 2009. Facultative versus obligate nitrogen fixation strategies and their ecosystem consequences. The American Naturalist 174:465–477.
Menge, D. N. L., J. W. Lichstein, and G. Ángeles-Pérez. 2014. Nitrogen fixation strategies can explain the latitudinal shift in nitrogen-fixing tree abundance. Ecology 95:2236–2245.
Menge, D. N. L., A. A. Wolf, and J. L. Funk. 2015. Diversity of nitrogen fixation strategies in Mediterranean legumes. Nature Plants:1–5.
Mylona, P., K. Pawlowski, and T. Bisseling. 1995. Symbiotic nitrogen fixation. The Plant Cell 7:869–885.
Nagata, K. M. 1985. Early plant introductions in Hawaiʻi. Hawaiian Journal of History 19:35-61.
Pearson, H. L., and P. M. Vitousek. 2001. Stand dynamics, nitrogen accumulation, and symbiotic nitrogen fixation in regenerating stands of *Acacia koa*. Ecological Applications 11:1381–1394.
Plant Industry Division. 2017. Import program: Plant guidelines. State of Hawaiʻi.
RStudio Team 2015. RStudio: Integrated development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.
Richards, C. L., O. Bossdorf, N. Z. Muth, J. Gurevitch, and M. Pigliucci. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters 9:981–993.
Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93–107.
Schulten, J.R., T.C. Cole, S. Cordell, K.M. Publico, R. Ostertag, J.E. Enoka, J.D. Michaud. 2014. Persistence of native trees in an invaded Hawaiian lowland wet forest: Experimental evaluation of light and water constraints. Pacific Science 68:267-285.
Simberloff, D. 2013. Invasive Species: What Everyone Needs to Know. Oxford University Press, New York.

Sprent, J. I., and P. Sprent. 1990. Nitrogen Fixing Organisms: Pure and Applied Aspects. 1st edition. Chapman and Hall, London.

Staples, G. W., and C. R. Elevitch. 2006. *Samanea saman* (rain tree). Page 15. Species profiles for Pacific Island agroforestry. www.traditionaltree.org.

Thomson, L. A. J. 2006. *Pterocarpus indicus* (narra). Page 17. Species profiles for Pacific Island agroforestry. www.traditionaltree.org.

Udvardi, M., and P. S. Poole. 2013. Transport and metabolism in legume-rhizobia symbioses. Annual Reviews in Plant Biology 64:781–805.

US Forest Service, Pacific Island Ecosystems at Risk (PIER). Online resource at http://www.hear.org/pier/ accessed on 02-04-2020.

van Kleunen, M., E. Weber, and M. Fischer. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13:235–245.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. Oikos 57:7-13.

Vitousek, P. M., K. Cassman, C. C. Cleveland, T. Crews, C. B. Field, N. B. Grimm, R. W. Howarth, R. Marino, L. A. Martinelli, E. B. Rastetter, and J. I. Sprent. 2002. Towards an ecological understanding of biological nitrogen fixation. Biogeochemistry 57/58:1–45.

Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238:802–804.

Vitousek, P. M., and R. L. Jr. Sanford. 1986. Nutrient cycling in moist tropical forest. Annual Review of Ecology and Systematics 17:137–167.

Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999. Manual of the flowering plants of Hawaii. Page (S. W. Mill, Ed.). Revised. Bishop Museum and University of Hawaii, Honolulu, HI.

Whistler, W. A., and C. R. Elevitch. 2006. *Erythrina variegata* (coral tree). Page 16. Species Profiles for Pacific Island Agroforestry. www.traditionaltree.org.

Wurzburger, N., and L. O. Hedin. 2015. Taxonomic identity determines N_2 fixation by canopy trees across lowland tropical forests. Ecology Letters 19:62–70.

Yelenik, S., S. Perakis, and D. Hibbs. 2013. Regional constraints to biological nitrogen fixation in post-fire forest communities. Ecology 94:739–750.