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UNIVERSITY OF MIAMI

PLASTICITY AND ONTOGENY IN DYNAMIC ENVIRONMENTS: A CASE STUDY OF TWO NEOTROPICAL UNDERSTORY HERBS

By

Andrea C. Westerband

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PLASTICITY AND ONTOGENY IN DYNAMIC ENVIRONMENTS: A CASE STUDY OF TWO NEOTROPICAL UNDERSTORY HERBS

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For understory plants in tropical forests, light strongly influences rates of growth, survival, and reproduction, i.e., vital rates. To better understand how light availability influences the vital rates of two co-occurring understory herbs, *Calathea crotalifera* and *Heliconia tortuosa*, I monitored their growth, survival, and reproduction in forest plots. Plant size influenced the effect of light on vital rates, and increasing light did not always increase vital rates. Both species grew at small sizes but shrank at larger sizes, and larger individuals were more sensitive to changes in light than small individuals. I also found evidence of tradeoffs among vital rates, which were influenced by the interaction between plant size and light. These results support the hypothesis that life stage (ontogeny) influences the ability to capture and utilize light, and reveal that high light may negatively influence the demographic performance of plants that are adapted to deep shade.

To better understand how the ability to capture and utilize light influences growth, I estimated photosynthetic light responses for individuals in the forest plots and used model averaging to determine the importance of size, light, and photosynthetic responses for estimating future size. I found minor differences between the species in their

photosynthetic traits, but found significant differences in the importance of size, light, and physiology on growth. *Calathea* that diminished in size had one of two combinations of photosynthetic efficiency and respiratory costs, either higher respiratory costs coupled with lower photosynthetic efficiency, or, higher efficiency coupled with maximum photosynthetic capacity compared to individuals that increased in size. *Heliconia* that diminished in size also had different combinations, lower respiratory costs coupled with photosynthetic capacity or lower efficiency, coupled with lower respiration, and lower photosynthetic capacity than individuals that increased in size. These results do not support the hypothesis that that shade tolerant species should have high efficiency but low respiration and low photosynthetic capacity and therefore they indicate differences in mechanisms and degrees of shade tolerance among species.

I used a shadehouse experiment to determine whether demographic traits and functional traits were positively influenced by variability in light, light availability during the seedling stage, and soil moisture. I measured growth, survival, leaf lifespan, photosynthetic capacity, and biomass allocation of *Heliconia* and *Calathea* over two years. Plants in a variable light environment had greater growth than those in a constant light environment when moisture was low. At low moisture, a variable light environment increased growth when individuals started in low light and had no influence on growth when individuals started in high light. At high moisture, a constant light environment increased growth whether individuals started in low or high light. Survival decreased with increasing environmental variability but more so at high moisture. Photosynthetic capacity decreased for individuals in a variable light environment, when they had lived in high light as seedlings, but was unaffected by environmental variability when they had lived in low light as seedlings. *Calathea* had a significantly greater proportion of its total biomass aboveground than *Heliconia*. Leaf lifespan was unaffected by the treatments. Thus, although these species inhabit highly heterogeneous and variable light environments, these results do not support the hypothesis that environmental variability positively influences demographic and functional traits. Instead they reveal that environmentmal variability may be stressful even for plants found in intrinsically heterogeneous environments. They may have low plasticity, i.e., a low capacity to acclimate.

To determine the effects of static and dynamic light environments on population growth rates, I used Integral Projection Models. Growth was modelled as a function of plant size, maximum photosynthetic capacity (A_{max}), and light, and all other vital rates were modelled as functions of plant size and light. I estimated the population growth rates for both species over a range of light levels and A_{max} values. Finally, I evaluated three types of elasticity (proportional sensitivity) of the population growth rate for three levels of A_{max}: perturbations in the mean and variance of vital rates (E^S), increased variance of vital rates ($E^{S\sigma}$), environment-specific perturbations of vital rates ($E^S{}_\beta$). The latter are especially of interest as it addresses the relative impact on overall fitness of events that occur in different light environments, in other words the potential strength of selection of events that occur in high light vs shady environments. Adaptation to shady environments means a higher impact of events that occur in the shade on fitness whereas adaptation to high light environments means a higher impact of events that occur in high light on fitness.

As light availability increased, the population growth rate (λ) increased for *Calathea* but shrank for *Heliconia*, and increasing A_{max} had no effect on λ for *Calathea* but increased λ for *Heliconia* in low light. As A_{max} increased, the population growth rate in a dynamic light environment (λ_S) increased for *Heliconia*, but not *Calathea*. These results suggest that *Calathea* is more strongly adapted to shade than *Heliconia* and indicates that increasing the ability to use light has a direct positive influence on population growth, and therefore fitness.

Photosynthetic capacity (A_{max}) had an impact on how sensitive the population growth rate was to changes in life history rates for *Heliconia*, but not *Calathea*. *Calathea* λ_S was most sensitive to perturbations in intermediate-sized individuals under high light, and changing A_{max} had little effect on this relationship. When light availability was low, elasticities were more widely distributed among the size classes, but λ_S was much more sensitive to seeds and seedlings. In contrast, *Heliconia* λ_S was sensitive to intermediate- and large-sized individuals when light availability was low, and became much more sensitive to seeds and seedlings as light availability increased. Changing A_{max} had much more of an effect on elasticity of *Heliconia* when light was abundant than when light was scarce. These results demonstrate that photosynthetic physiology can have large consequences for the population dynamics of plants in both static and dynamic light environments, and that the effect of light on population dynamics is influenced by photosynthetic rates.

In conclusion, I found that increasing light and increasing the capacity to use light does not always improve demographic performance for plants adapted to living in the shade. Plant size interacts with light availability to influence rates of growth, survival,

and reproduction. Growth is in turn influenced by different combinations of physiological responses for my study species. I found that the effect of light variability is influenced by soil moisture and early life conditions. Finally, population growth rates, an indicator of fitness, are significantly influenced by photosynthetic capacity for one species but not the other, and reflect differences in the ability to use light. The broader impact of this study is that physiological responses can be used to predict the fates of species in temporally variable environments.

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Chapter I: Introduction

Resources vital to life often vary both temporally and spatially within the environment, limiting rates of growth, survival, and reproduction (hereafter, vital rates). For understory plants in tropical forests, vital rates are most strongly limited by the availability of light (Denslow et al. 1990). Light becomes abundant in the forest understory when gaps in the tree canopy form, most often due to treefalls (Brokaw 1985). However, canopy gaps are rare and ephemeral (Denslow et al. 1998), resulting in strong selective pressure for morphological and physiological plant adaptations that promote shade tolerance. Shade tolerance is defined as the minimum amount of light necessary for survival (Valladares and Niinemets 2008).

Tropical plants possess a wide range of morphological and physiological adaptations that influence degrees of shade tolerance, dictating the amount of resources invested in growth, maintenance, and reproduction. Plants adapted to take advantage of short-lived gaps in the tree canopy are generally referred to as gap species. Gap species are known as shade-intolerant, and will often grow both faster and larger than shade-tolerant species, hereafter referred to as understory species. Although this adaptive strategy has allowed gap species to maximize usage of an ephemeral resource, it comes at a cost. Because gap species are adapted to thrive under high levels of sunlight, their fitness has been shown to decrease once light abundance decreases, as typically occurs with closure of a canopy gap. This tradeoff is thought to result from the high cost of maintaining the photosynthetic machinery needed to harness and utilize large quantities of light (Givnish 1988). Contrary to gap species, understory species are highly shade tolerant and able to survive under very low levels of sunlight. One consequence of being highly shade adapted, however, is having photosynthetic machinery that is easily damaged at very high light levels, as occurs when gaps form.

Between these extremes, moderately shade tolerant species are able to exploit and survive within a greater range of light conditions than shade tolerant and shade-intolerant species. Moderately shade tolerant species are thought to be habitat generalists because of their ability to maintain high fitness in a variety of environments (Futuyma and Moreno 1988). To maintain fitness when the environment is temporally variable requires a broad tolerance to the environment or trait plasticity. Plasticity in plant traits refers to a trait's ability to be molded or altered to suit environmental conditions. Plasticity is different from variability among individuals in a population because it involves regulating the range of homeostatic conditions. We expect moderately shade tolerant species to possess a greater degree of plasticity in physiological and morphological traits for harnessing light, compared to strictly gap or strictly understory species (Ellsworth and Reich 1996).

Ontogenetic changes in morphological and physiological traits can heavily influence the demographic parameters that determine fitness. The production of carbohydrates in leaves is regulated by rates of gas exchange from pores known as stomata. Within leaves, net photosynthesis and gas exchange have been shown to peak early in development and subsequently decline with age (Jurik et al. 1979, Kubien et al. 2007). An early study (Jurik et al. 1979) found that young leaves exhibited greater plasticity in gas exchange and net photosynthesis across different light levels than old leaves. Reductions in rates of gas exchange are thought to result from shifts in resource allocation (away from leaves), or alternatively, senescence. Several studies of angiosperms have found that photosynthetic rates decrease with age, size, and the transition to a reproductive life stage (Donovan and Ehleringer 1991, Bond 2000). As plants change in size, their allocation patterns may also change, for example, greater investment in structural tissue to support larger leaves.

Morphologically, traits that increase total carbon gain under one light environment may not be as beneficial under a different light environment. For example, a plant which increases its leaf area in order to utilize light from a canopy gap will incur large respiratory costs once that gap closes. To reduce those costs, a plant may drop leaves, produce thinner leaves, or shift allocation away from future leaf production, i.e., growth. Leaf toughness (an indicator of thickness) and low turnover rates in tropical tree species have been associated with better survival in shade, but not in gaps (Kitajima et al. 2012) because having longer-lived leaves helps recoup resources invested in leaf production (Coley et al. 1985). Furthermore, changes in leaf architecture have been shown to be light dependent, influencing future light capture and thus carbon gain in gaps as well as the understory (Naumburg 2001). When light is not limiting, we expect natural selection to favor fast growth and leaf turnover rates, and a high maximum photosynthetic capacity (Bongers and Popma 1990). These leaf level traits work in conjunction to produce the functional trait syndrome used to explain the well observed tradeoffs between growth and mortality rates, in forest tree species (Kitajima 1994, Wright et al. 2010).

The utilization of light is also directly influenced by intrinsic leaf level properties relating to photochemistry and light use efficiency. One such property, maximum photosynthetic capacity (A_{max}), represents the uppermost photosynthetic limit, i.e., the point at which the rate limiting step for carbon gain shifts from light availability to leaf chemistry. A_{max} is higher for shade intolerant species than it is for shade tolerant species. Another important leaf level property, quantum efficiency (alpha) is defined as the absorption and release of high energy light via protein complexes known as photosystems. High quantum efficiency allows shade intolerant gap species to avoid damaging their photosystems due to overabundance of light, known as photoinhibition. Because adaptation to high light can only be accomplished with large investments in photosynthetic efficiency, sun leaves have been shown to possess a higher respiration rate (R_d) per unit leaf area than shade leaves (Sims and Pearcy 1994). The amount of light needed to offset respiration is known as the 'light compensation point' (LCP). Plants that encounter light environments at or below the LCP are incapable of producing a net gain in carbon and should exhibit a reduction in long term survival (Baltzer and Thomas 2007). Shade intolerant species have been shown to have a higher LCP than shade tolerant species (Givnish 1988).

Because plant architecture and carbon allocation patterns directly impact how plants utilize light (Valladares et al. 2002), it has been hypothesized that these two factors are more important drivers of adaptation to light than photosynthetic acclimation (Sims and Pearcy 1994). As plants age, the position of their leaves determines the degree of self-shading, and therefore light uptake. Leaf architecture may therefore influence future changes in morphology such as, high leaf turnover, or elongation of stems to reach light higher up in the forest canopy. Plant architecture may also change in accordance with mode of reproduction. For example, many herbaceous plants are known to form dense thickets of clonal growth, resulting in a few large (high total leaf area), genetically isolated individuals, which may have increased probabilities of survival compared to individuals that do not exhibit an asexual growth form. Belowground architecture may work in conjunction with changes in aboveground morphology, to increase carbon gain per individual. Roots may lengthen to increase stabilization as both height and leaf area increase. Increases in root biomass also aid in the absorption of water and nutrients (Bloom et al. 1985). Although soil water is typically not a limiting resource in tropical rainforests, plants within gap environments may experience a greater degree of drought stress compared to understory plants (Becker et al. 1988).

Variability in the amount of available light has been studied with respect to vital rates and plant population dynamics (Tuljapurkar and Horvitz 2006, Metcalf et al. 2009). Translating leaf level responses to population dynamics relies on understanding the links between photosynthetic performance and demographic performance, and can be accomplished using mathematical models that incorporate the effects of light availability across these scales. Demographic rates are directly influenced by how individuals that compose a population utilize resources in the environment. Thus, to model the effects of a dynamic light environment on fitness, a chain of rate relationships can be used to link light availability to population growth.

A population's growth rate, λ, can be used as a measure of average fitness (Charlesworth 1974), allowing us to make predictions regarding the effects of fluctuating light and light-adapted traits on plant fitness. Estimating a plant's fitness when the environment changes randomly over time is estimated using λ_S (Rees and Ellner 2009) and depends on correctly translating physiological responses into demographic rates (probabilities of growth, survival, and reproduction) over a plant's lifetime. For plants, life stage and size are often interlinked and have been shown to be better predictors of demographic rates, and therefore fitness, than age (Caswell and Werner 1978, Cochran and Ellner 1992). In order to incorporate physiological responses into a demographic model, individuals must be monitored at each life stage and under different environmental conditions. Using different levels of light availability, we can determine how demography relates to stage, size, and physiological responses, and how these factors relate to one another.

Evaluating the sensitivity of λ with respect to light availability, can be used to predict how future changes in light availability might influence the long term success of co-existing species. Tropical forest environments worldwide are expected to undergo major shifts in spatial extent and resource availability resulting from anthropogenic disturbance and global climate change. As gaps open and close in the forest canopy, species that are favored by the current light conditions may experience population growth, while those that are not favored will experience a decline. Although several moderately shade tolerant species survive under similar light environments, the physiological mechanisms allowing them to do so may differ. Mechanistic explanations for how plant species coexist have been heavily studied in the forest environments with regards to coexistence among gap and shade species and possible impacts on community composition (Ishii and Asano 2009). However, to elucidate the variety of mechanisms tropical understory species use to cope with dynamic environments requires development of a mathematical model integrating experimentally determined responses to light.

The primary objectives of this dissertation are 1) to understand how the availability of light interacts with plant size to influence probabilities of growth, survival, and reproduction 2) to model the effects of changes in physiological traits on growth rates 3) to understand how functional traits and demographic rates respond to changes in resource availability, and 4) to integrate morphological and physiological parameters into stage-specific demographic models that estimate fitness in temporally variable environments. The study species are two moderately shade tolerant perennial species, *Heliconia tortuosa* and *Calathea crotalifera* (order Zingiberales), which are widespread in a mid-elevation tropical rainforest in Costa Rica. Understory herbaceous plants within the order Zingiberales are well suited to demographic and physiological studies due to their wide availability in the tropics, fast growth rates, and degrees of shade tolerance. This dissertation research bridges the gap in translating leaf level responses to plant population dynamics by incorporating stage-specific morphological and physiological traits into estimation of vital rates.

Chapter II: Interactions between plant size and canopy openness influence vital rates and life-history tradeoffs in two Neotropical understory herbs[1]

Overview

For tropical forest understory plants, the ability to grow, survive, and reproduce is limited by the availability of light. The extent to which reproduction incurs a survival or growth cost may change with light availability, plant size, and adaptation to shade, and may vary among similar species. We estimated size-specific rates of growth, survival, and reproduction (vital rates), for two Neotropical understory herbs (order Zingiberales) in a premontane tropical rainforest in Costa Rica. During three annual censuses we monitored 1278 plants, measuring leaf area, number of inflorescences, and canopy openness. We fit regression models of all vital rates and evaluated them over a range of light levels. The best fitting models were selected using Akaike's Information Criterion. All vital rates were significantly influenced by size in both species, but not always by light. Increasing light resulted in higher growth and a higher probability of reproduction in both species, but lower survival in one species. Both species grew at small sizes but shrank at larger sizes. The size at which shrinkage began differed among species and light environments. Vital rates of large individuals were more sensitive to changes in light than small individuals. Increasing light does not always positively influence vital rates; the extent to which light affects vital rates depends on plant size. Differences among species in their abilities to thrive under different light conditions and thus occupy distinct niches may contribute to the maintenance of species diversity.

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[1] Westerband, A. C. and C. C. Horvitz. 2015. Interactions between plant size and canopy openness influence vital rates and life-history tradeoffs in two Neotropical understory herbs. American Journal of Botany **102**:1290-1299.

Background

In tropical forests, light is a major limiting resource for plant growth, survival, and reproduction (Chazdon, 1988). The availability of light in moist tropical forests is strongly influenced by the opening and closing of gaps in the tree canopy (Denslow et al., 1990; Dirzo et al., 1992), as well as brief and often unpredictable pulses of direct light, known as sunflecks (Chazdon and Pearcy, 1991). Thus, for plants living in the dark forest understory, the ephemeral nature of light sources may promote morphological and physiological adaptations that efficiently maximize light capture (Givnish, 1988) while minimizing respiration costs (Givnish, 1988; Walters and Reich, 2000). Adaptations to shade increase the fitness of plants in low light environments, and plant fitness should change as the degree of canopy openness changes over an individual's lifetime. Here we empirically estimate per capita rates of growth, survival, and reproduction in two Neotropical understory herbs, hereafter vital rates. Vital rates are strongly influenced by the availability of light for tropical trees (Alvarez-Buylla and Martinez-Ramos, 1992; Clark and Clark, 1992) and understory herbs (Mulkey, Smith, and Wright, 1991; Horvitz and Schemske, 1994, 1995; Gagnon et al., 2011).

The vital rates of plants are size-dependent (Horvitz and Schemske, 1995; Metcalf et al., 2009), likely due to ontogenetic shifts in resource acquisition and allocation (Worley and Harder, 1996; Lusk, 2004), as well as size-associated shifts in physiological performance (Bond, 2000). In herbaceous perennials, leaf area ratio (ratio of leaves to total biomass) has been shown to decrease from the juvenile to the senile stage, resulting in a reduction in the ability to capture light (Niinemets, 2004, 2005), while allocation to belowground growth generally increases with size in both annuals and perennials (Geng et al., 2007). Thus, plant size and life stage can be a strong predictor of allocation strategy as well as physiological performance, and is likely to be driven by the availability of limiting resources. Under stressful conditions, reductions in size (hereafter shrinkage) could be adaptive; populations with shrinkage have been shown to have a faster recovery after disturbance than populations without shrinkage, as measured by their damping ratios (Salguero-Gomez and Casper, 2010). Therefore, interpreting the size-dependency of vital rates across varying light levels can provide crucial insight regarding how tropical understory species cope with dynamic light environments.

Life history evolution theory posits that costs are paid in the currency of fitness when beneficial changes in one life history trait results in detrimental changes in another, defined as a life history tradeoff (Stearns, 1989). The tradeoffs themselves result from differences in allocation of resources towards growth, survival, and reproduction. Investment of resources into these categories is often determined by the degree of shade tolerance for understory plants. We characterize the relative shade tolerance of species by quantifying how they differ in the minimum amount of light they require to survive (Valladares and Niinemets, 2008). Using this metric, a plant species that can survive in the least amount of light is considered the most shade tolerant. The ability to tolerate shade is often negatively associated with the ability to take advantage of high light (Givnish, 1988). As the degree of shade tolerance increases among species, the ability to efficiently use light will often decrease as proteins become more sensitive to degradation, a process known as photoinhibition (Long, Humphries, and Falkowski, 1994; Valladares and Niinemets, 2008). Several studies have found that plants that allocate resources towards survival in low light environments are able to persist and “wait” for gaps to open in the canopy (Mulkey, Smith, and Wright, 1991). Differences in species in their ability to persist in low light versus their ability to colonize gaps is a key determinant of successional patterns in forest communities (Rees et al., 2001). Additionally, the ability to tolerate light may be important in determining the success of understory species adapted to shade, as high light can have detrimental effects on leaves (see Discussion).

Despite the significant contribution of herbs to the diversity (Gentry and Dodson, 1987) and functioning of tropical forests (e.g. soil nutrient dynamics, succession, etc.), they remain understudied with respect to their demographic responses to gap dynamics. Our objective was to estimate size-specific per capita rates of growth, survival, and reproduction for two co-occurring Neotropical herbs (*Heliconia tortuosa* and *Calathea crotalifera*) across a naturally occurring continuum of light environments. We parameterized regression models for effects of two continuous variables, size and light, on future size, survival, and reproduction. Light, measured by canopy openness, was assayed for each individual in the study and it spanned the range of natural variation in light availability for our study species within our study site, a tropical rainforest. Our chosen study species are common at our study site and inhabit a wide range of light environments, facilitating comparisons of demographic responses in response to natural light environments. Vital rates were measured over a three-year period and coupled with measures of canopy openness to investigate the following (1) Does canopy openness, a metric of light availability, influence the vital rates of two widespread understory herbs? (2) Do vital rates change with plant size? (3) Do *Heliconia* and *Calathea* show evidence of tradeoffs between growth, survival, and reproduction? (4) Do tradeoffs in resource allocation depend upon canopy openness, in particular, do plants in low light experience high survival but low growth, while in high light can there be both high survival and high growth?

Interspecific differences in shade tolerance have been postulated as a mechanism responsible for coexistence among tropical forest species (Sterck et al., 2011). Due to their similar evolutionary history and widespread abundance within the forest understory at our study site, we hypothesized that the vital rates of these co-occurring species would be similar to those reported in the literature for shade-adapted species, i.e., high survival in low light, low growth in high light (Kobe et al., 1995), and high reproduction in high light. However, based on morphological differences among the two species, we predict that *Calathea* is more shade-tolerant than *Heliconia*, and should exhibit a greater tradeoff between growth and reproduction than *Heliconia* (in particular, in the shade, *Calathea* should reproduce relatively less but grow more than *Heliconia*). Morphologically, *Calathea* shoots branch out from rhizomes at a distance much lower to the ground than *Heliconia* (Kennedy, 1973), decreasing the degree of clumping in leaves and increasing light interception efficiency, which generally increases with shade-tolerance (Niinemets, 2006; Duursma et al., 2012). Additionally, *Calathea* leaf bases are thickened into a pulvinus, which aids in regulating the capture of light throughout the day (Herbert and Larsen, 1985). Thus, differences in morphology (and possibly physiological performance) may confer different degrees of shade tolerance between our study species, allowing them to coexist locally over a range of light environments.

Methods

STUDY SYSTEM—*Heliconia tortuosa* is a perennial, herbaceous understory monocot that exhibits rhizomatous growth, and ramets grow 1-2 m tall. Individuals reproduce sexually via seeds, and asexually via clonal shoots that are connected by subterranean stems called rhizomes, and can spread laterally to form clumps. Inflorescences are characterized by bright red floral bracts (Linhart, 1973) and bright yellow flowers are produced in these bracts resulting in blue fruits that are held in the bract until the ramet falls to the ground, dispersing the fruit. Each fruit produces two to three seeds. *Calathea crotalifera* is a perennial, herbaceous understory monocot that is also rhizomatous, and ramets grow 1-3 m tall. Inflorescences possess yellow, erect floral bracts (reminiscent of a rattlesnake's rattle) that grow up to 25 cm long. *Calathea* reproduces sexually and asexually and several clonal shoots arise from a sympodially branched rhizome near the ground (Kennedy, 1973), resulting in greater spatial spread among leaves on a ramet, compared to *Heliconia*. *Calathea* flowers are yellow-white and produce seed capsules containing one dark blue seed surrounded by white flesh, and do not persist on the inflorescence. *Heliconia* is hummingbird pollinated whereas *Calathea* is pollinated by bees. Both species have been considered moderately shade tolerant, although no quantitative assessment of their abilities to tolerate low light were previously made (Berry and Kress, 1991). These study species were chosen because they are among the most common understory plants at our study site, they occupy a large range of light environments (including under large gaps and completely closed canopies), and they reach large enough sizes (up to 3 m tall) to compete with tree saplings and other herbaceous species for light, making them likely contributors to the process of forest succession in our plots.

Although both species have clonal growth, we did not account for clonality in our estimates of vital rates because our field observations led us to the conclusion that a majority of the individuals in our study plots arose from seed. Vascular connections among clonal shoots has been to shown to strongly influence the transfer of resources in a closely related species, *Calathea marantifolia* (Matlaga and da, 2009).

This study was conducted at the Las Cruces Biological Station, located 1200 m above sea level (8° 47' 7" N, 82° 57' 32" W) in Coto Brus county, southern Costa Rica. This region is designated as mid-elevation premontane forest and receives approximately 4 m of annual rainfall. There is a dry season from January to March and mean diurnal temperature over the year is between 13 and 26°C. Our study sites were located in primary, secondary, and selectively logged forest, within the station.

In June 2012, we established 17 circular plots (each 314 m^2), centered on areas containing both study species. Six plots were established within the selectively logged primary forest, six in the secondary forest, and five in the primary forest, although we do not focus on these distinctions of logging history in the current analyses. Out of 17 plots, seven had gaps ranging in size from 63 to 132 m^2 in July 2012. In these plots, 1278 individual plants were tagged. Of these, 482 were *Calathea crotalifera* and 796 were *Heliconia tortuosa*. For each individual, we measured the length of each leaf and the number of inflorescences in the month of June, from 2012 to 2014. We measured leaf lengths in the field and estimated leaf areas for each species using a regression relationship specific to our study site (Horvitz and Corff, 1993). Areas of individual leaves were then summed to give total leaf area per plant, used here as an indicator of plant size. Survival was determined by the presence or absence of individuals at the next annual census. The probability of reproducing was determined using presence/absence of inflorescences. Reproductive output was calculated as the number of inflorescences per individual. We also measured canopy openness over each individual plant on a scale of 1 to 25, using a rapid assessment technique known as the canopy scope (Brown et al., 2000). With this technique, a clear sheet of plexiglass is imprinted with an array of 25 dots, which is pointed towards the largest canopy gap. The number of dots in the gap are counted, and indicate degree of canopy openness, used here as a metric of light availability. Estimates of canopy openness with hemispherical photographs have been shown to strongly correlate with canopy openness scores using the canopy scope (Brown et al., 2000, $r=0.95$, $p<0.01$, $n=16$). The highest observed canopy openness in 2014 was approximately 30% (canopy score of 25) and the lowest was 1% (canopy score of 1)(Brown et al., 2000). We used the full range of observed light to quantify the dependence of vital rates on light and size. However, to visualize the interaction of light with size, we subsequently examined the effects of size on vital rates at each of seven light levels, evaluating the regression equations at each one. We chose canopy scores 1 through 7 because this range spans the 5th to 95th percentile of canopy openness scores at our study site.

DATA ANALYSIS—We evaluated the effect of plant size (total leaf area) and light levels (canopy openness) on growth, survival, and reproduction (vital rates) using regression models. We evaluated the effect of species (factor), size (continuous variable), and light (continuous variable) and all combinations thereof on vital rates, by testing 13 models (Table 1). For each vital rate, we selected the best model using Akaike's Information

Criterion (AIC) values (Akaike, 1974). Although models with a ΔAIC ≤2 are statistically identical, we focus principally on the best model because its coefficients were used to examine and plot the effects of light level on demographic rates. We then tested the effects of light on the vital rates of each species independently, using three models (Tables 2 and 3) that included size, light, and their interaction.

For example, to estimate the effects of size, light and their interaction on growth we constructed three nested models, with current size as a predictor of future size:

$$Size_{t+1} = x_0 + x_1 Size_t \tag{1}$$

$$Size_{t+1} = x_0 + x_1 Size_t + x_2 Light_t \tag{2}$$

$$Size_{t+1} = x_0 + x_1 Size_t + x_2 Light_t + x_3 Size_t Light_t \tag{3}$$

Similarly, the probabilities of surviving and reproducing were estimated using nested logistic regression models, where the model with all the main effects and the interaction was

$$Logit(probability\ of\ survival) = x_0 + x_1 Size_t + x_2 Light_t + x_3 Size_t Light_t \tag{4}$$

Inflorescence production was estimated using nested poisson models, where the model with all the main effects and their interaction was

$$Log(Number\ of\ inflorescences) = x_0 + x_1 Size_t + x_2 Light_t + x_3 Size_t Light_t \tag{5}$$

We used the regression coefficients from Tables 2 and 3 to evaluate the vital rate responses over a range of light levels (canopy scores 1 through 7) for each species.

Growth was statistically modelled, as total leaf area at time t+1 versus total leaf area at time t. The parameters obtained from this model were then employed to examine the predicted change in total leaf area between t and t+1 versus total leaf area at t. Total leaf area was converted to a log scale to improve statistical model fit. It was back-transformed to calculate the change in leaf area (square centimeters), defined as the difference obtained by subtracting leaf area at time *t*+1 from leaf area at time *t*. A negative change in leaf area from *t* to *t*+1 means that plants shrink, which is quite reasonable biologically in these species. All statistical analyses were conducted using the program R v. 3.0.2 (R Core Team, Vienna, Austria, http://www.R-project.org/).

To determine differences in effect sizes due to species, we used the slope coefficients from the regression models with size, light, and species as factors, and all interactions (Table 2.1). We divided the sum of the slope coefficients of both species by the slope coefficient of *Calathea* to determine the proportional change in the slope in *Heliconia* relative to *Calathea*. For example, the slope coefficient of the size by light interaction for *Calathea* was 0.0714, and was calculated for *Heliconia* by adding 0.0714 and -0.121 to get -0.0496. These values were exponentiated, and then divided as follows:

$$Exp(-0.0496)/Exp(0.0714) = 0.886 \tag{6}$$

Finally, we subtracted 0.886 from 1, which translates to an 11% increase in the odds of reproducing in *Heliconia* relative to *Calathea*. We exponentiated these coefficients for all models except growth, since the data were log transformed (Cooper, Hedges, and Valentine, 2009).

To assess tradeoffs among growth, survival, and reproduction, we modeled the growth of reproductive and non-reproductive individuals above the threshold size at which we observed reproduction, and selected the best model using AIC values. We could not model survival of either group because of the low number of deaths (less than 5% of the variation in survival was explained by our models). The best models of growth were used to plot the results for each species.

Results

When data from both species were pooled, we found that the best models of growth and reproduction (probability of reproduction as well as number of inflorescences) included species as a factor (Table 2.1). For survival, even though species was not a factor in the best model, it was a factor in other highly ranked models which did not differ significantly from the best model in AIC, for example in the third best model (ΔAIC=1.68, Table 2.1). We conducted separate regression analyses for each species with size, light, and all combinations thereof, and constructed figures using coefficients from the best models for each species (Tables 2.2 and 2.3). We found a very large difference between the likelihoods of the best model and of the second best model for our analyses of the probability of reproduction in both species, and of inflorescence production conditional on being reproductive in *Heliconia*. Strong support for the best model was indicated by ΔAIC greater than 8 for the second best model. Effect sizes were calculated using the regression coefficients from the model that included size, light, species, and all interactions, and are reported only when supported by the best models of growth, survival, and reproduction for both species.

Current size was a strong predictor of future size in both species (Figure 2.1). Over the range of light levels, *Calathea* experienced less shrinkage than *Heliconia* (Figure 2.1A and 2.1B respectively), even in the highest light. Size and light influenced growth in both species. The effect of light on growth was influenced by size in *Calathea*, but its effect was independent of size in *Heliconia* (Tables 2.2 and 2.3). The relationship between current size and change in size was made apparent by back-transforming the log-scaled values of size (Figure 2.1C and 2.1D are *Calathea* and *Heliconia*, respectively).

Both species experienced minimal growth at small sizes, and then began shrinking after a threshold size, with the exception of *Calathea* in the highest light environment (canopy score of 7, corresponding to 7% openness). This threshold size varied with light availability (Figure 2.1) and species. Threshold sizes for *Calathea* were 9-10 times greater than those of *Heliconia* for canopy scores ≤4, 13 times greater at a canopy score of 5, and 44 times greater at a canopy score of 6. Threshold sizes for *Heliconia* were far less sensitive to changes in light than in *Calathea*. In both species, large individuals shrank less as the availability of light increased, while the growth of small individuals was far less responsive to changes in light availability (Figure 2.1c and 2.1d). For both species, the best model of future plant size (lowest AIC) included current plant size and light environment, explaining 89% of the variation for *Calathea*, and 66% of the variation for *Heliconia*. The effect of size on growth was influenced by light (an interaction) by a factor of 0.9 in *Calathea* whereas the best model of growth in *Heliconia* did not include this interaction.

In *Calathea*, the effect of light on survival was influenced by size and light but the effect of light on future size was not influenced by current size (no interaction). Both species show increasing survival with size (Figures 2.3A and 2.3B). With increasing size, the proportional odds of survival were 16% higher in *Heliconia* relative to *Calathea*. In *Calathea* of all sizes, survival was slightly higher in low light than high light, whereas in *Heliconia*, the best model of survival included size but not light (Figure 2.3). In *Calathea*, survival was less sensitive to changes in light than growth (Figure 2.1). The best model for each species explained only 20% of the variation in survival in *Heliconia*, compared to 25% of the variation in survival in *Calathea* (Tables 2.2 and 2.3).

The probability of reproducing, and reproductive output was strongly, positively influenced by size in both species (Table 2.2, Table 2.3). In *Calathea*, the odds of reproducing increased 4.7 times for every one unit increase in size, while the odds increased by a factor of 6.8 in *Heliconia*. Increasing light also positively influenced the probability of reproduction in both species, but reproduction in large individuals was more sensitive to light than small individuals. Furthermore, the probability of large *Calathea* reproducing (Figure 2.4A) was more sensitive to changes in light than the probability of large *Heliconia* reproducing (Figure 2.4B). Small *Heliconia* had a slightly higher probability of reproducing in high light than small *Calathea* in high light. The best models explain 34% of the variation in the data for *Calathea* and 31% of the variation in *Heliconia* (Table 2.2, Table 2.3).

The number of inflorescences produced (for those individuals that reproduce) increased with size in both species (Figures 2.4C and 2.4D). With increasing size, reproductive output increased by a factor of 2.3 in *Calathea*, and 1.3 in *Heliconia*. The best models of inflorescence production included the interaction between size and light in *Heliconia*, but only included size for *Calathea* (Tables 2.2 and 2.3). Inflorescence production conditional on being reproductive increased with light availability in large *Heliconia* but decreased with light in small *Heliconia* (Figure 2.4D). *Calathea* reproduce equally well regardless of their light environment, over their range of sizes (Figure 2.4C). The best model for *Calathea* explains 50% of the variation in the data, while the best model for *Heliconia* explains only 28% of the variation.

To better assess tradeoffs among the vital rates, we also modelled the effects of size and light on growth in reproductive and non-reproductive individuals above the threshold size of reproduction (1378 cm^2 and 130 cm^2 in *Calathea* versus *Heliconia*, respectively). The effects of size and light on survival could not be modelled in either group because of the low number of deaths among individuals above this threshold size. For non-reproductive *Calathea*, light and size influenced growth but did not interact (Appendix 1), whereas size was the only factor that influenced growth in non-reproductive *Heliconia* (Appendix 2). In reproductive *Calathea*, light had no effect on growth, but size did (Appendix 3), whereas growth in reproductive *Heliconia* was affected by size and light, but not by their interaction (Appendix 4). Increasing light negatively influenced growth in non-reproductive *Calathea*, and individuals shrank over all sizes and light environments (Appendix 5). In contrast, growth in non-reproductive *Heliconia* was not affected by light (Appendix 5). Increasing size had a slightly positive effect on growth in reproductive *Calathea* (Appendices 3, 6), and increasing light positively influenced growth in reproductive *Heliconia* of all sizes (Appendices 4, 6). The size at which reproductive *Heliconia* began shrinking was nearly doubled compared to the model that combined both reproductive and non-reproductive individuals (not pictured).

In summary, linear regression analyses demonstrated that vital rates were strongly dependent on size in both species. Survival and reproduction increased with size in both species. For growth, the availability of light determined the threshold size at which individuals would grow or shrink, in both species. Over all evaluated light levels, *Heliconia* transitioned from growing to shrinking at relatively small sizes while *Calathea* did not exhibit shrinking until reaching somewhat larger sizes. Increasing light positively affected growth and reproduction in *Calathea* but negatively affected survival. These effects were much more pronounced in large individuals than small individuals. Conversely, increasing light had little influence on growth in *Heliconia*, did not affect survival, and positively affected reproduction. Similar to *Calathea*, the effect on reproduction was more evident in large individuals than small individuals. The availability of light had no effect on growth in reproductive *Calathea* but did affect growth in reproductive *Heliconia* (Appendix 7). In contrast, the availability of light influenced growth in non-reproductive *Calathea* (negatively) but did not influence growth in non-reproductive *Heliconia* (Appendix 7).

Discussion

EFFECT OF LIGHT ON VITAL RATES—Light is thought to be a key limiting resource for plant growth, survival, and reproduction in tropical forests (Chazdon, 1988). Its availability in the understory is strongly influenced by tree fall gap dynamics (Denslow et al., 1990). We estimated per capita rates of growth, survival, and reproduction for two Neotropical herbs common in the forest understory, and found that increasing light availability did not always translate into higher vital rates. In general, size significantly influenced the vital rates of both species, as in other herbaceous plants (Horvitz and Schemske, 1995; Bruna, 2003). Both species showed positive growth when small, but exhibited shrinkage at very large sizes in most light conditions. For each species and light level, there was a characteristic threshold size below which plants grew and above which they shrank. *Heliconia* started shrinking at smaller sizes: threshold sizes were 9 to 44 -fold greater in *Calathea* relative to *Heliconia* depending upon light levels. At the highest light level in the data set (7% canopy openness), *Calathea* did not exhibit shrinkage at any size. These results support our hypothesis that *Calathea* is better adapted to moderate shade than *Heliconia*, maintaining positive growth over a wider range of sizes and light conditions.

Shrinkage is common in herbaceous perennials; Salguero-Gomez and Casper (2010) reported shrinkage in 87.5% of 80 species belonging to 29 families. Here, we consider five explanations of shrinkage. First, the ability to shrink may be adaptive under stressful conditions, such as resource-limited environments (Salguero-Gomez and Casper, 2010). In our study, medium to large-sized individuals shrank less as light increased. Thus, increasing light may result in less stressful conditions for medium and large individuals, decreasing their need to shrink. In fact, small plants grew rather than shrank even in low light. Our result is consistent with other tropical plants that exhibited declines in growth as they increased in age and developmental stage. This was attributed to the decreasing ratio of leaf area to biomass (Lusk, 2004; Niinemets, 2005); as leaf area ratio decreased, respiratory costs increased relative to carbon gains from photosynthesis. As a result, small plants more easily achieved net growth under low light than large plants. Such high respiratory costs of large individuals appears to have been offset in the highest light environment in our study for *Calathea* (7% canopy openness), resulting in net growth, whereas large individuals in low light were unable to offset these costs. A second perspective on shrinkage: our metric of plant size is based on leaf tissue, not on any measure of belowground biomass. We cannot rule out the possibility that individuals with lots of leaf tissue in low light are increasing investment in belowground growth (i.e., rhizomes and roots) rather than increasing or maintaining leaf tissue. As the availability of light increases, the investment of resources may then shift back to the production of leaves. In another perennial herb, *Pimpinella saxifraga*, the fraction of plant biomass devoted to leaves decreased with age while belowground biomass increased (Niinemets, 2005). Third, diurnal and seasonal decrease in plant biomass may result from internal water stress, and not represent an adaptive response *per se* but instead a physical consequence of tissue dehydration (Kozlowski, 1965); such a scenario would be more likely in individuals exposed to high light. Fourth, because large individuals are more exposed to high light than small individuals, their leaves may have greater transpiration rates, which could promote leaf loss and shrinkage. Finally, because we measured changes in size using leaf area and not biomass, we cannot rule out the possibility that large individuals are producing fewer thicker leaves in low light. In such a scenario, the ability to capture light may decrease but the ability to use light photosynthetically could be enhanced, negating the effects of a reduction in size.

Similar to growth, survival and reproduction were significantly influenced by plant size in both species. Large plants had a higher probability of surviving and reproducing than small plants. *Calathea* survival was higher in low light than in high light over all sizes, whereas *Heliconia* survival was similar among light levels. Thus increasing light does not always translate into beneficial changes in vital rates. In particular, *Calathea* may be more shade-adapted than *Heliconia*. A possible explanation for slightly lower survival in high light is photoinhibition; other understory herbs that were suddenly exposed to large quantities of light have been seen to experience photoinhibition (Gouallec, Cornic, and Blanc, 1990; Lovelock, Jebb, and Osmond, 1994). Photoinhibition is a reduction in the efficiency of photosynthesis resulting from damage to proteins in the photosystems or from the dissipation of excess energy (Krause, 1988), and is often associated with rapid leaf senescence (Lovelock, Jebb, and Osmond, 1994). If leaf senescence is high but leaf production is also high, although individuals would experience a net positive change in size over time, the increased stress could result in lower survival. We did not measure leaf turnover in this study, however, we argue that because *Calathea* in high light are growing more but surviving less as light increases, that photoinhibition is a plausible mechanistic explanation. Differences in the degree of photoinhibition between our study species may be an example of how light tolerance plays a role in determining the success of different species under varying light levels.

Contrary to survival, the probability of reproduction was positively influenced by light and size in both species. Large individuals had a higher probability of reproducing than small individuals, but the probabilities were significantly higher as light increased. Thus, both species do not start reproducing until they reach a minimum size, but once *Heliconia* achieve this size they produce more inflorescences in high light than in low light, whereas production in *Calathea* is unaffected by light.

POPULATION DYNAMICS—The regression analyses of vital rates on plant size that we present in this paper for each species in each light environment could be used as components of constant environment integral projection models (IPM) (Easterling, Ellner, and Dixon, 2000) of population dynamics in each light environment. These results could also be integrated into population dynamics models in dynamic environment models, which are far more realistic for this study system. To construct such models would require data on dynamic changes in light environment and data on dynamic feedback between light and plant size.

RESOURCE ALLOCATION AND LIFE HISTORY TRADEOFFS—Resource allocation strategies may shift as plants age and change size (Worley and Harder, 1996), and are also likely to interact with light availability. Although our study species establish and persist in low light they only experienced net growth at very small sizes. *Calathea* in high light experienced a net positive change in leaf area over all sizes. In contrast to growth, the number of inflorescences produced was not influenced by light in *Calathea* even though increasing light increased the probability of reproducing, whereas *Heliconia* were more likely to reproduce, reproduced more, and grew more with increasing light. Comparisons of growth between reproductive and non-reproductive individuals revealed that when *Calathea* were reproducing, their ability to grow was not influenced by the amount of light they received, whereas when *Heliconia* were reproducing they were able to grow as in higher light and after attaining a certain size (small individuals shrank in the lowest light environment).

Availability of resources has been shown to influence life history tradeoffs (Kitajima, 1994; Hansen, Garcia, and Ehlers, 2013). We found evidence that some vital rates varied across light environments. In low light, *Calathea* grew only at small sizes while in high light *Calathea* grew over all sizes. *Calathea* survived better in low light than in high light, but inflorescence production was not affected by light. In low light, *Heliconia* grew only at very small sizes, whereas in high light *Heliconia* grew to somewhat larger, but still small sizes. *Heliconia* survived equally well in low and high light, but reproduced more in high light. *Heliconia* survival and *Calathea* inflorescence production were the only vital rates not influenced by light in the best models; these rates were not light-limited. Furthermore, there was no survival cost of reproduction; of 511 reproductive plants, only six died during the study period. Comparing to plants of the same size that were non-reproductive, the survival rates in the two groups were similarly high. There was also no cost of reproduction with respect to growth. Reproductive *Calathea* shrank less than similar sized non-reproductives across all light environments, whereas reproductive *Heliconia* shrank less than non-reproductives as the availability of light increased.

As shade tolerance increases, species are expected grow less and exhibit increased survival in low light vs in high light (Kobe et al., 1995), while reproducing more in high light. Contrary to this expectation, neither species demonstrated this pattern. Increasing light positively affected growth and reproduction, but survival was positively influenced by light only in *Calathea*. However, *Heliconia* required more light to grow than *Calathea*, evidence that *Calathea* is more shade-adapted than *Heliconia*.

MORPHOLOGICAL ADAPTATIONS PROMOTE SHADE TOLERANCE AND COEXISTENCE—Plant architecture can influence the efficiency with which light is captured for photosynthesis (Pearcy, Muraoka, and Valladares, 2005). In *Calathea*, several shoots arise from a sympodially branched rhizome near the ground (Kennedy, 1973) in contrast to *Heliconia*, whose stems are generated in clusters, at a higher distance above the ground; *Calathea*'s arrangement is thought to result in more efficient interception of light (Duursma et al., 2012). In addition, *Calathea* leaves possess a pulvinus, a gland that alters the position of *Calathea* leaves as the sun moves throughout the day (Herbert and Larsen, 1985), helping to regulate leaf temperature and transpirational water loss, increasing the efficiency of photosynthetic processes, and minimizing damage from photoinhibition (Geller and Smith, 1982; He, Chee, and Goh, 1996; Valladares and Pearcy, 1999). Therefore, *Calathea* may be more adept at capturing light than *Heliconia* simply due to inherent differences in morphology and architecture. The effects of these differences on carbon gain could be empirically tested in future studies (Pearcy and Yang, 1996; Duursma et al., 2012). Differences in morphological and physiological adaptations to heterogeneity in light may reduce niche overlap in understory herbs. Future work should integrate physiological measures of performance under different light levels, and studies of leaf turnover and belowground growth in the two study species and consider how such differences promote their coexistence.

CONCLUSIONS—Our results demonstrate that light often interacts with plant size in its effects on vital rates (per capita rates of growth, survival, and reproduction) of two understory herbs. For the study species, current size and canopy openness strongly influence whether plants will grow or shrink and how well they survive and reproduce. We found some evidence of adaptation to shade in both species based on their vital rates, although the tradeoffs did not exactly match those expected based on the literature, and we found support for our hypothesis that *Calathea* is more shade-tolerant than *Heliconia*, likely due to its morphology. Increasing light is not always beneficial for plants adapted to shade, highlighting the importance of light tolerance in determining the success of shade-adapted understory species under varying light conditions. Future demographic studies should aim to incorporate morphological and physiological adaptations when estimating vital rate responses under different environmental conditions.

Table 2.1 Summary of regression analyses for all vital rates. Global model is defined as the model with all factors and interactions. + denotes model components are additive, × denotes components are multiplicative and have an interaction. Sample sizes of regressions are as follows: growth n=780, survival n=861, reproduction n=863, inflorescence n=222. Grey shading indicates optimal models selected using AIC.

		Baseline effects in *Calathea,* the reference group				Incremental changes associated with *Heliconia*						
		Intercept	Size (S)	Light (L)	Species (Sp)	Size × Light	Species × Light	Size × Species	Size × Light × Species	R^2	df	ΔAIC
Growth	No 3-way interaction	0.5822	0.9322	-0.0774	0.6503	0.0095	0.0405	-0.1273	--	0.79	8	0
	Global model	0.5792	0.9326	-0.0764	0.6591	0.0094	0.0372	-0.1286	0.0005	0.79	9	1.998
	No size×light or three way	0.3589	0.9612	-0.0010	0.7030	--	0.0316	-0.1312	--	0.79	7	3.475
Probability of Survival	Size	-2.6916	0.8846	--	--	--	--	--	--	0.53	2	0
	Size and light	-2.6059	0.8921	-0.0495	--	--	--	--	--	0.53	3	0.026
	Size and species	-2.6362	0.8877	--	-0.1025	--	--	--	--	0.53	3	1.675
	Size, light, and their interaction	-2.5980	0.8906	-0.0527	--	0.0006	--	--	--	0.53	4	2.025
Probability of Reproduction	All single factors + species×light	-16.3505	1.7708	0.1449	1.9002	--	-0.0752	--	--	0.47	5	0
	All single factors + size×light	-15.3534	1.6580	-0.1314	1.6481	0.0315	--	--	--	0.47	5	0.729
	All single factors + size×light + light×species	-15.7621	1.6984	-0.0337	1.8577	0.0223	-0.0660	--	--	0.47	6	1.395
	Global model	-14.4577	1.5383	-0.4276	-1.0581	0.0714	0.8757	0.3734	-0.1210	0.47	8	1.625
	All single factors + species×light + size×species	-16.5439	1.7927	0.1456	2.1871	--	-0.0753	-0.0343	--	0.47	6	1.967
	All single factors + species×size	-16.3106	1.7760	0.1184	1.9130	--	--	-0.0302	--	0.47	5	1.974
	All single factors + size×light + size×species	-15.3710	1.6601	-0.1309	1.6725	0.0315	--	-0.0029	--	0.47	6	2.728
No. of Inflorescences	All single factors + species×size	-6.7227	0.8282	0.0137	3.3766	--	--	-0.3887	--	0.35	5	0
	All single factors + species×light + size×species	-6.7183	0.8294	0.0103	3.4235	--	0.0265	-0.4059	--	0.35	6	0.421
	Global model	-6.6023	0.8175	-0.0140	4.8106	0.0025	-0.3651	-0.5686	0.0449	0.35	8	1.08
	Size, species, and their interaction	-6.7080	0.8335	--	3.3324	--	--	-0.3849	--	0.34	4	1.663
	No 3-way interaction	-6.4286	0.7997	-0.0507	3.3328	0.0062	0.0333	-0.3993	--	0.35	7	1.75
	All single factors + size×light + size×species	-6.6178	0.8173	-0.0078	3.3366	0.0022	--	-0.3845	--	0.35	6	1.899
	All single factors + size×light	-5.0979	0.6631	-0.0873	-0.1579	0.0103	--	--	--	0.33	5	32.23

Table 2.2 Summary of regression analysis for *Calathea crotalifera* (see Figures 1 through 3). Definitions and abbreviations are S (Size = total leaf area) and L (Light, measured by canopy openness). Sample sizes are as follows: growth n=780, survival n=861, reproduction n=863, inflorescence n=222. Grey shading indicates best models selected using AIC.

		Intercept	Size	Light	Size × Light	R^2	df	ΔAIC
Growth	Size×Light	0.579	0.933	-0.076	0.009	0.89	5	0
	Size	0.358	0.961	--	--	0.89	3	2.123
	Size+Light	0.359	0.961	-0.001	--	0.89	4	4.1
Probability of Survival	Size+Light	0.448	0.066	-0.005	--	0.25	4	0
	Size×Light	0.423	0.069	0.004	-0.001	0.26	5	1.276
	Size	0.440	0.065	--	--	0.25	3	2.126
Probability of Reproduction	Size×Light	-0.323	0.072	-0.060	0.010	0.34	5	0
	Size+Light	-0.548	0.102	0.021	--	0.31	4	26.55
	Size	-0.516	0.107	--	--	0.29	3	55.79
No. of Inflorescences	Size	-28.569	3.475	--	--	0.50	3	0
	Size+Light	-28.582	3.458	0.038	--	0.50	4	1.211
	Size×Light	-26.737	3.254	-0.337	0.041	0.50	5	2.435

Table 2.3 Summary of regression analysis for *Heliconia tortuosa* (see Figures 1 through 3). Definitions and abbreviations are S (Size = total leaf area) and L (Light = Estimates of light availability based on canopy openness scores). Sample sizes are as follows: growth n=1222, survival n=1378, reproduction n=1380, inflorescence n=277. Grey shading indicates best models selected using AIC.

		Intercept	Size	Light	Size × Light	R^2	df	ΔAIC
Growth	Size+Light	1.062	0.830	0.031	--	0.66	4	0
	Size×Light	1.238	0.804	-0.039	0.010	0.66	5	0.676
	Size	1.080	0.839	--	--	0.66	3	3.263
Probability of Survival	Size	0.381	0.080	--	--	0.20	3	0
	Size+Light	0.386	0.081	-0.005	--	0.20	4	0.118
	Size×Light	0.338	0.089	0.014	-0.003	0.20	5	0.504
Probability of Reproduction	Size×Light	-0.414	0.090	-0.063	0.012	0.31	5	0
	Size+Light	-0.622	0.121	0.020	--	0.30	4	19.3
	Size	-0.601	0.126	--	--	0.29	3	35.89
No. of Inflorescences	Size×Light	-0.769	0.250	-0.778	0.100	0.28	5	0
	Size+Light	-3.679	0.599	0.073	--	0.25	4	8.43
	Size	-3.746	0.637	--	--	0.23	3	12.96

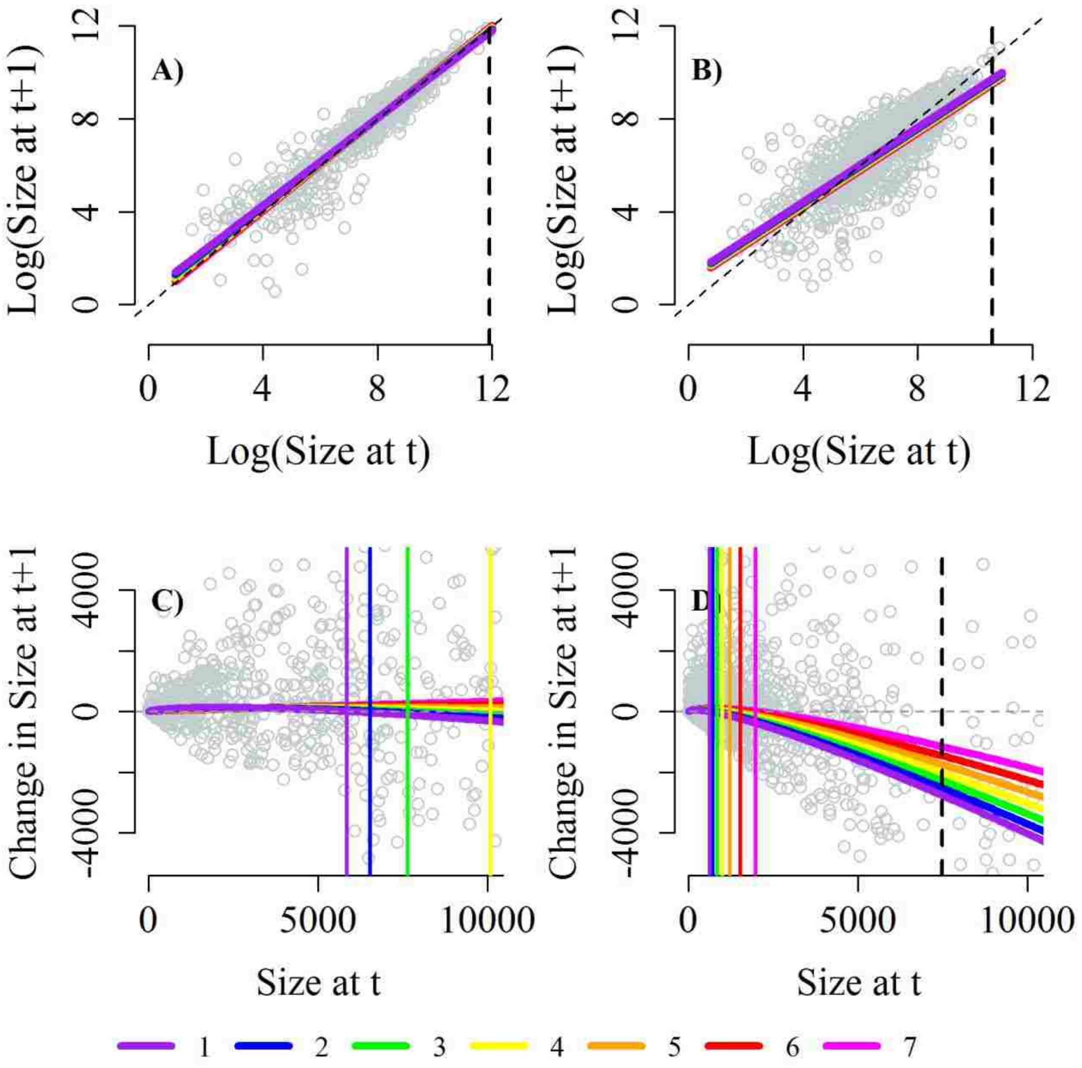

Figure 2.1 Future size as predicted by current size in A) *Calathea crotalifera* and B) *Heliconia tortuosa*. Size was log transformed to improve normality. Light gray dashed lines in A) and B) represent identity line (*i.e.,* the line where size at time t+1= size at time t) and black dashed vertical lines indicate largest observed size on log scale. Change in size was calculated by back transforming the log of size (see *Methods*) for C) *Calathea crotalifera* and D) *Heliconia tortuosa*. Black dashed vertical line in D) indicates the 80th quantile of size (maximum for *Calathea* occurs at 18012 cm^2 and therefore occurs outside the scope of figure); gray circles in C) and D) represent the 80th quantile of data; vertical colored lines in C) and D) indicate points at which individuals transition from growing to shrinking (see *Results* for values associated with canopy scores 5 through 7). Figures created using regression coefficients from best models in Tables 2 and 3. Different colors represent different canopy openness scores.

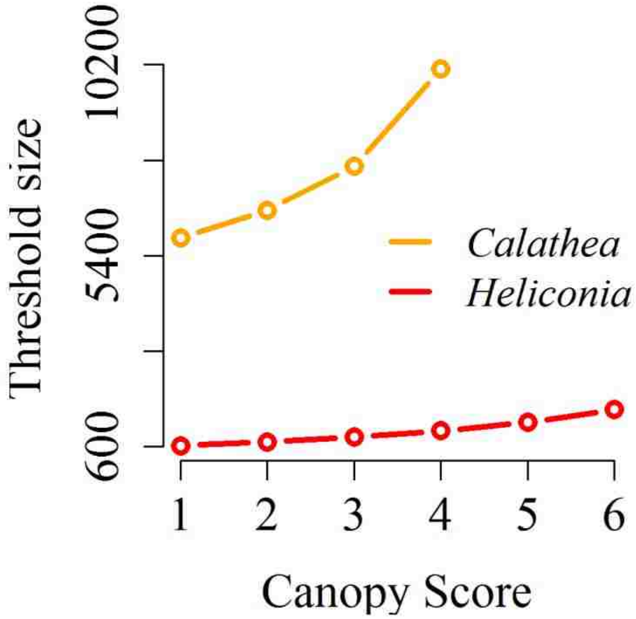

Figure 2.2 The threshold size at which individuals transition from growing to shrinking increases as the availability of light increases in *Heliconia tortuosa* (red line) and *Calathea crotalifera* (orange line). The threshold size for *Calathea* was 13 times greater than *Heliconia* at a canopy score of 5 and 44 times greater at a canopy score of 6 (not pictured). *Calathea* did not exhibit shrinkage at any size in the observed size range above a canopy score of 6.

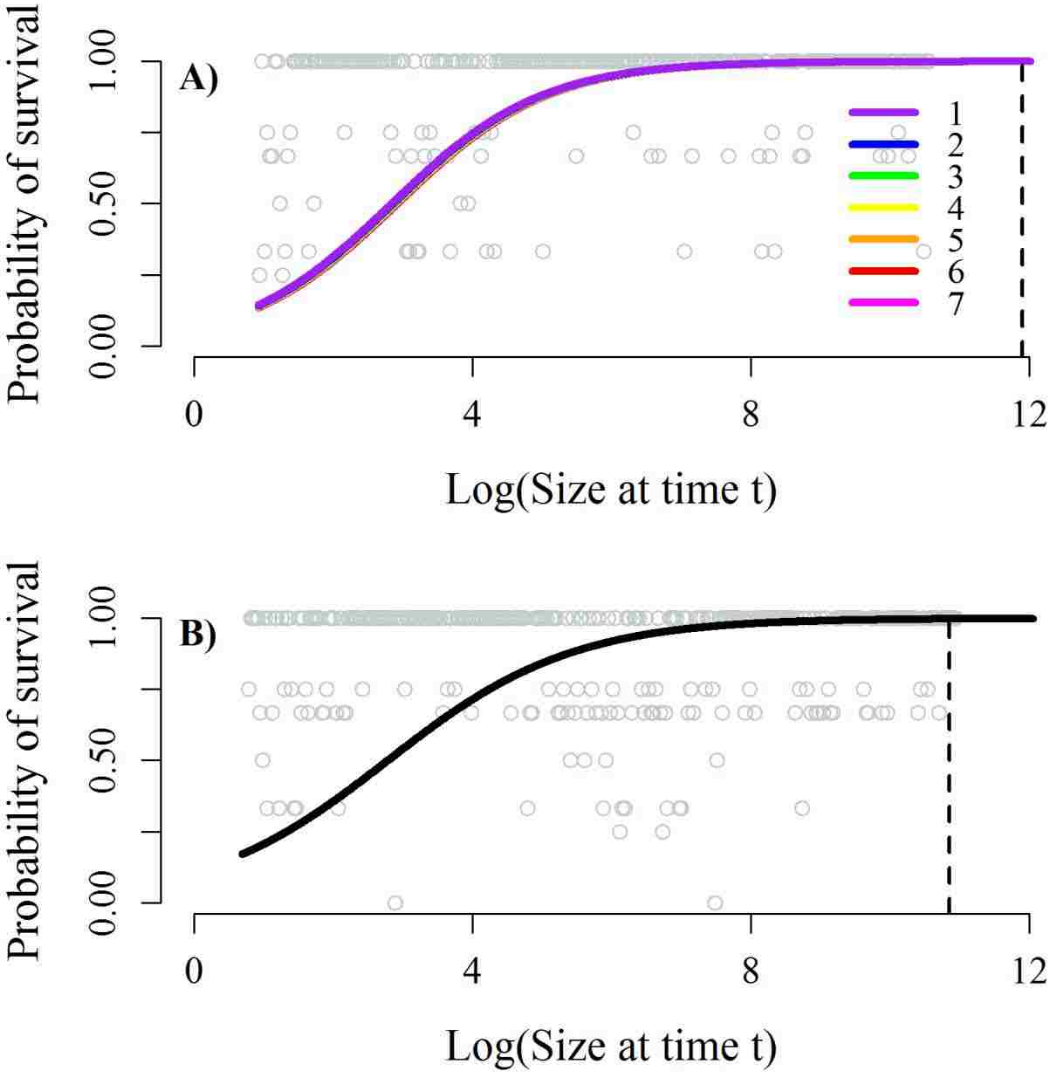

Figure 2.3 Probability of survival based on presence/absence of individuals in A) *Calathea crotalifera* and B) *Heliconia tortuosa*. Survival is higher in low light than high light, for large individuals but equal among light environments in small individuals of *Calathea*. Survival was influenced by size but not light in *Heliconia*, therefore only one line is present. Black dashed lines indicate largest observed sizes. Different colors represent different canopy openness scores. Figures created using regression coefficients from best models in Tables 2 and 3.

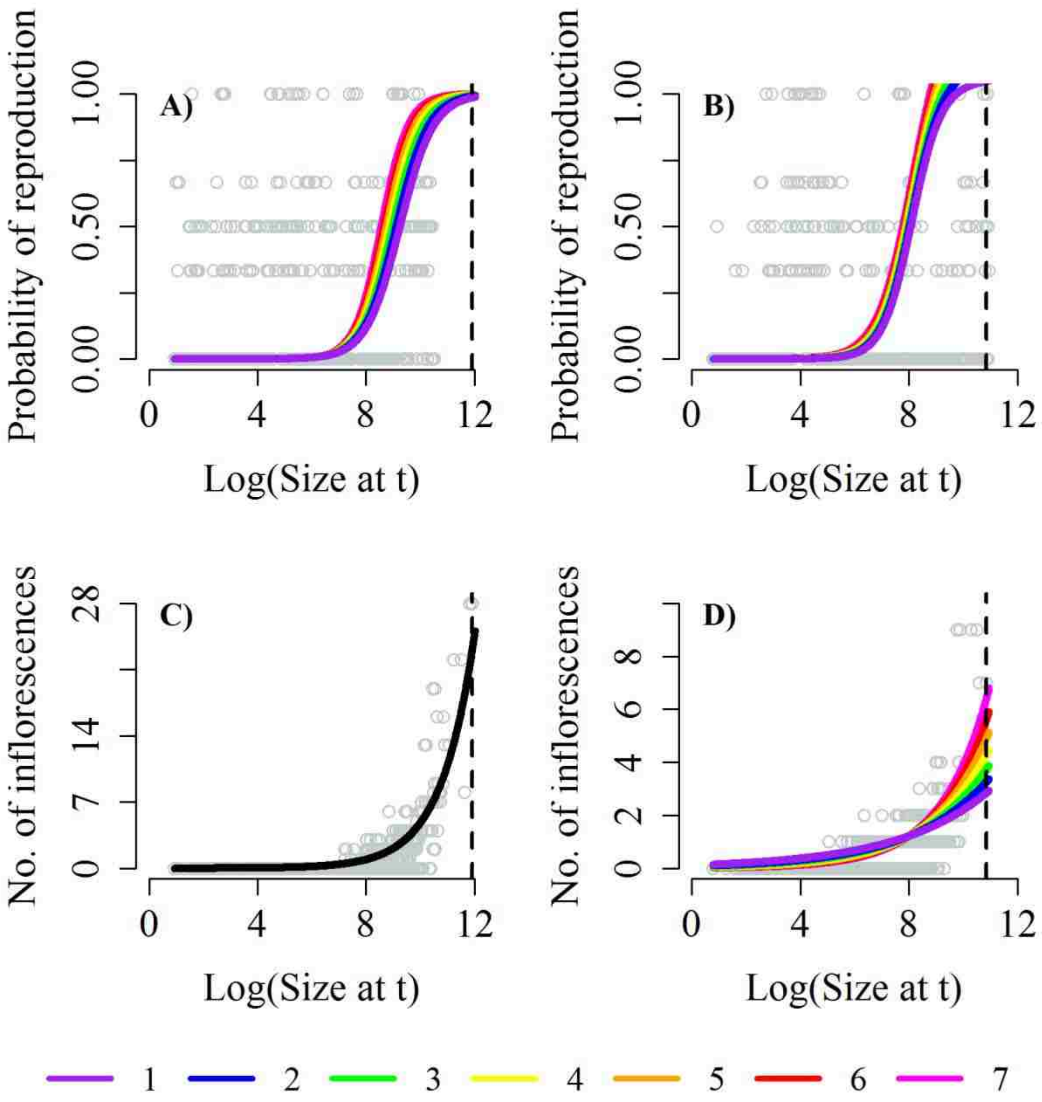

Figure 2.4 Probability of reproducing based on presence/absence of inflorescences for A) *Calathea crotalifera* and B) *Heliconia tortuosa*. There was a significant species effect. The probability of reproducing is higher in high light than in low light over all plant sizes and for both species, but the effect of light was statistically different from zero only in *Heliconia*. Reproductive output based on number of inflorescences for C) *Calathea crotalifera* and D) *Heliconia tortuosa*. Black dashed lines indicate largest observed sizes. Different colors represent different canopy openness scores.Figures created using regression coefficients from best models in Tables 2 and 3.

Chapter III: The interactive effects of photosynthetic physiology and forest canopy openness in growth models of two Neotropical understory herbs

Overview

The availability of light from tree canopy gaps may influence variability in the growth rates of perennial herbs in the understory by regulating carbon gained via photosynthesis. We modelled growth as a function of plant size, light availability, and light response parameters, for two understory herbs, *Heliconia tortuosa* and *Calathea crotalifera*. Principal components analysis (PCA) and correlation tests were used to determine relationships among four physiological parameters: net photosynthetic capacity (A_{max}), quantum efficiency (*alpha*), respiration (R_d), and light compensation point (*LCP*). For shade tolerant species, it is expected that A_{max}, *LCP*, and R_d are low when *alpha* values are high. Model averaging was used to determine the importance of size, light, and the composite light response parameters (the first and second principal component axis scores). PCA revealed only minor differences between the species; the first principal component axis was most strongly associated with *LCP*, and R_d while the second axis was most strongly associated with A_{max} and *alpha*. However, in the average model of growth for *Heliconia*, current size was the most important predictor of future size, followed by PC2, whereas current size and light were the most important predictors for *Calathea*. *Calathea* that diminished in size had either higher *LCP* and R_d and lower *alpha*, or, higher *alpha* and A_{max} versus individuals that grew. *Heliconia* that diminished in size had lower *LCP*, R_d, and A_{max} or low *alpha*, R_d, and A_{max} versus individuals that grew. Thus, the relationships among the light response parameters of two locally coexisting herbs differ significantly, in a way that does not match predictions for shade-adapted species, and their growth is regulated by different suites of light response parameters. Our results provide a physiological mechanism that explains why *Calathea* may be more shade tolerant than *Heliconia*.

Background

The availability of light strongly influences the growth, survival, and reproduction of plants in the tropical forest understory. In tropical forests, the dense tree canopy allows less than 5% of total sunlight to reach the forest floor, mostly in the form of diffuse sunlight punctuated by short duration sunflecks (Bruna 2003). When canopy gaps open, the amount of available energy for carbon gain increases greatly (Pearcy 1987), but often is accompanied by increased temperature and reduced humidity that can induce physiological stress in shade-adapted herbaceous species (Herbert and Larsen 1985). Thus, the availability of light from tree canopy gaps alters plant physiological responses (Chazdon 1992, Sims and Pearcy 1992), influencing rates of growth, survival, and reproduction of understory species (Gravel et al. 2010, Gagnon et al. 2011). As the size of a canopy gap increases, so should the availability of both direct and indirect light (here, light is defined as photosynthetically active radiation, PAR)(Dirzo et al. 1992).

To successfully establish and persist in such heterogeneous and dynamic environments, understory plants have adapted both morphologically and physiologically. Morphological adaptations to shade may include reduced self-shading via changes in leaf architecture and arrangement, and the production of large, thin leaves to increase light capture (Ehleringer and Forseth 1980, Valladares and Niinemets 2008). Light-adapted plants produce large, thick leaves with high stomatal densities for increased gas exchange

(Pearcy et al. 2005). Physiologically, plants that tolerate deep shade often have low dark respiration rates (R_d) and a low net photosynthetic rate (A_{max}), but their photosystems are highly efficient (α, alpha) and little light is required to offset the costs of respiration, known as the light compensation point (LCP) (Valladares and Niinemets 2008). In contrast, plants adapted to bright light have high respiration rates and a high net photosynthetic rate, but often have less efficient photosystems and higher light compensation points than shade-tolerant plants (Pearcy et al. 2005, Valladares and Niinemets 2008)(Table 1).

These morphological and physiological adaptations can change with plant age and are associated with shifts in resource allocation (Lusk et al. 2011), maturation of leaf tissue and leaf expansion (He et al. 1996), and leaf senescence (Geller and Smith 1982). Additionally, with increasing plant size the ability to capture light generally increases, provided that self-shading is low (Valladares and Niinemets 2008). Because adaptations that confer shade tolerance often are incompatible with adaptations that maximize usage of light (Valladares and Niinemets 2008), understory plant species (both trees and herbs) may be segregated by their degree of shade tolerance, promoting coexistence (Gravel et al. 2010). Thus, light drives morphological and physiological adaptations, which influences the partitioning of light environments by co-occurring understory species.

Whether shade tolerance is conferred by traits that maximize carbon gain or minimize respiratory losses under low light is under great debate (Valladares and Niinemets 2008). When the amount of carbon gained by leaves is greater than the carbon used to construct, maintain, and defend those leaves against herbivores, plants should grow (Eckstein et al. 1996). Carbon is gained via photosynthesis when light is abundant and ambient conditions, such as temperature and humidity, are optimal (Eckstein et al. 1996). However, under full sunlight, leaves adapted to deep shade can experience a dramatic reduction in their efficiency of light utilization (the quantum efficiency, *alpha*), and a simultaneous reduction in their net photosynthetic rate, a process known as photoinhibition (Valladares and Pearcy 1999). In extreme cases, photoinhibition can result in permanent leaf damage, although leaves often can recover within a few minutes to several hours (Krause 1988). Over long periods of photoinhibition, plants may promote leaf senescence to replace old “shade-grown” leaves with new “sun-grown” leaves (Lovelock et al. 1994). However, this latter strategy relies on having sufficient resources to produce new leaves, which often are more susceptible to herbivory than mature leaves (Coley 1983). Thus, for understory species, their net change in size will be influenced by their physiological responses to light.

The demographic responses of understory herbs to changing light environments remain understudied, despite the ecological importance and diversity of understory herbs in tropical forests (Gilbert et al. 2006). Understory perennial herbs also are known to influence forest succession (Swanson et al. 2010) by competing with trees for light (Tsvuura et al. 2010). Here we investigate the relationship between photosynthetic physiology and inter-annual growth in two locally coexisting tropical forest understory herbs, *Calathea crotalifera* and *Heliconia tortuosa*. Previously, the demographic rates of these species were quantified across a range of forest light environments (Gagnon et al. 2011). To better understand the role of light in shaping the demographic responses of these species, we measured their rates of photosynthesis within the forest during two annual censuses and used statistical modelling to predict future size as a function of current size (hereafter, growth), canopy openness (a proxy for light availability), and photosynthetic responses. To our knowledge, this is the first study to model growth as a linear function of the photosynthetic light curve parameters (A_{max}, LCP, R_d, and alpha), although there exist mechanistic models of long term forest dynamics that include photosynthesis, respiration and plant growth, such as the HYBRID and FIRE-BGC models (see Bugmann 2001 for review).

We hypothesized that (1) although *Calathea* and *Heliconia* are functionally similar and coexist locally, they will differ in how they respond photosynthetically to the availability of light. This hypothesis is based on the results of a companion study on the same species, which found that the two species differed in their demographic rates under varying light levels (Gagnon et al. 2011). (2) individuals under relatively open canopies will have a higher photosynthetic capacity, a higher respiration rate, a higher light compensation point, but a lower quantum efficiency than those under closed canopies, (3) both canopy openness and physiology should be equally important predictors of future size for these understory herbs, and (4) individuals with different physiological profiles (e.g. low respiration and high quantum efficiency versus high respiration and low quantum efficiency) should have different rates of growth under similar light environments.

Methods

SITE DESCRIPTION—This study was conducted at the Las Cruces Biological Station, located 1200 m above sea level (8° 47' 7" N, 82° 57' 32" W) in Coto Brus county, southern Costa Rica. This region is designated as mid-elevation premontane forest and receives approximately 4 m of annual rainfall. There is a dry season from January to March and mean diurnal temperature over the year is between 13 and 26°C. We sampled individuals across 17 study sites within the biological station, located in primary, secondary, and selectively logged forest, but we do not focus on these distinctions of logging history in the current analyses.

STUDY SPECIES—*Heliconia tortuosa* is a perennial, herbaceous understory monocot, which grows 1-2 m tall and is characterized by bright red floral bracts (Linhart 1973). *Calathea crotalifera* is a perennial, herbaceous understory monocot, which grows 1-3 m tall and possesses yellow, erect floral bracts (reminiscent of a rattlesnake's rattle) that grow up to 25 cm long. Both species have been considered moderately shade tolerant, although their abilities to tolerate low light have not been quantitatively assessed (Berry and Kress 1991). Detailed descriptions of the life history of these species can be found in Gagnon et al. (2011).

EXPERIMENTAL DESIGN—We estimated plant size, canopy openness, and photosynthetic performance for 39 individuals in June and July 2013 (n=18 for *Heliconia*, n=21 for *Calathea*) and 40 individuals in 2014 (n=20 for *Heliconia*, n=20 for *Calathea*). Of the 39 individuals measured in 2013, three died and four were added to the study the following year. To determine whether the estimates of each of the four physiological parameters differed between years, we used linear mixed models with year as the independent variable (the fixed effect), the physiological parameter as the dependent variable, and individuals as a random effect variable. Each parameter was tested separately. We also tested the effect of current light environment and species on each physiological parameter, using linear mixed models. In this analysis, the physiological parameter was the dependent variable, while species and current light environment (canopy openness) were the independent variables. Each parameter was again tested separately.

To estimate plant size, we measured the length of each leaf for each individual. We measured leaf lengths in the field and estimated leaf areas for each species using a regression relationship specific to our study site (Appendix 8). Areas of individual leaves were then summed to give total leaf area per plant, used here as a metric of size. To determine the effect of physiology on future plant size, we conducted a linear regression analysis with future size as the dependent variable and the four independent variables: species, current light environment, principal component scores from the first axis, and principal component scores from the second axis (see *Statistical Analyses* for regression equation). The principal component scores were derived from the PCA that included both species.

We measured canopy openness over each individual plant on a scale of 1 to 25, using a rapid assessment technique (Brown et al. 2000). Canopy openness is used here as a metric of light availability and has been found to correlate strongly with estimates of light availability, determined using hemispherical photographs (Brown et al. 2000). At our study site, canopy scores were strongly and positively correlated with the amount of photosynthetically active radiation in μmol m^{-2} s^{-1} (*rho*=0.72, p<0.001) measured with a quantum sensor on a LI-6400 (Li-Cor, Lincoln, NE, USA). The highest observed canopy openness over both years was approximately 30% (canopy openness score of 25) and the lowest was 1% (canopy openness score of 1)(Brown et al. 2000).

Photosynthetic performance was assessed in the field based on rates of gas exchange, using a portable gas exchange system (LI-6400; Li-Cor, Lincoln, NE, USA). On one leaf per individual, we measured a light response curve between 0900 and 1100 hours to minimize any confounding effects of sampling during the hottest hours of the day. Only mature leaves were used, and were selected to have little or no damage (evidence of senescence or herbivory) in addition to maximum exposure to sunlight. Leaves were exposed to a gradient of eight light levels from 0 to 1000 µmol PAR m^{-2} s^{-1} (starting at high light and decreasing to zero) and we measured the rate of exchange of CO_2 and H_2O from the leaf at each light level to construct a light curve. We fit the data to the rectangular hyperbola model (Thornley 1976) to estimate three parameters (Equation 1): the assimilation rate at saturating light (A_{max}, units are µmol m^{-2} s^{-1}), the assimilation rate when no light was present (dark respiration, R_d, units are µmol m^{-2} s^{-1}), and the quantum efficiency of the photosystems (alpha, unitless), described by the initial slope of the curve. *I* represents the light intensity (µmol PAR m^{-2} s^{-1}).

$$Net\ Photosynthesis = \frac{alpha \times A_{max} \times I}{alpha \times I + A_{max}} - R_d \qquad (1)$$

We then algebraically calculated the leaf light compensation point (LCP, units are µmol m^{-2} s^{-1}), the light level where assimilation is zero (Equation 2). Across all photosynthesis measurements, CO_2 concentration was 400 µmol m^{-2} s^{-1}, leaf temperature was 25°C±2, and average relative humidity was 58%±8.

Stomatal conductance (g_{wmax}) at each light level was not estimated using the LICOR 6400 because we did not allow sufficient time (300 seconds per light level)

$$LCP = \frac{A_{max} \times R_d}{(alpha \times A_{max}) - (alpha \times R_d)} \qquad (2)$$

between light levels for the stomata to respond, resulting in overestimation of conductance at low light by this method. Therefore, to estimate differences in maximum stomatal conductance between species, we collected leaf tissue from 60 individuals at our study site (n=30 *Heliconia*, and n=30 *Calathea*) in July 2014, and measured stomate size and density from microscopic images. Each individual (*Calathea*: 15 juvenile, 15 adult; *Heliconia*: 15 juvenile, 15 adult) was categorized as small non-reproductive or large reproductive (we did not measure leaf area) and all individuals were located under closed canopies (approx. 1% canopy openness using the canopy scope technique). Mature leaves were carefully selected for maximum exposure to light (not covered by other leaves), and with minimal damage. We cut one small square section from the middle of each leaf, avoiding the central vein, and wiped the surface clean. Leaf samples were then placed in methanol for up to 72 h before being processed. To capture images, the leaf squares were placed on slides with the underside of the leaf facing down. Images were prepared using a high-resolution confocal microscope (Leica Microsystems Inc., Buffalo Grove, IL, USA), which fluoresces photosynthetic tissue via a helium neon laser at a wavelength of 458 nm. We estimated stomatal size by measuring the length and width of the guard cell pair for twenty randomly selected stomata per image, and we used the mean values for each sample in all subsequent analyses. Ten stomata were chosen randomly to measure width, and another ten were chosen to measure length (Franks and Beerling, 2009).

We estimated maximum stomatal conductance to water vapor, defined as the rate at which water vapor exits the stomata in mol $m^{-2}s^{-1}$, using Equation 3 (following Franks and Beerling 2009).

$$g_{wmax} = \frac{\frac{d}{v} \times D \times a_{max}}{(l + \frac{\pi}{2}\sqrt{a_{max}/\pi})} \qquad (3)$$

Where d is the diffusivity of water vapor in air at 25°C, 0.26×10^{-4} m^2 s^{-1}, v is the molar volume of air at 25°C, 0.02479 m^3 mol^{-1}, D represents stomatal density (mm^{-2}), a_{max} is maximum stomatal area (μm^2), and l is stomatal pore depth (µm), taken as guard cell width/2.

STATISTICAL ANALYSES—Parameters of the light response models (Equation 1) were estimated using nonlinear least-squares regression conducted in the statistical software program, R (R Core Team 2013), resulting in the fitting of one light curve per individual. We also estimated parameters using the nonrectangular hyperbola (Wright 2002), which includes a parameter of convexity (Θ) but AIC model selection determined that there was no significant improvement in model fits for all but two individuals, therefore we used the simpler model, the rectangular hyperbola (Appendix 9 for results from 2013, Appendix 10 for results from 2014). Three individuals were excluded from the remaining analyses as outliers, resulting in a sample size of 76. These individuals were excluded because they had either A_{max} values greater than 15 or alpha values greater than 2.

Variability in parameters of the photosynthetic curves: Differences among each of the four parameters of the photosynthetic curves between years were tested using mixed effects models, where individuals were considered as random factors. We found no significant effect of year ($p>0.05$), therefore data from both years were combined in all subsequent analyses. Mixed effects models (with forest type and individual plants as random factors, and species and canopy openness as fixed factors) were used to determine whether there was a significant effect of species and canopy openness on any of the four parameters of the photosynthesis curves. Also, we investigated if the correlations among the four parameters of the photosynthetic curves followed the hypothesized association for shade tolerant species and whether the correlations differed by species, using Spearman Rank Correlation analyses. PCA then was conducted on the correlation matrix for both species combined to investigate the relationships among the four parameters (A_{max}, LCP, R_d, and alpha) and reduce the dimensionality of the physiological measurements. Lastly, we tested for correlations between the principal component axis scores and each of the light response parameters using Spearman Rank tests. We report the signs of the associations for relationships that were statistically significant ($p<0.05$, Table 3).

Variability in size at time t+1: The principal component scores from the PCA of the pooled data (both species combined) were then used as predictor variables in linear regression models where size at *t*+1 is a function of size at time *t*, canopy openness at time *t*, and both principal component scores at time *t* (Equation 4). We used the reduced physiological data (PC1 and PC2) as composite measures of photosynthetic performance in our analyses, rather than including the four physiological parameters as separate predictors, because of the strong correlations among the variables (Table 2).

$$\begin{gathered} Size_{t+1} = x_0 + x_1 Size_t + x_2 Canopy\ Openness_t + x_3 PC\ 1_t + x_4 PC\ 2_t + x_5 Size_t \\ Canopy\ Openness_t + x_6 Size_t PC1_t + x_7 Size_t PC2_t + x_8 Canopy\ Openness_t PC1_t + \\ x_9 Canopy\ Openness_t PC2_t + x_{10} PC1_t PC2_t + x_{11} Size_t CanopyOpenness_t PC1_t + \end{gathered}$$

$$x_{12}Size_tCanopyOpenness_tPC2_t + x_{13}CanopyOpenness_tPC1_tPC2_t +$$

$$x_{14}Size_tPC1_tPC2_t + x_{15}Size_tCanopyOpennesstPC1_tPC2_t \tag{4}$$

The importance of size, canopy openness, and the composite photosynthetic responses (PC1 and PC2) to future size was estimated using model averaging (Burnham and Anderson 2002). There were 127 nested models derived from the full model (Equation 4). The relative importance of each variable then was estimated over all models using the sum of the AIC weights across all the models in the set of 127 models where the variable occurs (Burnham and Anderson 2002). Because it is a relative term, values are between 0 and 1. We also calculated the values of all model coefficients in the average model. Finally, we evaluated the effect of changing PC1 and PC2 scores on size at *t*+1 by plotting the average model using regression coefficients obtained above. In these plots, light was kept constant (at a value of 1) and we evaluated future size over the range of observed plant sizes. We evaluated growth using PC1 and PC2 scores ranging from -3 to 4, based on the PCA plots. It is important to note that the two species differ in the signs of association between the light curve parameters and the principal component axes (see Table 3, *Results*).

We tested for differences in maximum stomatal conductance between species, stages (juvenile or adult), and forest type using ANOVA, and analyzed multiple pairwise comparisons using Tukey HSD. We found no significant difference due to forest type therefore we did not include this factor in subsequent analyses.

Results

The mean values (± SD) of the photosynthetic parameters for *Heliconia* are: $\mu A_{max}=6.3 \pm 2.3$, $\mu R_d=0.39 \pm 0.32$, $\mu LCP=3.5 \pm 2.6$, $\mu alpha=0.13 \pm 0.06$. For *Calathea*, the means are: $\mu A_{max}=6.6 \pm 1.7$, $\mu R_d=0.35 \pm 0.16$, $\mu LCP=3.6 \pm 2.2$, $\mu alpha=0.14 \pm 0.13$. Spearman Rank correlation analyses revealed significant positive relationships between LCP and A_{max}, LCP and R_d, and A_{max} and R_d, and a negative relationship between LCP and alpha for *Calathea* (Table 3.2). For *Heliconia*, LCP and R_d were the only variables that were significantly correlated, and the relationship was positive (Table 3.2). Neither species matched the syndrome expected for shade-adapted species (Table 3.2). When the species were combined, the strength and directions of the correlations matched those of *Calathea*; there was a positive relationship between LCP and A_{max}, LCP and R_d, and A_{max} and R_d, and a negative relationship between LCP and alpha. The mixed effects models with species and current light environment as the independent variables, and the physiological parameters as the dependent variables, revealed that the study species did not differ in their photosynthetic response curve parameters ($p_{Amax} = 0.7$, $p_{alpha} = 0.94$, $p_{Rd} = 0.34$, $p_{LCP} = 0.51$). From the same model output, current light environment (canopy openness) had no effect on the parameters of the photosynthetic curves of either species models ($p>0.05$). We also found no evidence of grouping among parameters of the photosynthetic curves by canopy openness scores in a PCA analysis (not shown). Maximum stomatal conductance was significantly higher for *Calathea* than *Heliconia* ($p<0.0001$, Figure 3.1). *Calathea* had smaller stomata but at a higher density (ca. 30% greater) than those of *Heliconia* (Appendix 11, 12). Additionally, adults had a significantly greater maximum stomatal conductance ($p<0.0001$, Figure 3.1), because of larger and more numerous stomata (ca. 30% greater) than those of juveniles.

Principal component analysis supported these findings; the parameters of the photosynthetic curves of both species grouped similarly (Figure 3.2). When both species were included in one correlation matrix (not shown), its PCA showed that R_d and LCP loaded most heavily onto the first axis (65 and 70%, respectively), whereas alpha loaded most heavily (77%) onto the second axis, followed by A_{max} (59%)(Figure 3.2). Together, the first two axes explain 78% of the cumulative variance. Although the two species overlapped on the PCA plot, the species differed in terms of which light response parameters were significantly correlated with the PCA axes (Table 3.3). Individuals of *Calathea* that had high PC1 scores had high R_d, high LCP, but low alpha. Individuals of *Heliconia* with high PC1 scores had high R_d and LCP and also had high A_{max}. Individuals of *Calathea* that had high PC2 scores had high alpha and A_{max} while *Heliconia* with high PC2 scores had high A_{max}, alpha, and R_d. To simplify future discussion, we hereafter refer to PC1 as the photosynthetic "costs" axis (light compensation point, *LCP*, and dark respiration, R_d), and PC2 as the photosynthetic "gains" axis (quantum efficiency, alpha, and photosynthetic capacity, A_{max}). The latter are "gains" in the sense that if they increase while all other parameters stay equal, the net amount of energy obtained should increase, which should result in a positive change in future size. The former are "costs" in the sense that if they increase, the net amount of energy obtained decreases, which could result in stasis or a negative change in future size (shrinkage). However, this interpretation must be tempered with the observation that, based on the PCA, to achieve a net carbon gain, *Calathea* should require a decrease in PC1 values and an increase in PC2 values, because of the directions of the variables associated with each axis. For *Calathea*, a decrease in PC1 values is associated with a decrease in LCP and R_d, with a concurrent increase in alpha, while an increase in PC2 values is associated with an increase in A_{max} and alpha. These scenarios should result in a net carbon gain and the first scenario matches the prediction for shade-adapted species. For *Heliconia*, the light response parameters do not load onto the PC axes as they do for *Calathea*, so that the effect of changing PC1 and PC2 values is not clear (we have no expectation regarding the effects of changing PC1 and PC2 on growth). Although a decrease in PC1 is associated with reductions in LCP and R_d (these should have a positive effect on net carbon gain), A_{max} also decreases. A decrease in PC2 would result in a low R_d, which could positively influence carbon gain, but also a low A_{max} and alpha, which could result in a net carbon loss. (See *Discussion* for explanations regarding predictions). Thus, we have no expectations regarding the effects of changing PC1 and PC2 values for *Heliconia* because the combinations of variables associated with the PC1 and PC2 axes have conflicting consequences for carbon gain.

Model averaging revealed significant differences between *Calathea* and *Heliconia* in the importance of photosynthetic responses for predicting future size. Current size and canopy openness were the most important predictors of future size for *Calathea*, whereas current size and the photosynthetic gains axis were the most important predictors of future size for *Heliconia*, and were equally important (Figure 3.3). When comparing the two species, current size and canopy openness had nearly equal importance for predicting future size, but parameters associated with both increasing and decreasing carbon gains were more important predictors of future size for *Heliconia* than for *Calathea* (Figure 3.3). In both species, parameters associated with increasing carbon gains (A_{max} and alpha) were more important predictors of future size than parameters associated with decreasing carbon gains (R_d and LCP), but the difference was greater for *Heliconia* than for *Calathea*. In both species, the effect of current size on future size was influenced by the photosynthetic gains axis and this two-way interaction was the most important predictor of future size among all other two-way interactions (Figure 3.4). The importance of this interaction was nearly three times greater for *Heliconia* than for *Calathea* (Figure 3.4). All two-way interactions were more important predictors of future size for *Heliconia* than for *Calathea*, with the exception of the interaction between the photosynthetic costs axis and the gains axis (Figure 3.4). The importance of the three-way interactions for predicting future size was negligible in both species (importance <0.03)(Figure 3.5), although the size by light by photosynthetic gains interaction for *Heliconia* was more than five times higher in importance (0.02 versus <0.004) than all other three way-interactions. The four-way interactions were not important predictors of future size for either species (importance of 0) (not shown).

The values of the parameters in the average model of future size for each species also differed significantly by species (Table 3.4). In terms of the model coefficients, the greatest differences between the species were the values of the intercept (x_0 in Equation 4) and the values representing the effect of the photosynthetic gains axis (PC2), which was nearly 80 times greater in magnitude for *Heliconia* than for *Calathea* (Table 3.4). For *Calathea*, the values of the two-way interactions (coefficients x_5 through x_{10}) were up to 30 times lower than those of *Heliconia* (Table 3.4). The coefficients associated with the size by canopy openness interaction, size by cost interaction, and cost by gain interaction were negligible for both species (Figure 3.4). Similarly, the values of the coefficients for the three- and four-way interactions all were low for both species (<0.02, Table 3.4, not shown).

Using the coefficients of the average model of future size for each species (Table 3.4), we plotted future size as a function of current size while changing the values of both the photosynthetic cost axis and gain axis to determine their effect on future size (Figures 3.6 and 3.7). In these figures, light is held constant at a value of 1. For *Calathea*, individuals shrank as the photosynthetic cost axis (PC1) values increased (their future size was smaller than their current size), but they grew as the photosynthetic cost axis values diminished (Table 3.3, Figure 3.6A). The opposite was true of *Heliconia*; individuals grew as photosynthetic cost axis values increased and shrank as the photosynthetic cost axis values decreased (Table 3.3, Figure 3.6B). The effect of photosynthetic cost on growth thus was greater for *Heliconia* than for *Calathea*, which agreed with the parameter importance values. The net effect of changing the photosynthetic gains axis (PC2) values on growth differed from the net effect of changing photosynthetic costs (PC1) axis values for *Heliconia* but not *Calathea*; *Calathea* shrank as the values of the photosynthetic gains axis (PC2) increased and grew as gains axis values decreased, but the reverse was true of *Heliconia* (Table 3.3, Figures 3.7A and 3.7B). The effect of photosynthetic gains on growth was greater than the effect of photosynthetic costs on growth for both species, which agreed with the parameter importance values. Thus, (referring to Table 3.3) *Calathea* that diminished in size had higher R_d and LCP but lower alpha than individuals that grew, in terms of PC1 parameters. In terms of PC2 parameters, *Calathea* that diminished in size had lower alpha, and A_{max} than individuals that grew. *Heliconia* that diminished in size had lower LCP, R_d, and A_{max}, in terms of PC1 parameters than individuals that grew. In terms of

PC2, *Heliconia* that diminished in size had lower A_{max}, alpha and R_d than individuals that grew.

Discussion

RELATIONSHIPS AMONG PHYSIOLOGICAL VARIABLES—Of six possible combinations, correlation tests revealed four significant relationships among photosynthetic curve parameters for *Calathea*, but only one significant relationship among photosynthetic curve parameters for *Heliconia*. For *Calathea*, as well as both species combined, there was a significant positive relationship between A_{max} and R_d, supporting previous findings that as plants increase their capacity to use light (by developing and maintaining the photosynthetic machinery needed to do so), they increase their respiratory costs (Valladares et al. 2000). A physiological study of nine tropical tree species across three light levels found significant positive correlations between A_{max} and R_d but only for plants grown in high light (Valladares et al. 2000). Similarly, A_{max} was positively correlated with LCP, defined as the amount of light necessary to offset the costs of respiration. LCP and R_d were the most strongly correlated, as expected, given that both parameters reflect metabolic costs. This relationship was the only significant relationship among the four physiological parameters for *Heliconia*, which may be because of *Heliconia's* high variability in physiological performance. LCP and alpha were negatively correlated for *Calathea*, which implies that individuals that were the most efficient at using light required relatively little light to offset the costs of respiration, an adaptation that would be beneficial for shade-adapted species. We were surprised not to find a correlation between alpha and A_{max} in either species and in the correlation matrix for both species combined, given that several studies of tropical understory herbs have reported a strong inverse relationship between the two variables (Valladares and Pugnaire 1999, Walters and Reich 2000). We again attribute the lack of correlation to the high variability in the physiological responses. High variability in physiological responses may represent an adaptation to a variable environment, as has been argued for early successional or pioneer species (Bazzaz and Pickett 1980). Individuals that exhibit a narrow range of responses over a light gradient may be less able to respond to abrupt changes in light availability, i.e., a lower plasticity. Therefore, variability in physiological performance across light environments could be an important attribute supporting the successful establishment and persistence of these species (see below). A study of nine tropical trees reported high variability and plasticity in leaf level ecophysiological performance (Valladares et al. 2000).

Principal component analyses of the correlations among the photosynthetic curve parameters revealed minor differences between the species, despite *Calathea* having more significant correlations among its variables. The PCA that combined both species revealed grouping of LCP and R_d on the first axis, and of A_{max} and alpha on the second axis. This separation of the variables in the PCA agrees with the biological interpretations of these variables. LCP and R_d reflect respiratory costs, while A_{max} may be considered the maximum ability to offset these costs because increasing A_{max} values will always increase carbon gains when respiration is held constant. The efficiency of a leaf's photosynthetic machinery is reflected by alpha which is not directly related to respiratory cost; increasing alpha does not necessarily increase carbon gains. A previous study on tropical trees found that A_{max} and stomatal conductance loaded onto a first principal component axis, while alpha and R_d loaded onto the second axis (Valladares et al. 2000). Although R_d loaded with LCP and not alpha in our study, the differences could be attributed to physiological differences between herbs and trees, because respiration (scaled by mass) is significantly higher in herbs than in trees (Reich et al. 1998). In terms of the light response parameters, we found no statistical difference between the species based on the PCA and mixed effects models. These results indicate that these functionally similar species have highly similar physiological responses to light under different levels of canopy openness.

Based on morphology, *Calathea* has higher maximum stomatal conductance than *Heliconia*, but *in situ* measurements of A_{max}, R_d, alpha, and LCP, revealed no significant differences between the species across the measured light environments. Under periods of drought, darkness, elevated CO_2, or low humidity, guard cells experience a loss of turgor pressure that results in stomatal closure and low stomatal conductance (Shimazaki et al. 2007). The lack of significant differences in the measured photosynthetic parameters (A_{max}, R_d, alpha, and LCP) between species may indicate that despite *Calathea*'s increased morphological capacity to exchange gases due to higher stomatal density, stomatal closure and opening may be more sensitive to changes in abiotic conditions than that of *Heliconia*.

Previous studies have demonstrated that as the vapor pressure deficit (VPD) between a leaf and air increases (often associated with low relative humidity), transpiration rates increase, inducing stomatal closure (Mott and Parkhurst 1991). Stomatal opening also is directly regulated by light, including blue and red light (Shimazaki et al. 2007), of particular importance for plants in the forest understory.

Shade-adapted leaves have been shown to have higher rates of photosynthetic induction compared to sun-adapted leaves in response to sunflecks, resulting from faster stomatal opening (Rees et al. 2001). Thus, while under optimal conditions (high humidity, high light, etc) *Calathea* appears to have the ability to maximize carbon gain, we cannot rule out the possibility that stomatal opening by *Calathea* is slower than by *Heliconia*, resulting in no difference in net photosynthesis.

EFFECTS OF CANOPY OPENNESS ON PHYSIOLOGY—There was no significant effect of canopy openness at time *t* on physiological responses at time *t* or *t*+1 according to our mixed effects models, and we found no grouping among light response parameters by canopy openness according to the PCA. This may suggest that forest canopy openness does not directly influence physiological responses to light in our study system. As already noted, our estimates of the light response parameters were highly variable for both species, which may be a consequence of variability in the amount of photosynthetically active radiation (PAR) within the canopy gaps at our study site. Although our assessment of canopy openness was strongly, positively correlated with PAR (*rho*=0.72), some individuals may be sensitive to small fluctuations in PAR, resulting in high variability in physiological performance. Thus, while individuals under relatively closed canopies are not receiving as much direct sunlight as those in canopy gaps, diffuse sunlight and sunflecks could provide sufficient light for photosynthesis by these shade-adapted species, which our sampling method would not detect. To better determine the extent to which diffuse light influences photosynthesis would require sampling individuals only under closed canopies, rather than over a complete range of light environments.

MODELS OF GROWTH AS FUNCTIONS OF SIZE, LIGHT, AND LIGHT RESPONSE PARAMETERS— Model averaging revealed significant differences between the species in terms of which variables were the most important predictors of growth. For both species, current size was a very strong predictor of future size, as has been demonstrated in other understory herbs (Horvitz and Schemske 2002). However, for *Calathea*, light was the second most important predictor of growth, whereas size and the photosynthetic gains axis (PC2) values were the most important predictors for *Heliconia*, and were equally important. Because an increase in PC2 values for *Heliconia* is associated with an increase in respiration rate, maximum photosynthetic capacity, and quantum efficiency, these results may indicate that for *Heliconia*, accurate predictions of growth are dependent on measuring an individual's ability to capitalize on bursts of light and manipulate rates of respiration rather than how much light is present in the current environment. For *Calathea*, the light response parameters were less important predictors of growth than how much light actually was present, suggesting that photosynthetic physiology does not have a strong direct effect on aboveground growth. Nevertheless, we cannot rule out the possibility that the carbohydrates produced via photosynthesis are being invested in the production of roots or thicker leaves, which we did not quantify. In our study, although physiological responses did not differ significantly between the species, their effects on growth did differ. Interestingly, the second principal component axis (associated with

A_{max} and alpha for *Calathea*, and with A_{max} , alpha, and Rd for *Heliconia*) was a more important predictor of growth than the first principal component axis (associated with LCP, R_d, and alpha for *Calathea* but LCP, R_d, and A_{max} for *Heliconia*) for both species, indicating that different suites of traits influence future size in these two locally coexisting species. For *Calathea*, future size is more strongly influenced by the ability to maximize carbon gains (via A_{max} and alpha) rather than minimize costs (LCP, R_d, and alpha), while future size for *Heliconia* is more strongly influenced by the combined effects of A_{max}, R_d, and alpha, than by the combined effects of A_{max}, R_d, and LCP.

The two-way interaction between size and the second principal component axis (photosynthetic gains axis) was the most important interaction for both species, and more so for *Heliconia* than *Calathea*. This finding agreed with our previous results for *Heliconia* since PC2 was the most important single predictor following size. Therefore, for *Heliconia*, the effect of PC2 (A_{max}, alpha, and R_d) and size were equally important in terms of predicting growth. However, this finding contradicted our previous results for *Calathea* since light was the most important single predictor of growth, following plant size, and the effect of PC2 was the third most important predictor.

Despite the significant effects of size, light, and physiology, the three-way and four-way interactions among these variables were not important predictors of growth for our study species. The most important interaction was among size, light, and the photosynthetic gains (PC2) axis values, but even this interaction had an importance of less than 5%. A significant three-way interaction among size, light, and light response parameters could mean that, for example, the effect of current size on future size (i.e., growth) is mediated by light response parameters, which change with the degree of canopy openness. Thus, the absence of such an interaction may indicate that canopy openness does not strongly influence how these species physiologically respond to light across their size range, but we cannot rule out the possibility that the lack of an effect is due to low sample size across the full spectrum of light environments.

In the average models of growth, there were significant differences between species. For *Heliconia*, the model coefficient associated with the photosynthetic gains axis (PC2) values (A_{max}, alpha, and R_d) was much more negative than for *Calathea* (A_{max} and alpha), although changing the PC2 values produced the same effects on growth in both species. As this coefficient became more negative, growth decreased dramatically for *Heliconia* and decreased minimally *Calathea*. Therefore, the joint effects of A_{max}, alpha, and R_d have a stronger effect on growth for *Heliconia* than the joint effects of A_{max} and alpha for *Calathea*. The effect of changing PC1 values was reversed for the two species. For *Calathea*, increasing PC1 axis values (associated with high LCP and R_d but low alpha) resulted in a reduction in future size, but for *Heliconia*, increasing PC1 axis values (associated with high A_{max}, LCP, and R_d) resulted in a net increase in size. In summary, compared to *Calathea* that grew, *Calathea* that diminished in size had higher respiratory costs, required more light to offset respiration, and had less efficient photosystems, or, had high efficiency and high photosynthetic capacity. The two scenarios correspond to the effects of PC1 and PC2, respectively (Table 3). If a high net carbon gain results in an increase in future size, compared to a low net carbon gain, the latter scenario contradicts our prediction that increasing A_{max} and alpha will result in a high growth via carbon gain, all other parameters staying equal. Compared to *Heliconia* that grew, *Heliconia* that diminished in size had low respiratory costs, required less light to offset respiration costs, and had less efficient photosystems, or, had low photosynthetic capacity, low respiration, and low efficiency. The two scenarios correspond to the effects of PC1 and PC2, respectively (Table 3). Thus, when pooled over all light environments, the shapes of the light response curves differ between individuals that grew versus those that diminished in size, again indicating that growth is likely to be regulated by different suites of physiological adaptations to light in these species.

Interestingly, the effects of the light response parameters associated with PC1 (LCP, R_d, and alpha) for *Calathea* matched those expected for species adapted to shaded environments (minimize R_d, A_{max}, and LCP while maximizing alpha (Valladares and Niinemets 2008)); *Calathea* that grew had low LCP, low R_d, and high alpha. There was no significant association with A_{max}, which would be expected to decrease with LCP and R_d. *Calathea* that diminished in size had the opposite syndrome, high LCP, high R_d, and low alpha. The effects of the light response parameters associated with PC2 had the opposite effect of what we would expect for shade-adapted species. *Calathea* that grew had low A_{max} and low alpha, while those that shrank had high A_{max} and high alpha. For *Heliconia*, the effects of the light response parameters associated with PC1 and PC2 also more closely matched to those expected for light-adapted species. We did not have any expectations regarding the effects of changing PC1 and PC2 values because the combinations of variables have conflicting consequences for carbon gain. *Heliconia* that grew had high LCP, R_d and A_{max} while those that shrank had low LCP, R_d, and A_{max}. There was no significant association of PC1 with alpha, which is expected to be high for shade-adapted species. The effects of the light response parameters associated with PC2 were also a closer match to those expected for light-adapted species. *Heliconia* that grew had high A_{max} and high R_d but a low alpha. There was no significant association of PC2 with LCP, and LCP should be low for shade-adapted species. These results support previous findings that *Calathea* is the more shade tolerant species of the two species (although the effects of PC2 did not match our expectation for *Calathea*), and describes two mechanisms resulting in growth for both species. We offer two explanations of these results. First, the effects of PC2 on growth for *Calathea* do not match those expected for shade-adapted species because *Calathea* have adapted their physiology to take advantage of light pulses, resulting in growth even in very low light environments. This type of adaptation may be more necessary for moderately shade tolerant species, which inhabit a wide range of light environments. Second, for *Heliconia*, individuals that grow may tend to be in areas of high light compared to *Calathea* that grow, resulting in light response parameters and their associated effects which are more similar to those expected for light adapted species. Without rates of photosynthetic induction (which assesses the rate at which stomata open) for both species, we also cannot rule out the possibility that the rates of photosynthesis between the species would differ even more than they do currently. Furthermore, photoinhibition also could have depressed our estimates of the light response parameters.

CONCLUSIONS —A companion study of these species found that *Calathea* was more shade tolerant than *Heliconia* because *Calathea* had higher survival in low light than in high light and less size loss (shrinkage) over the range of observed light environments. In contrast, *Heliconia* survival was unaffected by light availability and *Heliconia* experienced more shrinkage than *Calathea* over all light environments (Gagnon et al.

2011). The authors attributed these findings to differences in physiology and morphology, because *Calathea* is likely to intercept more light than *Heliconia* due to its growth form. Our results support these findings by providing a physiological mechanism that explains why *Calathea* is more shade tolerant than *Heliconia*.

Table 3.1 Expected values of photosynthetic light response parameters for a shade-adapted and a light-adapted species, following Valladares and Niinemets (2008). A_{max}, LCP, and R_d should be positively correlated with one another and negatively correlated with alpha for both shade-adapted and light-adapted species.

	Shade-adapted	Light-adapted
A_{max}	Low	High
LCP	Low	High
R_d	Low	High
alpha	High	Low

Table 3.2 Spearman Rank correlations among physiological parameters. First row contains correlation values expected for a shade-adapted species. The following rows contain data for *Calathea crotalifera*, *Heliconia tortuosa*, and both species combined. Statistically significant relationships ($p<0.05$) are marked in bold. A_{max}, LCP, and R_d should be positively correlated with one another and negatively correlated with alpha for both shade-adapted and light-adapted species.

		alpha	A_{max}	R_d
Expected for shade-adapted species	LCP	–	+	+
	alpha		–	–
	A_{max}			+
Calathea	LCP	**-0.43**	**0.34**	**0.72**
	alpha		-0.05	0.17
	A_{max}			**0.44**
Heliconia	LCP	-0.32	0.14	**0.81**
	alpha		0.15	0.16
	A_{max}			0.19
Both species	LCP	**-0.37**	**0.28**	**0.79**
	alpha		0.06	0.15
	A_{max}			**0.34**

Table 3.3 Associations between principal component scores and physiological parameters for *Calathea* and *Heliconia*, and their effects (expected and observed) on future size. The signs of the parameter values were obtained using a Spearman Rank correlation of each principal component axis against the parameter. + indicates a significant positive association, – indicates a significant negative association. 'weak' indicates correlations were not statistically significant (p>0.05), therefore signs are not shown. ? indicates the lack of an expectation (see *Discussion*). See figures 6 and 7 for graphical representation.

		Sign of Association				Growth	
		A_{max}	alpha	LCP	R_d	Expected	Observed
Calathea	PC1 values	weak	–	+	+	–	–
	PC2 values	+	+	weak	weak	+	–
Heliconia	PC1 values	+	weak	+	+	?	+
	PC2 values	+	+	weak	+	?	–

Table 3.4 Values of coefficients in the average model of future size for *Calathea crotalifera* and *Heliconia tortuosa*. Model coefficients correspond to those listed in Equation 3. PC1 represents the photosynthetic costs axis and PC2 represents the photosynthetic gains axis.

	Model coefficients	*Calathea*	*Heliconia*
Intercept	x_0, *intercept*	1.11	2.64
Main effects	x_1, *size*	0.877	0.645
	x_2, *light*	-0.064	-0.204
	x_3, *PC1*	-0.132	0.577
	x_4, *PC2*	-0.083	-6.721
Two way interactions	x_5, *size×light*	0.002	0.011
	x_6, *size×PC1*	0.005	-0.013
	x_7, *size×PC2*	0.008	0.750
	x_8, *light×PC1*	-0.027	0.613
	x_9, *light×PC2*	0.065	-2.013
	x_{10}, *PC1×PC2*	-0.001	0.000
Three-way interactions	x_{11}, *Size×Light×PC1*	0.000	0.000
	x_{12}, *Size×Light×PC2*	0.000	0.012
	x_{13}, *Light×PC1×PC2*	-0.002	0.009
	x_{14}, *Size×PC1×PC2*	0.000	0.000
Four way interaction	x_{15}, *Size×Light×PC1×PC2*	0	0

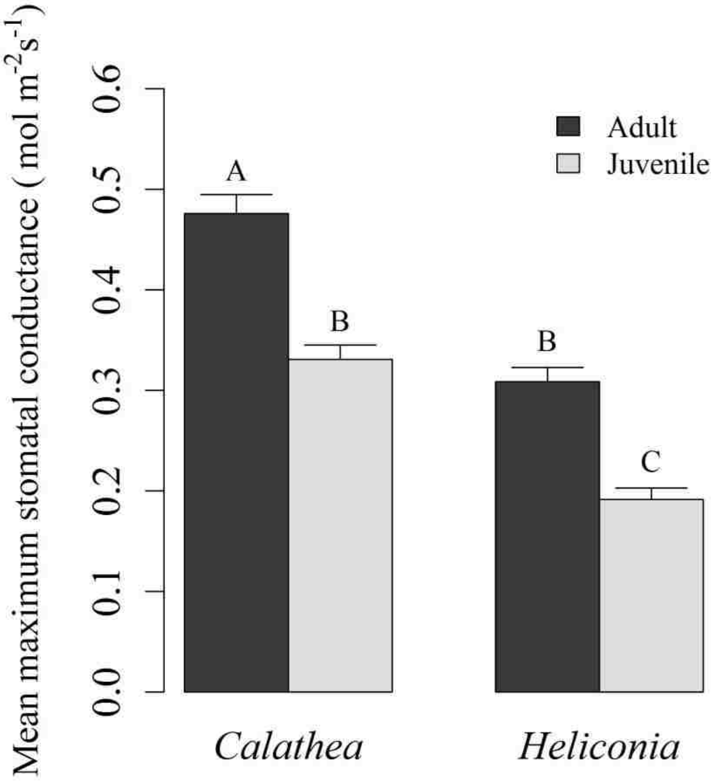

Figure 3.1 Mean maximum stomatal conductance (mol m^{-2} s^{-1}) was significantly higher ($p<0.05$) for *Calathea* than for *Heliconia* ($p<0.05$), and was higher for adults than for juveniles of each species. Bars topped by the same letter do not differ significantly by Tukey's HSD test. Conductance was estimated from stomate size and density.

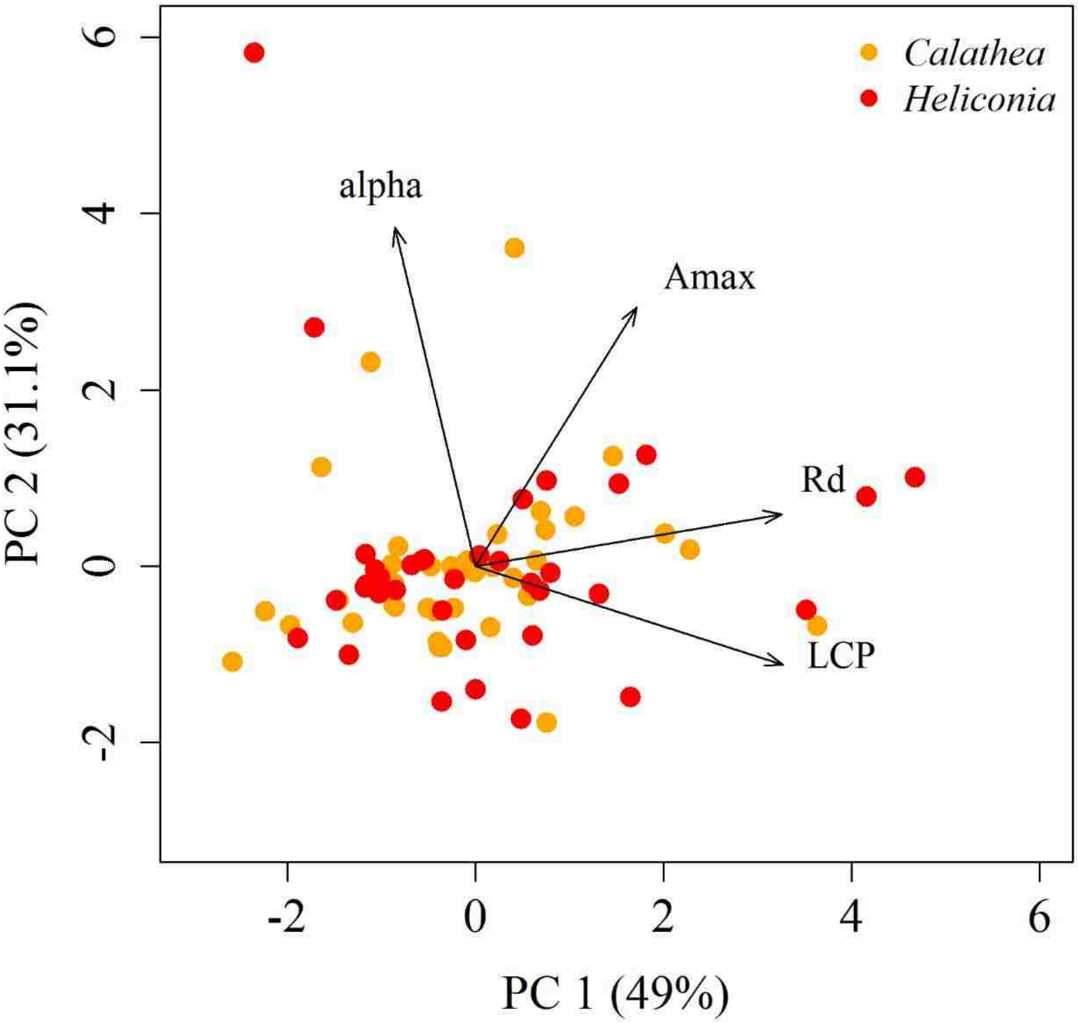

Figure 3.2 Principal components analysis of photosynthetic responses. There was no separation of species by physiological responses.

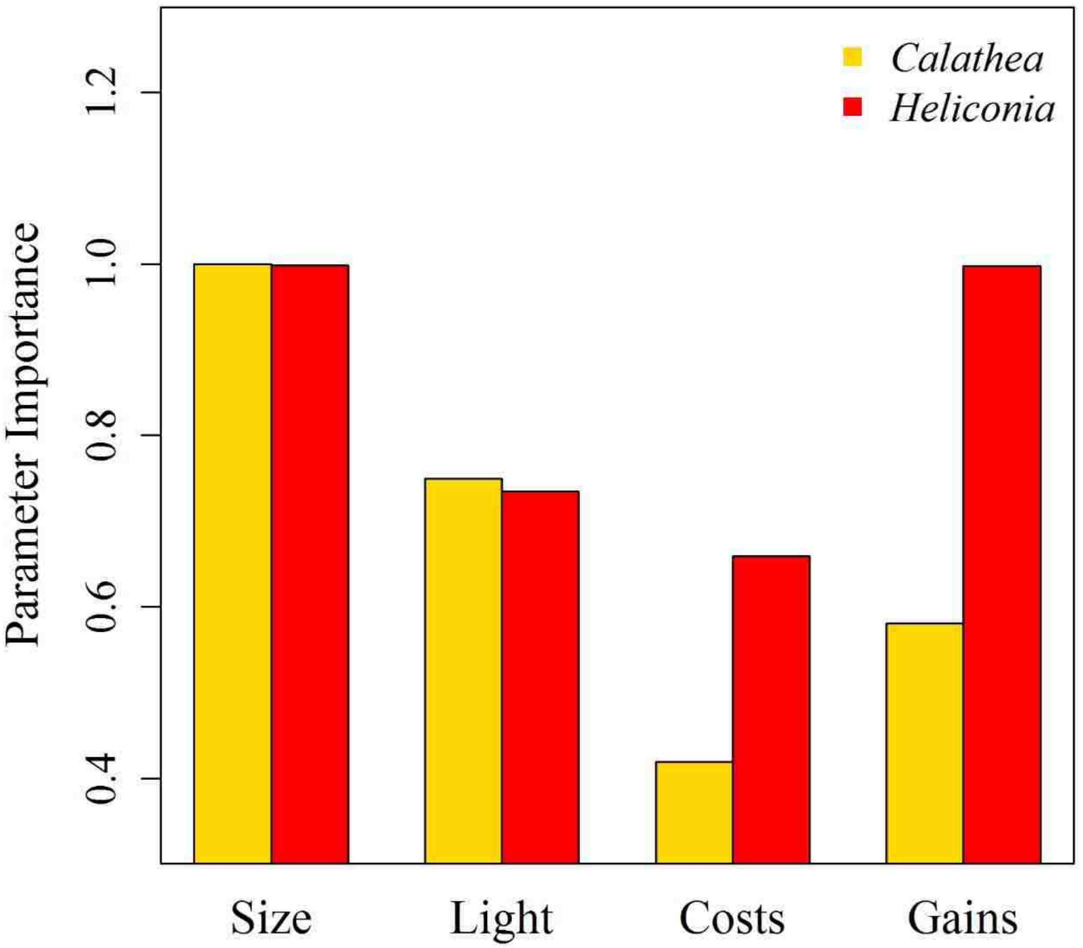

Figure 3.3 Relative importance of plant size, light, and the principal component scores of the photosynthetic costs (PC1) axis and photosynthetic gains (PC2) axis for determining future size. The importance values are relative to one another and are thus scaled to be between 0 and 1. The principal component scores are derived from the PCA in Fig 3.1.

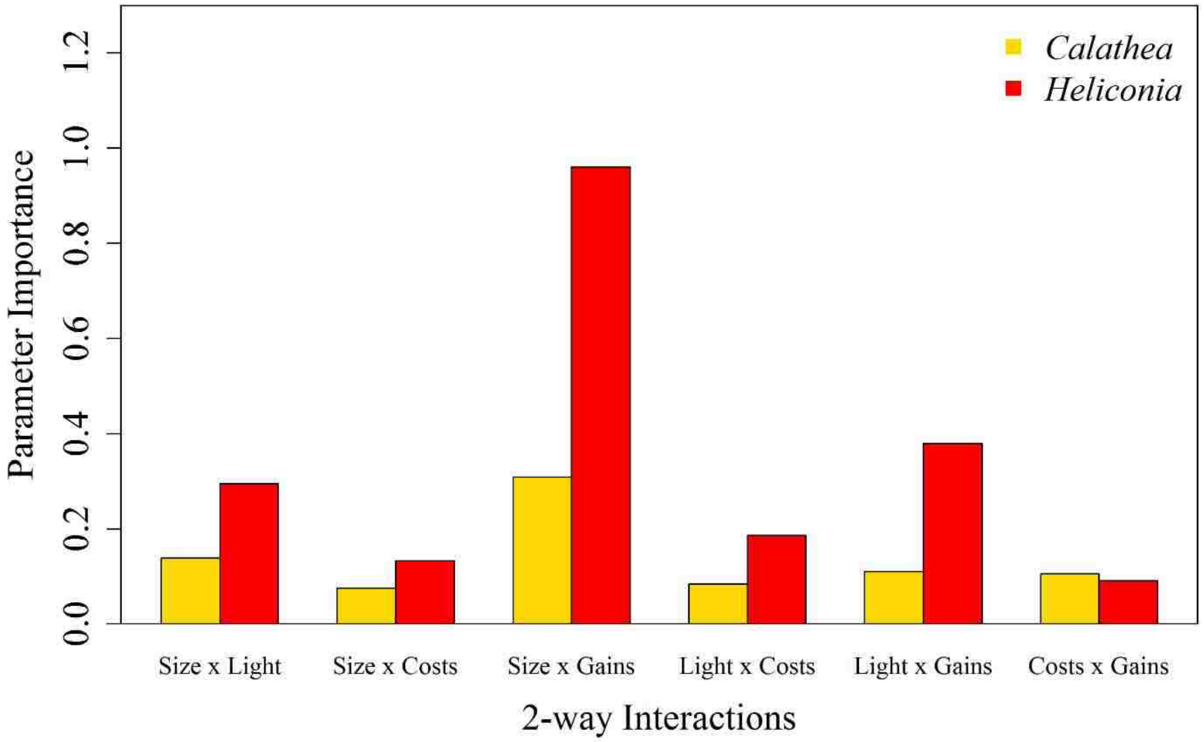

Figure 3.4 Relative importance of two-way interactions among current size (size_t), light, and photosynthetic costs (PC1) axis and photosynthetic gains (PC2) axis for determining future size (size_{t+1}). The importance values are relative to one another and are thus scaled to be between 0 and 1. The principal component scores are derived from the PCA depicted in Fig 3.1.

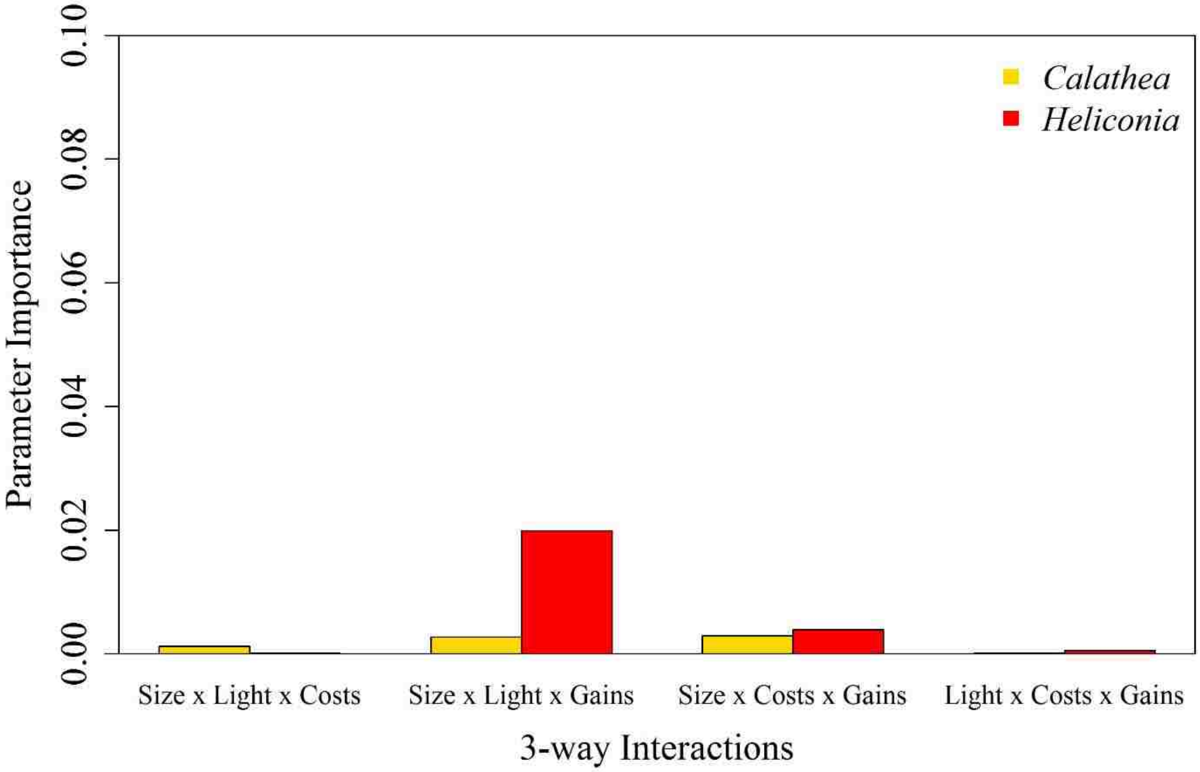

Figure 3.5 Relative importance of all three-way interactions among current size (size$_t$), light, and the principal component scores of the photosynthetic costs (PC1) axis and photosynthetic gains (PC2) axis, for determining future size (size$_{t+1}$). Note the change in the range of the vertical axis. The importance values are relative to one another and are thus scaled to be between 0 and 1. The principal component scores are derived from the PCA depicted in Fig 3.1.

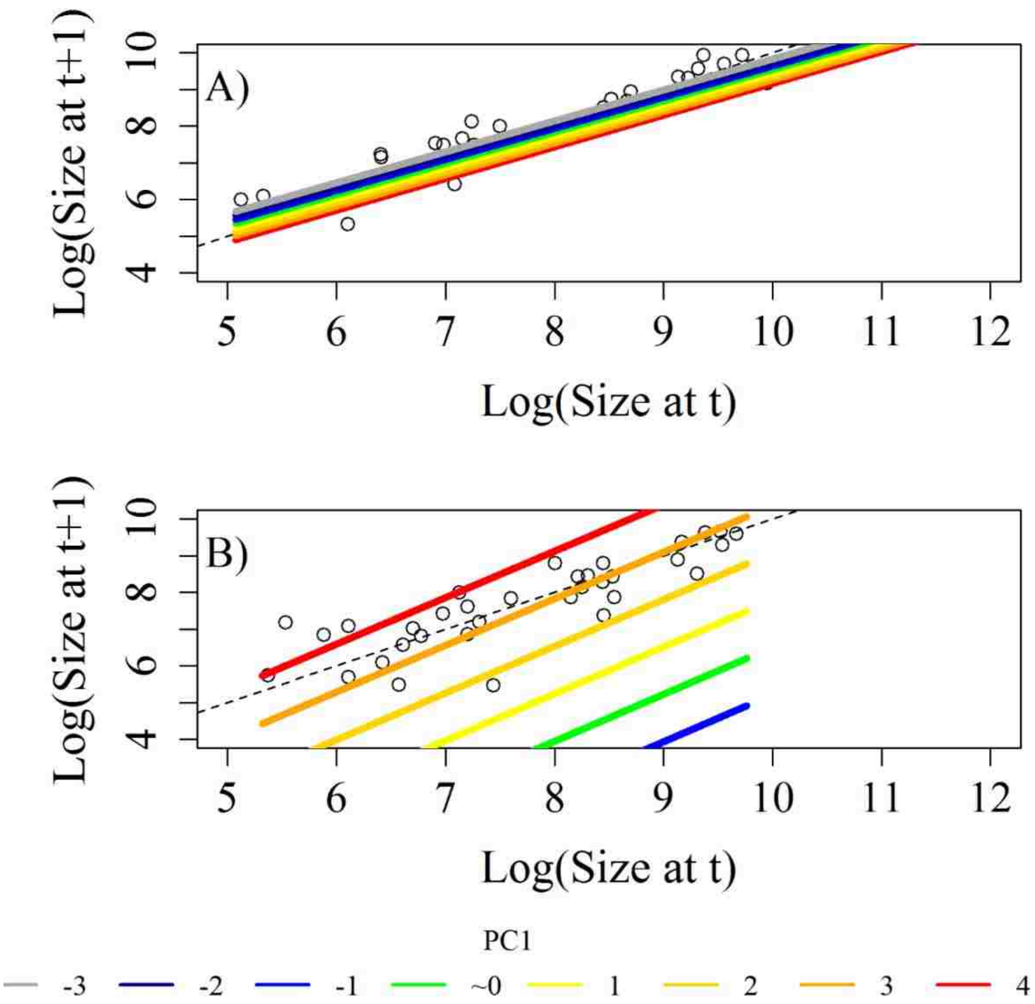

Figure 3.6 Average model of future size as a function of current size, light, and composite physiological responses (PC1 and PC2) for A) *Calathea crotalifera* and B) *Heliconia tortuosa*. Colored lines represent the values of the average model when photosynthetic cost (PC1) is changed and canopy openness is held constant (value of 1). Open circles represent data and dashed lines represent identity line. Colored lines below the identity line are diminishing in size, while those above the dashed line are growing.

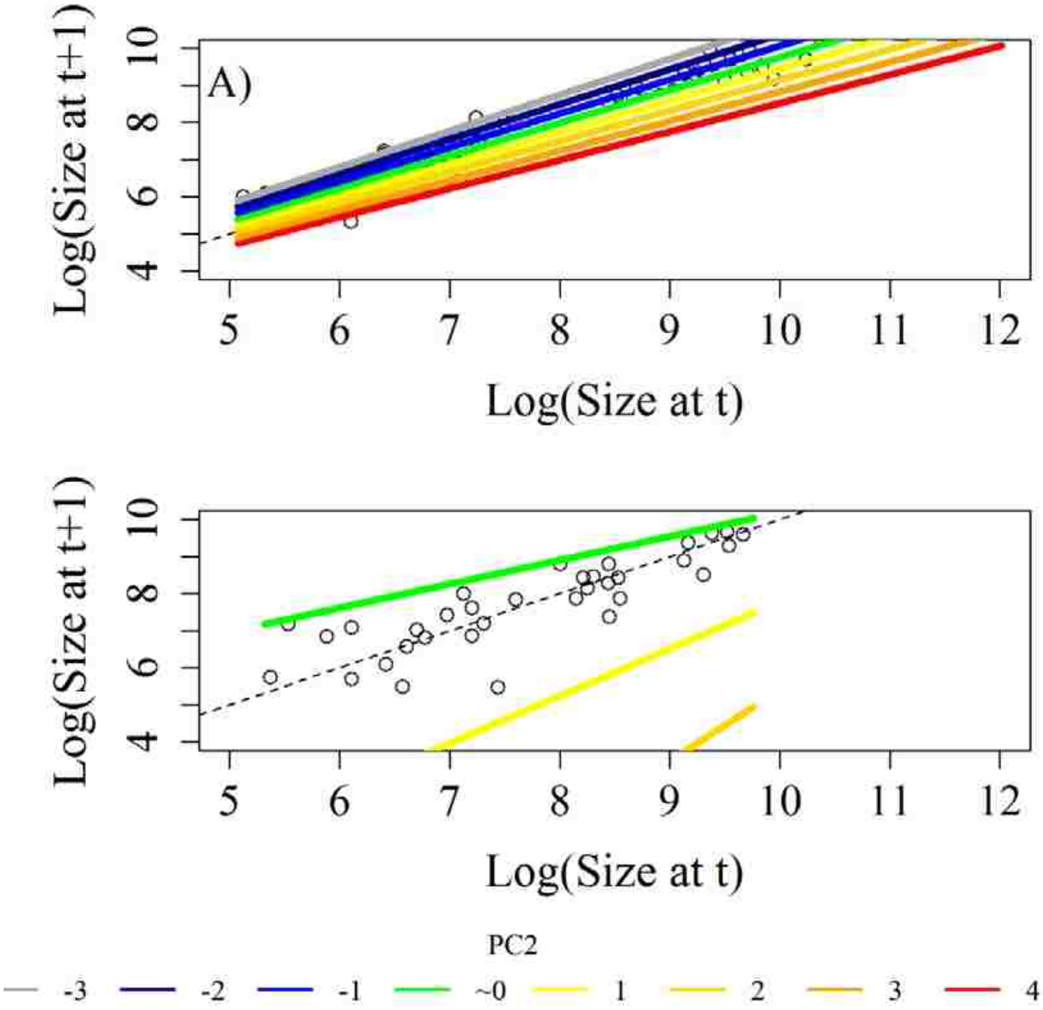

Figure 3.7 Average model of future size as a function of current size, light, and composite physiological responses (PC1 and PC2) for A) *Calathea crotalifera* and B) *Heliconia tortuosa*. Colored lines represent the values of the model when photosynthetic gain (PC2) is changed and canopy openness is held constant (value of 1). Open circles represent data and dashed lines represent identity line. Colored lines below the identity line are diminishing in size, while those above the dashed line are growing.

Chapter IV: Demographic and functional traits of two tropical, understory herbs are influenced by variability in light and precipitation in a shadehouse experiment

Overview

The availability of light from tree canopy gaps strongly influences demographic and functional traits of plants in the tropical forest understory. The forest understory is a highly variable environment, which should promote plasticity in traits that influence light capture and usage. We used a shadehouse experiment to test the hypothesis that demographic and functional traits are positively influenced by light variability. We measured growth, survival, leaf lifespan, photosynthetic capacity, and biomass allocation of two understory perennial herbs, *Heliconia tortuosa* and *Calathea crotalifera* over two years, in response to three independent factors: light availability at the seedling stage, precipitation level, and whether individuals experienced a constant or a variable light environment. Individuals that were assigned to the variable light environment switched between low and high light levels every six months. Individuals assigned to the constant light environments remained at either a low (90% shade) or high (60% shade) light level throughout their lifetimes. Individuals were also assigned to one of two precipitation treatments: constant at low or constant at high precipitation. We used linear regression analyses with mixed effects models to determine the effect of each factor independently and jointly. Compared to *Heliconia*, *Calathea* grew faster and less individuals survived, independent of the treatment. *Calathea* grew more at high precipitation than low precipitation while *Heliconia* grew more at low precipitation than high precipitation. *Calathea* had a significantly greater proportion of its total biomass aboveground versus that of *Heliconia*. Plants in a variable light environment had greater growth than those in

a constant light environment when precipitation was low. At low precipitation, a variable light environment increased growth when individuals started in low light and had no influence on growth when individuals started in high light. At high precipitation, a constant light environment resulted in higher growth whether individuals started in low or high light. Survival decreased with increasing environmental variability but more so at high precipitation. Photosynthetic capacity decreased for individuals in a variable light environment, when they had lived in high light as seedlings, but was unaffected by environmental variability when they had lived in low light as seedlings. Leaf lifespan was not significantly affected by the treatments. Although these species inhabit highly heterogeneous and variable light environments, environmental variability does not always have positive effects on demographic and functional traits and may be stressful if plants have low plasticity, i.e., a low capacity to acclimate.

Background

Light in tropical rainforests is both a spatially heterogeneous and temporally variable resource, the availability of which fluctuates with the opening and closing of gaps in the tree canopy (Chazdon and Fetcher 1984). The presence of gaps also influences soil moisture availability in the gap itself and in the surrounding microhabitat (Denslow et al. 1990, Camargo and Kapos 1995); gaps have higher soil moisture and temperature than the adjacent forest understory (Denslow et al. 1998). The availability of light and moisture has been shown to limit demographic, morphological, physiological, and functional traits of tropical plants (Kitajima et al. 1997, Rundel et al. 1998, Valladares et al. 2000, Aragao et al. 2005, Chazdon et al. 2005). Therefore, the need to capture and efficiently use light and soil moisture as they fluctuate should promote high trait plasticity for plants restricted to the forest understory. Furthermore, the availability of resources early in life may influence growth, survival, and functional traits later in life, because trait plasticity has been observed to change with ontogeny (Martinez-Garza and Howe 2005, Lasky et al. 2015). Thus, a better understanding of how shifting resource availability influences the fitness of understory species requires studies that monitor both light and moisture over an individual's lifetime.

For plants that establish and persist in both low and high light environments, a necessary requirement is to possess flexible traits that change quickly enough to increase an individual's fitness as the environment changes. Plants adapted to living in shade may possess one of two adaptive strategies allowing them to persist in low light environments: minimizing respiratory costs while waiting for gaps to open, increasing their efficiency of light capture and usage (Valladares and Niinemets 2008) in low light. Trait plasticity may allow species to alternate between these strategies, and may be achieved by a combination of morphological and physiological adaptations. For example, high physiological plasticity may express itself as a high potential to acclimate to changes in light availability (Chazdon et al. 1996) or as high variability in a response to changes in light availability. Acclimation to changing light levels may be achieved via changes 1) in whole plant structure, such as leaf lifespan and self-shading, 2) leaf morphology, such as regulation of stomatal density, mesophyll layer thickness, and chlorophyll content, and 3) leaf biochemistry, via functioning of proteins within the photosynthetic apparatus (Demmigadams and Adams 1992, Valladares and Niinemets 2008). Photosynthetic capacity, chlorophyll content, and stomatal conductance, have been shown to exhibit plasticity in response to changing light conditions (Valladares et al. 2002, Walters 2005, Portes et al. 2010) and to change with ontogeny (Valladares and Niinemets 2008).

Physiological plasticity and acclimation to early life conditions may influence demographic and physiological performance later in life. Physiological plasticity is greater when seedlings are adapted to high light as opposed to low light (Valladares et al. 2002), and similarly, has been shown to be greater in shade-intolerant species than in shade-tolerant species (Straussdebenedetti and Bazzaz 1991, Valladares and Niinemets 2008). When shade-grown plants shift from low to high light, mature leaves often show signs of photoinhibition while newly-produced leaves exhibit a range of responses if plasticity is high (Chazdon et al. 1996). Therefore, when seedlings of shade-intolerant species are grown in low light they exhibit high photosynthetic plasticity, which may increase survival in the short term, but if light availability does not increase, the positive effects of plasticity are offset by high metabolic costs, reducing survival (Chazdon et al. 1996). Although shade-intolerant species have been found to have greater plasticity in leaf production and photosynthetic capacity than shade-tolerant species, shade tolerant species have been found to be more plastic than shade-intolerant species in terms of leaf traits such as specific leaf mass, leaf display, and leaf nitrogen concentration (Lei and Lechowicz 1990, Kubiske and Pregitzer 1996). Previously, researchers have reported that shade-intolerant species grown in low light and transferred to high light have a similar or higher relative growth rate and photosynthetic capacity than shade-intolerant species growing in a constant high light environment, and shade-grown plants acclimated faster to increasing light availability than sun-grown plants did to decreasing light availability (Popma and Bongers 1991, Sims and Pearcy 1991, Straussdebenedetti and Bazzaz 1991).

Tradeoffs between growth and survival are likely to occur in resource-limited environments where allocation of resources towards growth to obtain additional resources, takes resources away from maintenance thus lowering survival (Wright et al. 2003). The allocation of resources to above versus belowground growth also is influenced by resource availability. Increasing allocation to aboveground biomass should increase the capture of light, while increasing investment in belowground biomass should increase the uptake of soil water and mineral nutrients (Davidson 1969, Bloom et al. 1985, Canham et al. 1996). Also, an increase in belowground biomass often reflects an increased allocation to storage, which benefits survival. Therefore, the availability of resources is likely to result in changes in resource allocation, influencing survival and growth. Growth-survival tradeoffs are also likely to be influenced by the propensity to store resources when resource supply exceeds demand. Chapin et al. (1990) defined storage as the build-up of resources that can be mobilized in the future to support biosynthesis for growth or other plant functions. The ability to store resources is common in woody and non-woody perennials (Kozlowski 1992, Landa et al. 1992), and may result in short term reductions in growth during the storage period. When resource demands begin to exceed supply, stored reserves can be used towards growth, and may increase rates of survival for plants in resource limited environments.

A tradeoff exists between the ability to adapt to shade and to withstand drought (Smith and Huston 1989). According to Smith and Huston (1989), shade tolerant species increase allocation to shoots rather than roots, and have a high specific leaf area, resulting in a large evaporative surface and reduced ability to capture water, decreasing drought tolerance. Therefore, whether plants invest resources in growth over survival and whether growth takes place above or below ground, depends on current resource availability and the need to withstand periods of deep shade or drought.

Our objective was to determine whether demographic and functional traits of plants that establish and persist in variable environments, are influenced by variability in light and how light variability interacts with precipitation. Our second objective was to determine how the availability of light during early life stages influences the effect of environmental variability and precipitation level on demographic and functional traits. The study species are two perennial herbs, *Calathea crotalifera* and *Heliconia tortuosa*, which are restricted to the tropical forest understory. To assess the role of environmental variability, we exposed plants to constant and variable environments in a shadehouse experiment. To assess the role of early life light availability, we exposed seedlings to high or low light and then assigned them to the variable or constant environment. The demographic traits of interest are relative growth and survival rates, and the functional traits of interest are photosynthetic capacity, leaf turnover, and the ratio of aboveground to total biomass. A key assumption of this study is that plants exposed to either low or high light during the seedling stage acclimated to the light environment to which they were exposed, over a period of several days to weeks, prior to being switched to the opposing light environment. Another key assumption is that our species are not employing ‘adaptive plasticity’ (Alpert and Simms 2002), whereby species increase plasticity in a trait (that strongly influences fitness) in only one or a few of the total set of environments. In other words, although we may not find evidence of plasticity due to our treatments, the study species may be plastic under another set of environmental conditions. Furthermore, traits may exhibit different degrees or patterns of plasticity at different development stages (Gedroc et al. 1996). The lack of phenotypic variation under different environmental conditions may also be evidence of ‘adaptive fixity’, as described by Alpert and Simms (2002), and are akin to a homeostatic or stabilizing strategy.

Our earlier study of the same species (*Heliconia tortuosa* and *Calathea crotalifera*) in wild populations in the field reported that both species added leaf area at a higher rate in low light than in high light and that relative growth was faster for small plants than large plants (Westerband and Horvitz 2015). Also, this study reported that *Calathea* survived better in low light than high light, *Heliconia* survived equally well across light environments. This is likely a result of adaptation to shade, or light intolerance, although both species occur over a wide range of environments in the forest. Thus, we offer four hypotheses: 1) the effect of variation in the light environment (hereafter environmental variability) will be influenced by light availability during early life stages. Specifically, plants exposed to a variable light environment and exposed to high light as seedlings should have higher growth, survival, leaf lifespan, ratio of aboveground to total biomass, and photosynthetic capacity, than those exposed to low light. 2) Because these study species occur over a wide range of light environments in the forest, we hypothesize that regardless of early life light conditions, a variable light environment will be favorable and therefore increase growth, survival, the ratio of aboveground to total biomass and photosynthetic capacity compared to a constant environment. 3) We hypothesize that high precipitation will increase growth, survival, photosynthetic capacity, and the ratio of aboveground to total biomass. 4) Lastly, we hypothesize that there will be interactions for all demographic and functional traits and that the species' responses will differ, because previous studies suggest that *Calathea* is more shade-adapted than *Heliconia*.

Methods

STUDY SPECIES—*Heliconia tortuosa* (Order Zingiberales: Family Heliconiaceae) is a perennial, herbaceous understory monocot that exhibits rhizomatous growth, with ramets 1-3 m tall. *Heliconia* reproduces both sexually via seeds and asexually via clonal shoots (Appendix 13). *Calathea crotalifera* (Order Zingiberales: Family Marantaceae) is a perennial, herbaceous understory monocot that is also rhizomatous, with ramets 1-3 m tall (Appendix 14). *Calathea* reproduces sexually and asexually with several clonal shoots arising from a sympodially branched rhizome near the ground (Kennedy 1973), resulting in greater spatial spread among leaves of a ramet, than for *Heliconia*. These study species were chosen because they are among the most common understory plants at our study site, they occupy a large range of light environments (including both large gaps and closed canopy understory), and they reach large enough sizes (up to 3 m tall) to compete with tree saplings and other herbaceous species for light, making them likely contributors to the process of forest succession.

STUDY SITE—This study was conducted at the Las Cruces Biological Station, located 1200 m above sea level (8° 47' 7" N, 82° 57' 32" W) in Coto Brus county, southern Costa

Rica. This region is designated as mid-elevation premontane forest, and it receives approximately 4 m of annual rainfall. There is a dry season from December to April and mean diurnal temperature over the year ranges from 13°C to 26°C.

SEEDLING SAMPLING DESIGN—In July 2013, we constructed a shadehouse at the biological station, and populated it with seedlings transplanted from the forest. A total of 1186 seedlings (614 *Calathea* and 572 *Heliconia*) were collected over a four-week period and transplanted into the shadehouse immediately. To remove any confounding effects of nutrient limitation, we collected soil from the forest to not more than 10 cm depth and mixed it with organic fertilizer. Large debris, including rocks and large roots, was removed from the soil by sieving. Plants were transferred to increasing larger pots as they grew in size, to reduce pot binding. We systematically assigned individuals collected from the forest to the light treatment groups Plants collected on days 1,3,5, etc. were assigned to the high light treatment, while plants collected on days 2,4,6, etc. were assigned to the low light treatment (these are the blocks in our randomized block design, see *Experimental design*).

EXPERIMENTAL DESIGN—The experimental design and sample sizes can be found in Table 1. Our experiment was a randomized block design, where the blocks were high or low light at the seedling stage (factor 1, two levels) and the plants in each block were then randomly assigned to high or low precipitation (factor 2, two levels) and to a variable or constant light environment (factor 3, two levels). Thus, the three factors, each with two levels, resulted in a total of eight treatment groups. Since there were two species, each with the same design, there were 16 distinct groups that we could compare. Each of the 16 groups was characterized by: 1) high or low light as seedlings, 2) constant or variable light after the seedling stage, 3) high or low precipitation throughout their life, and 4) species, *Calathea* or *Heliconia*. The independent variables (factors) in our analyses are initial light environment (high or low), environmental variability (yes or no), precipitation (high or low), and species (*Calathea* or *Heliconia*). The dependent variables were each of the demographic and functional traits (growth, survival, leaf lifespan, biomass, and photosynthetic capacity). We conducted a separate analysis for each trait (see *Statistical Analysis*). We waited 60 days before randomly assigning individuals within blocks to treatments, to allow individuals to acclimate to the shadehouse conditions. The plants in the variable light treatment were switched four times during the course of the two-year experiment. We haphazardly shifted the location of individuals within the treatments every two weeks to minimize any positional effects.

LIGHT AVAILABILITY AND ENVIRONMENTAL VARIABILITY—Photosynthetically active radiation (PAR) was adjusted to 60 and 90% shade by using different weaves of shadecloth to simulate light and dark forest environments, respectively. Individuals assigned to the variable environment treatment were switched between light environments every six months. We chose six month intervals to allow one switch during the dry season (December-April) and one switch during the wet season (May-November).

PRECIPITATION TREATMENT—Precipitation level was manipulated for plants assigned to the low precipitation treatment by excluding natural rainfall using clear plastic sheeting placed below the shadecloth roof, and watering one to two times weekly (depending on the treatment, Table 1). All plastic sheets were cleaned weekly to minimize unwanted shading from dirt and debris. Plants in the low precipitation treatment and high light were watered once a week at the onset of the experiment but because of high seedling mortality, the watering regime was changed so that plants were watered two times a week. This change occurred at the six month mark and the treatment remained constant for the duration of the experiment. When plants were watered, they were watered to field capacity, such that the soil surface was moist and water was dripping from the pot. We chose this method, rather than giving a finite amount of water because the amount of water necessary to fully wet the soil varied with plant size. We did not measure soil moisture in our pots, thus our precipitation treatments describe levels of watering, not soil water availability. Sample sizes ranged from 38 to 92 individuals per treatment.

MEASUREMENTS OF ABIOTIC CONDITIONS IN THE SHADEHOUSE—To ensure that plants in each treatment were indeed subject to different environmental conditions, we measured PAR, relative humidity, and ambient temperature in all treatments during the summer of 2014. In the month of July, four quantum sensors (Apogee Instruments, Inc) attached to a Campbell data logger (Campbell Scientific, Inc., Logan, UT) were installed in the low light treatment for 10 days and then switched to the high light treatment and for 11 days. Of the four sensors, two were placed in the low precipitation treatment (under plastic sheeting) and two were placed in the high precipitation treatment (not under sheeting). Four dual temperature and humidity sensors (DataQ instruments, Akron, OH, USA) were placed on the high light side for 25 days and then switched to the low light, where they remained for 27 days, with the exception of the sensor in the low-light high-precipitation treatment, which only logged five days after switching because of battery failure. Temperature, relative humidity, and PAR measurements for each treatment are described in Table 2 (*Results*). We tested for differences between treatments using ANOVA. Because the distributions of PAR values are not well represented by the mean values, we tested for differences in the distributions of PAR values between treatments using a series of Two-Sample Kolmogorov-Smirnov tests.

COLLECTION OF RELATIVE GROWTH RATE AND SURVIVAL DATA —Total leaf area for each individual was estimated by measuring the length of each leaf and using a regression relationship specific to our study species at this study site (Westerband and Horvitz 2015). We measured total leaf area during three annual censuses from 2013 to 2015. Relative growth rate (RGR) was estimated by log transforming the leaf area estimates and subtracting leaf area at time *t* from leaf area at time *t*+1, and dividing by the census interval (in this case, 1 year). Survival was determined by the presence of green, aboveground tissue at the conclusion of the experiment. Therefore, individuals with green stems but no leaves were considered still alive, although they had size zero at the time of census. During the experiment, only one individual reproduced.

PHOTOSYNTHETIC PERFORMANCE AND LEAF LIFESPAN—We estimated maximum photosynthetic capacity (A_{max}) in 363 randomly chosen individuals (165 *Calathea* and 198 *Heliconia*) using a LiCOR 6400 (Li-Cor, Lincoln, NE, USA) in 2014 and 2015. A_{max} was measured every six months, just before switching light environment for plants in the environmental variability treatment. The same individuals were measured, unless they had no leaves at the time of census or had died. In such cases, we replaced the plant with another randomly selected individual. Leaf life span was estimated for 289 randomly selected individuals (141 *Calathea* and 148 *Heliconia*) across the treatment groups. For each individual, we counted the initial number of leaves and subsequently counted the number of leaves produced and the number of leaves that died monthly, for up to 14 months. Leaf life span was then calculated as the inverse of the rate of leaf mortality (Wright et al. 2002) where the rate of leaf mortality is the number of leaves that died over the study period divided by the number of months the individual was sampled.

BIOMASS ESTIMATES—Above and belowground biomass was measured for 227 individuals. We sampled 7 *Calathea* that started in low light, switched between light environments, and experienced low precipitation and 10 *Heliconia* that started in low light, remained in low light, and experienced low precipitation. For the other 14 groups, we sampled 15 individuals. Aboveground biomass is here defined as all living leaves and stems; belowground biomass includes roots and rhizomes. We then estimated the ratio of aboveground biomass to total biomass.

STATISTICAL ANALYSES—To determine the main effects of treatments and their interactions on survival, we used a linear regression model with a binomial distribution and species, precipitation, environmental variability (constant or variable), and initial light environment as independent variables. Relative growth rate (RGR) was log transformed to achieve normality and was modelled using a generalized linear mixed effect model, where species, precipitation, environmental variability, and initial light environment, were used as independent variables with fixed effects. Plant size at time *t* was used a random effect in the model, because it accounted for a significant proportion of the variance in RGR (as determined by plots of residuals). We also tested the effect of plant size at time *t* (independent variable) on relative growth rate (dependent variable) using ANOVA and found no significant effect ($p<0.05$).

To determine the effects of the treatments on leaf lifespan, we log transformed the data to achieve normality, then used linear regression analysis to determine the effects of species, precipitation, environmental variability, and initial light environment on leaf lifespan. Differences in photosynthetic capacity attributable to treatments effects were examined using ANOVA, after determination with probability plots known as QQ plots (Quinn et al. 2002) that the data did not deviate significantly from normality. We tested effects of environmental variability, initial light environment, precipitation, and species.

We tested for differences in the ratios of aboveground to total biomass using a generalized linear model with a binomial distribution and the logit link function. All statistical analyses were conducted using R v 3.0.2 (R Core Team 2013). Although we used both parametric and nonparametric tests in our analyses, we present all traits as means with standard error bars to facilitate comparisons among traits, and to facilitate the comparison between treatments.

Results

ABIOTIC CONDITIONS—The shade cloth and watering treatments affected the abiotic environment in both intentional and unintentional ways. On the high light side of the shade house, humidity was significantly lower in the low precipitation treatments ($p<0.001$) and temperature was significantly greater ($p<0.001$). On the low light side, humidity was also significantly lower in the low precipitation treatments ($p<0.001$) and temperature was significantly greater ($p<0.001$). There were statistically significant differences in the distributions of PAR values between the low precipitation and high precipitation treatments on the high light side ($p<0.01$) and on the low light side ($p<0.01$), with the low precipitation treatments having lower PAR values than the high precipitation treatments. There were also statistically significant differences in the distributions of PAR values between the high light and low light treatments for the low precipitation ($p<0.01$) and high precipitation treatments ($p<0.01$), with the high light side having higher PAR values than the low light side. We also found that the distributions of PAR values for the two sensors within each precipitation treatment differed significantly ($p<0.05$) with the exception of the high precipitation treatment in low light ($p=0.43$). Because we moved plants within each treatment every two weeks, differences within treatments should not confound our results, because the differences between the low precipitation versus high precipitation treatments and the low light versus high light treatments are statistically significant.

DEMOGRAPHIC TRAITS —*No species differences:* We found that mean relative growth rate (RGR) and survival were significantly influenced by different combinations of the independent variables: species, initial light environment, environmental variability later in life, and precipitation. RGR was significantly higher for individuals that started in high light than for those that started in low light, and significantly lower for individuals in high precipitation versus those in low precipitation (Table 4.3, Figure 4.1). Under both low and high precipitation treatments, individuals that started in high light (Figure 4.1A and 4.1C) grew more rapidly than those that started in low light (Figure 4.1B and 4.1D), and the effect was amplified in the high precipitation treatment. The effect of being in a variable light environment was significantly influenced by precipitation and initial light environment (a three-way interaction) (Table 4.3, Figure 4.1). In low precipitation conditions (Figure 4.1A and 4.1B), having a variable light environment increased growth when individuals started in low light (Figure 4.1B) and had no influence on growth when individuals started in high light (Figure 4.1A). In high precipitation conditions (Figure 4.1C and 4.1D), a constant light environment resulted in slightly higher growth whether individuals started in low or high light. Individuals that started in low light had significantly lower survival than individuals that started in high light (not shown). Individuals in the high precipitation treatment had significantly higher survival than individuals in low precipitation (Table 4.3, Figure 4.3). The effect of environmental variability on survival was significantly influenced by the precipitation treatment (a two-way interaction) (Table 4.3, Figure 4.3). Although being in a variable light environment significantly decreased survival compared to a constant light environment in both low and high precipitation, the magnitude of the effect was greater for high precipitation than for low precipitation (Table 4.3, Figure 4.3).

Species differences: Relative growth rate was significantly higher in *Heliconia* than *Calathea* (Table 4.3, Figure 4.2). There was a significant difference between the species in terms of the effect of precipitation on relative growth rate; *Calathea* grew more in low precipitation than high precipitation while *Heliconia* grew slightly more in high precipitation than low precipitation (Table 4.3, Figure 4.2). Initial light conditions also influenced the interaction between precipitation and species (a three-way interaction, Table 4.3). For *Calathea*, plants that started in high light grew more than those that started in low light, but the effect of initial light availability was significantly greater for plants in the low precipitation treatment than in high precipitation (Figure 4.2A and 4.2B). For *Heliconia*, plants that started in high light grew more than those that started in low light and were not strongly influenced by precipitation (Figure 4.2C and 4.2D). Survival was significantly higher in *Heliconia* than *Calathea* (not shown), and there were no two-way or three-way interactions that included the effect of species.

FUNCTIONAL TRAITS—*No species differences*: Leaf lifespan did not differ significantly due to the treatments and did not differ by species (not shown). Leaf lifespan also had a large range for both species, from 0.5 to 7 months for *Calathea*, and from 0.3 to 6 months for *Heliconia*. The highest leaf lifespan for *Calathea* occurred for an individual in high light and high precipitation that switched between light environments. The lowest leaf lifespan for *Calathea* occurred for an individual in low light and low precipitation that remained in a constant light environment. The lowest leaf lifespan for *Heliconia* occurred for an individual in low light and high precipitation that switched between light environments. The highest leaf lifespan for *Heliconia* occurred for an individual in low light and low precipitation that remained in a constant light environment. The mean lifespan for *Calathea* was 1.8 months (± 0.08) and for *Heliconia* was 1.6 (± 0.05) months.

Photosynthetic capacity was significantly higher for individuals that started in high light than those that started in low light (Table 4.3, Figure 4.5). Photosynthetic capacity was also significantly lower for individuals in the low precipitation treatment than those in the high precipitation treatment (Table 4.3, not shown). There was a marginally significant interaction between environmental variability and initial light environment (Table 4.3, Figure 4.5). For plants that started in high light, photosynthetic capacity was lower for those in a variable light environment than a constant light environment, whereas plants that started in low light had a higher photosynthetic capacity in a variable than a constant light environment (Table 4.3, Figure 4.5).

Species differences: Aboveground biomass was not influenced by any of the treatments but there was a significant difference between species, in that *Calathea* had a greater proportion of aboveground biomass than *Heliconia* (Table 4.3, Figure 4.4).

Discussion

DEMOGRAPHIC TRAITS—The ability to change a trait in response to changes in the environment, i.e., trait plasticity, may increase the fitness of species in heterogeneous and variable environments (Alpert and Simms 2002). In this study, adaptation to a variable environment is defined by a positive effect of environmental variability on a trait, rather than the degree of change in a trait. Our objective was to understand the persistent effects of acclimation to resource availability at early life stages on performance later in life. We found that demographic and functional traits of two understory herbs are influenced by precipitation, by changes in light environment and light availability during the seedling stage, and that the species differed in their growth, survival, and resource allocation strategies. Previous studies have found that functional traits are often good predictors of fitness (Poorter and Bongers 2006) but in this study, functional traits were not necessarily influenced by the same factors as demographic traits.

The mean relative growth rate was significantly higher in *Heliconia* relative to *Calathea* and *Calathea* grew more when precipitation was low than when it was high, while *Heliconia* grew more in high precipitation than low precipitation treatments. These results support our hypothesis that the species would differ, although we predicted the opposite response. Smith and Huston (1989) hypothesized that a tradeoff exists been shade tolerance and drought tolerance, resulting in shade-tolerant plants being highly sensitive to drought. Westerband and Horvitz (2015) concluded that *Calathea* was more shade tolerant than *Heliconia*, based on demographic performance in low light versus high light. Our results here suggest that growth of *Heliconia* is more sensitive to drought than is growth of *Calathea*, which is not consistent with our previous findings. Another explanation is that drought and shade tolerance may not be as tightly coupled as we hypothesized, which has been suggested by more recent studies (Markesteijn and Poorter 2009, Holmgren et al. 2012) that argue that the two adaptations rely on different suites of morphological adaptations.

For both species, plants exposed to high light as seedlings grew more than plants exposed to low light, supporting our hypothesis that high light conditions early in life improves performance in a variable light environment. These results may also suggest that environmental variability had no main effect on growth, refuting our hypothesis that variable light environments are more favorable than constant light environments for these species. These results differ from those of Yamashita et al. (2002) who found that when seedlings of a pioneer tree species switched from high to low light, they had lower relative growth rates than those in constant low light. Our results suggest that the availability of light early in life is a more important determinant of resource allocation later in life, than is light availability later in life. These results may be attributed to a lag in the growth responses of these species. Martinez-Garza and Howe (2005) studied nonpioneer tropical trees and found that their leaf traits changed with ontogeny in response to the current conditions, but reflected the expected light conditions. Because our species will never reach the canopy and may be short-lived compared to trees, early life conditions should have a stronger influence on late life responses than expected future conditions.

Previous studies have found evidence of interactions between light availability and soil moisture affecting the relative growth rates and allocation strategies of herbs and tree seedlings (Canham et al. 1996, Baruch et al. 2000). Although soil moisture is known to influence nutrient availability in tropical forest soils (Wardle 1992), we did not test for differences in soil nutrients among our treatments and did not test for differences in soil moisture availability. Therefore, while we recognize that interactions may exist between soil macronutrients, precipitation (as it affects soil moisture), and light availability, we restrict our discussion to the effects of precipitation level and light availability. When data for each species were considered separately, differences were revealed in the nature of the interaction between precipitation and initial light. *Calathea* exposed to high light as seedlings grew more than those exposed to low light but the effect was greater for plants in low precipitation than in high precipitation, indicating that the positive effects of early life acclimation to high light conditions are most beneficial under periods of low precipitation. If low precipitation is a stressful abiotic condition for *Calathea*, our results suggest that high resource availability early in life may ameliorate the negative effects of resource poor conditions later in life and produce an overcompensation in growth. However, because *Calathea* grew more in low than in high precipitation, low precipitation may not be stressful (defining "stress" as defined as a decrease in the potential to acclimate to the environment or as a condition that results in a decrease in carbon gain (following Muraoka et al. (2002)). In contrast, *Heliconia* exposed to high light as seedlings grew more than those exposed to shade, and this relationship was *not* influenced by precipitation. Even though *Heliconia* grew best when precipitation was high, the positive effects of acclimating to high light early in life may negate the effects of low precipitation, resulting in similar growth rates under high and low precipitation. Sack and Grubb (2002) found no evidence of an interaction between moisture and irradiance in seedlings of three woody species, and argued that interactions were unlikely to occur if species were adapted to a broad range of environmental conditions.

When precipitation was low, environmental variability in our experiment increased growth for individuals exposed to low light but had no influence on growth for individuals exposed to high light. When precipitation was high, however, environmental variability decreased the relative growth rate for individuals exposed to low and high light and seedlings. Thus, our hypothesis that early life acclimation to high light will increase performance in a variable light environment is refuted. We offer three complementary explanations of these results. First, during early life stages, plants exposed to high light and high precipitation may have grown more belowground biomass than those acclimated to low light. Because we only measured root and shoot biomass at the end of the study, we cannot account for treatment effects during early life stages. Second, for plants in high precipitation, photosynthetic acclimation to high light during early life stages may have resulted in high maintenance costs. With large metabolic costs, environmental variability could be a stressful condition, because periods of darkness result in not enough carbon gains to offset costs (Chazdon et al. 1996). This latter scenario would result in reduced growth for plants photosynthetically acclimated to high light during early life stages. Third, plants exposed to high light as seedlings may be storing carbohydrates in the form of starch. Storage of resources is common in perennials (Kozlowski 1992, Landa et al. 1992), and is defined as the build-up of resources that can be mobilized in the future for growth or other plant functions (Chapin et al. 1990). Thus, when precipitation is high and light is readily available, resource supply may exceed demand, resulting in a short term accumulation of resources. The short term accumulation of stored resources would diminish growth between time *t* and *t*+1, but could promote growth when light is no longer readily available, acting as a buffer during periods of stressful abiotic conditions. Determining which of these scenarios is most likely would require a mechanistic plant growth model that estimates carbon gain, such as the YPLANT model (Pearcy and Yang 1996) and the model developed by Gross (1982),which integrates the presence of sunflecks in carbon gain estimates.

Survival was significantly higher for *Heliconia* than for *Calathea*, but high light availability early in life decreased survival, which supports the findings of Westerband and Horvitz (2015) that these species are shade-adapted. Increasing precipitation increased survival, which supports our hypothesis that that increasing precipitation positively influences survival, but adding environmental variability decreased survival, and more so when precipitation was high. This result was unexpected, given our prediction that these species should have improved performance in variable light environments. This suggests that environmental variability may be a stressful condition and if so, it is surprising that abundant precipitation amplifies its negative effects. Furthermore, the differential responses of growth and survival suggest that once these species acclimate to a light level, they can change their growth rates to suit the changing environmental conditions, i.e., growth is plastic, but survival is less plastic to changes in the environment. Plasticity in growth but not survival indicates the lack of a growth-survival tradeoff. Individuals that remained in the initial light environment to which they acclimated as seedlings survived better but grew equally well compared to those that experienced environmental variability. Tradeoffs between life history traits, such as growth and survival, may depend on plant size and life stage (Kunstler et al. 2009, Westerband and Horvitz 2015). Because we did not distinguish between survival of seedlings and later developmental stages, we cannot exclude the possibility that survival was temporarily increased by increasing environmental variability at the onset of the experiment.

We also cannot rule out the possibility that our study species have adapted to variable light environments by responding similarly regardless of the abiotic conditions, described by Alpert and Simms (2002) as ‘adaptive fixity’. This scenario would result in responses that are unaffected by environmental variability, and are akin to a homeostatic or stabilizing strategy. Under this scenario, we expect our species to have low trait plasticity because they perform equally well over a range of conditions. Palacio-Lopez et al. (2015) have found that phenotypic plasticity is not as ubiquitous in plants as a lack of plasticity, and a lack of plasticity may be expected for highly shade-tolerant species.

FUNCTIONAL TRAITS—Leaf longevity has been found to correlate with resource availability, influencing photosynthetic rates as well as the ability to defend against herbivory, pathogens, and extreme environmental conditions (Gusewell 2004). When resources are limited, plants should produce more durable, longer-lived leaves than when resources are abundant. Short-lived leaves tend to have higher photosynthetic rates than long-lived leaves and are less costly to produce and maintain (Gusewell 2004). In addition, long-lived leaves are correlated with reduced plasticity because individuals take longer to replace old leaves with phenotypically different new leaves as the environment changes (Valladares et al. 2000). Our results refuted our hypothesis that environmental variability decreases leaf lifespan compared to constant light environments because none of our treatments influenced leaf lifespan. Furthermore, we found that both species had very short-lived leaves (medians were 1.6-1.8 months), indicating that they should have high photosynthetic rates, as has been estimated for other broad-leaved species with similarly short leaf life lifespans (<2 months) (Reich et al. 1992). Similar leaf lifespans have been documented for broad-leaved forbs as wells as shrubs (Reich et al. 1998), and have been strongly and positively correlated with dark respiration rates (Reich et al. 1998). Thus, the lack of a treatment effect on leaf lifespan may indicate that aboveground allocation to leaves and its effect on carbon gain may not be as tightly coupled as has been documented for other species. Leaf lifespan did not reflect photosynthetic capacity for our study species and may not be plastic for these species, if plasticity increases performance in variable environments.

Individuals that started life in high light and were switched to low light had lower photosynthetic capacity than individuals who remained in high light throughout their lives. In contrast, individuals that started life in the shade and were switched to high light had the same photosynthetic capacity as individuals who remained in shade throughout their lives. These results support our hypothesis and suggest that photosynthetic acclimation during early life stages influences the ability to photosynthetically acclimate to a fluctuating light environment during later life stages. Ontogeny has been shown to influence physiological performance via changes in leaf chemistry, morphology, and architecture (Valladares and Niinemets 2008). When individuals acclimated to low light conditions during early stages, alternating between light environments may have had no influence on their photosynthetic rates because their photosynthetic machinery was attuned to low light and they were unable to use high light. Conversely, individuals that acclimated to high light maintained their ability to use high light but also had the ability to decrease their photosynthetic rates when they experienced a low light environment. Thus, early life acclimation to high light appears to promote plasticity because subsequent switching to low light resulted in a reduced photosynthetic capacity, whereas early life acclimation to low light produced no change in the photosynthetic capacity.

Yamashita et al. (2002) carried out a similar study on trees, and found that when plants transitioned from low to high light, their photosynthetic capacity decreased as leaves aged, but when plants transitioned from high to low light, there was an increase in photosynthetic capacity for two of the four study species and no effect for the other two species. These results support our findings; photoinhibition may be occurring when acclimation to low light happens early in development. We also found that photosynthetic capacity was high when initial light availability was high and was higher when precipitation was high than when precipitation was low, which agrees with our hypotheses. When precipitation is low, stomatal closure may reduce photosynthetic rates for plants even under periods of high light (Muraoka et al. 1997).

When precipitation and nutrients are plentiful, plants should invest resources in aboveground biomass to capture light, and when precipitation and nutrients are limiting, they should allocate resources towards growing roots (Alvarez-Buylla and Martinez Ramos 1992).We found no evidence of increased allocation to aboveground biomass due to light, precipitation, initial light environment, or environmental variability, refuting our hypotheses. We found that *Calathea* invested a significantly higher proportion of resources in aboveground biomass than *Heliconia*, over all treatments. These results indicate inherent morphological differences between the species and suggest low trait plasticity because changing the environment had no effect on the allocation of resources. It is important to note that because we mixed natural forest soil with organic fertilizer, soil nutrients and moisture may not have been limited. Thus, there may not have been any need to allocate more resources towards increased root production if belowground nutrient requirements were being met, even during periods between waterings. The lack of a response to light availability may indicate that changes in belowground morphology are not as sensitive to aboveground stimuli as changes in aboveground morphology. Alternatively, if our study species are storing large amounts of carbon, we would observe no net change in growth (above or belowground).

CONCLUSIONS—Our controlled experiment revealed that precipitation, light availability at early life stages, and environmental variability, influence demographic and functional traits in two understory herbs. Environmental variability influenced all traits except biomass allocation, indicating that for these understory herbs, fluctuations in resource availability may be an important determinant of fitness. The direction of the effect of increased environmental variability depended on the trait of interest, and at times decreased performance, indicating that environmental variability may be a stressful condition, often influenced by precipitation levels. A negative effect of environmental variability on demographic and functional traits is contrary to our hypothesis that these species are adapted to a wide range of light environments in the forest and could be indicative of low trait plasticity. The study species differed significantly in terms of their demographic traits and resources allocation strategies but not in any of their functional traits, which was unexpected, given that previous studies have described *Calathea* as being more shade tolerant than *Heliconia* (Westerband and Horvitz 2015). Thus, while some traits exhibit signs of plasticity, others do not, indicating that variable environments drive plasticity in some traits but not others. In conclusion, variable light environments are likely to be driving plasticity in some demographic and functional traits, key indicators of fitness, but early life conditions appear to be more important for later life performance than previously has been described for these understory herbs.

Table 4.1 Summary of experimental design of shadehouse experiment. N represents sample size at onset of experiment. Wet season occurs May-November, and dry season occurs December-April. * denotes a change in the treatment after the first year (see *Methods*).

Treatment	**Initial light environment**	**Environmental variability**	**Precipitation**	**Dry season watering regime**	**Wet season watering regime**	**N *Heliconia***	**N *Calathea***
1	High	No	Low	1x week, then 2x week*	1x week	38	66
2	High	Yes	Low	1x week	1x week	53	62
3	High	No	High	natural rainfall, plus 1x week	natural rainfall, plus 1x week	92	57
4	High	Yes	High	natural rainfall, plus 1x week	natural rainfall, plus 1x week	70	63
5	Low	No	Low	1x week	1x week	45	47
6	Low	Yes	Low	1x week, then 2x week*	1x week	84	67
7	Low	No	High	natural rainfall, plus 1x week	natural rainfall, plus 1x week	45	40
8	Low	Yes	High	natural rainfall, plus 1x week	natural rainfall, plus 1x week	65	83

Table 4.2 Abiotic conditions in each treatment of shadehouse experiment. Temperature, relative humidity, and photosynthetically active radiation (PAR) were estimated in the summer of 2014, over a period of 4 weeks.

Treatment	Initial light environment	Environmental variability	Precipitation	Mean Temperature (°C) ± SD [Range]	Mean Relative Humidity (%) ± SD [Range]	Mean PAR (μmol m^{-2} s^{-1}) ± SD [Range]
1	High	No	Low	20.8 ± 2.4 [16.5-33]	98.1 ± 6.6 [56-104.5]	44.4 ± 80.0 [0.2-511.1]
2	High	Yes	Low	20.6 ± 2 [16.5-28]	99.5 ± 5.0 [69.5-105.5]	39.4 ± 64.5 [0.2-683.6]
3	High	No	High	20.5 ± 2.5 [16.5-32.5]	99.6 ± 6.4 [62.5-105.5]	54.1 ± 86.8 [0.1-683.6]
4	High	Yes	High	20.4 ± 2.2 [16.5-29.5]	100.1 ± 5.8 [16.5-29.5]	48.7 ± 72.3 [0.1-404.6]
5	Low	No	Low	20.6 ± 2 [16.5-28]	99.5 ± 5.0 [69.5-105.5]	32.7 ± 32.0 [0.4-220]
6	Low	Yes	Low	20.8 ± 2.4 [16.5-33]	98.1 ± 6.6 [56-104.5]	39.4 ± 64.6 [0.2-683.6]
7	Low	No	High	20.4 ± 2.2 [16.5-29.5]	100.1 ± 5.8 [16.5-29.5]	48.7 ± 44.6 [0.7-404.6]
8	Low	Yes	High	20.5 ± 2.5 [16.5-32.5]	99.6 ± 6.4 [62.5-105.5]	41.3 ± 72.3 [0.1-511.1]

Table 4.3 Effects of species, precipitation, initial light environment, and environmental variability on demographic and functional traits for two species, *Calathea crotalifera* and *Heliconia tortuosa*. Of all possible main effects and interactions, only statistically significant effects are shown (no four-way interactions). Asterisks indicate significance level: · p<0.1, * p<0.05, **p<0.001, ***p<0.0001.

		Significant main effects	**Significant Two-Way Interactions**	**Significant Three-Way Interactions**
Demographic trait	**Relative Growth Rate**	Initial Light *** Precipitation *** Species**	Initial Light × Precipitation** Precipitation × Species**	Initial Light × Precipitation × Species* Initial Light × Precipitation × Variability*
	Survival	Initial Light*** Precipitation ** Species***	Precipitation × Variability**	
Functional trait	**Log(Leaf lifespan)**			
	Aboveground: total biomass	Species*		
	Photosynthetic capacity	Initial Light* Precipitation *	Initial Light × Variability·	

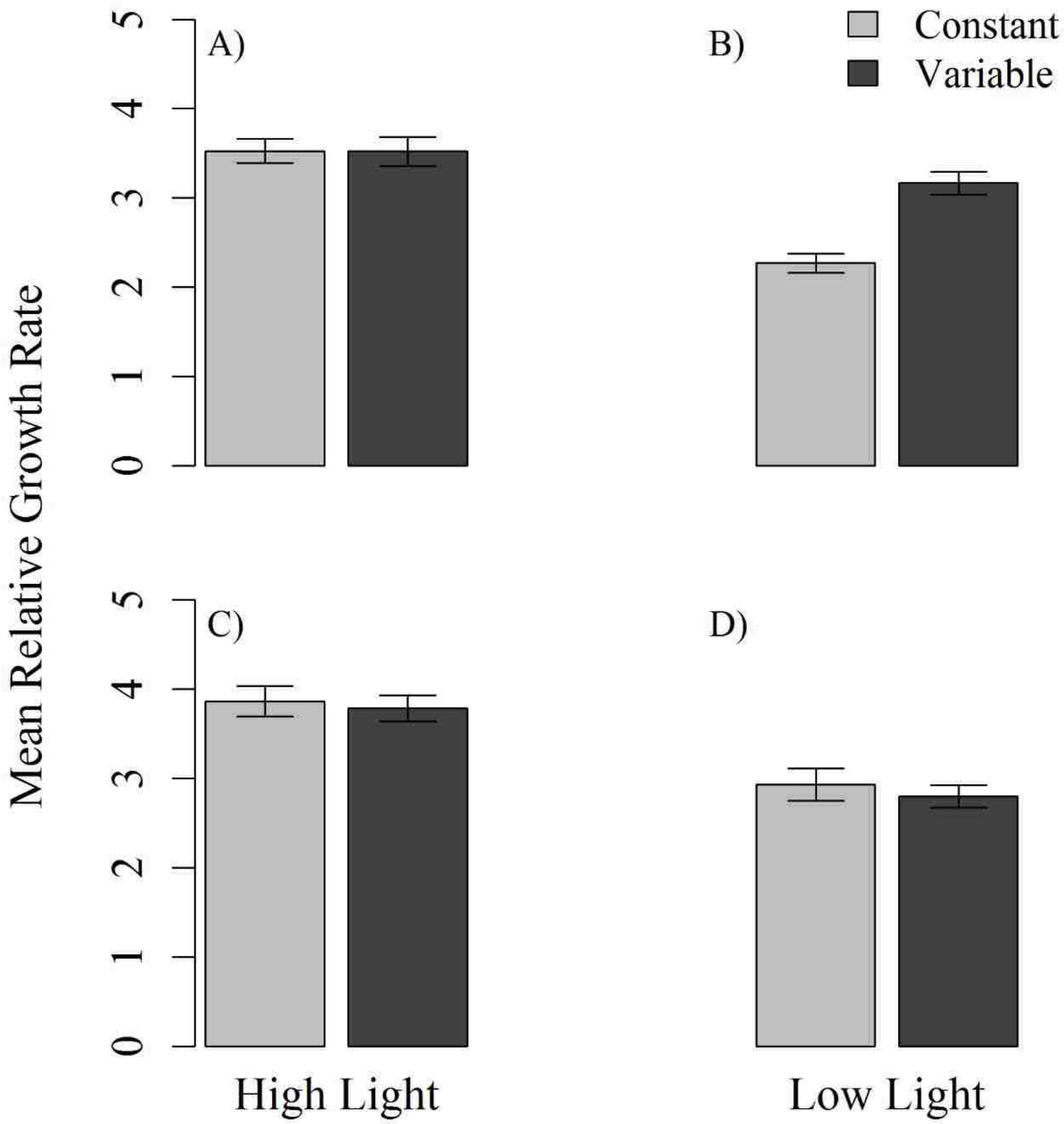

Figure 4.1 The effects of precipitation, initial light environment, and environmental variability on mean relative growth rate (leaf area yr^{-1}). A, B) are low precipitation; C, D) are high precipitation; A, C) high initial light; and B,D) are low initial light. There was a significant difference between the species (*Calathea* and *Heliconia*), but not a four-way interaction, therefore the species were combined. Bars represent mean growth ± 1 standard error.

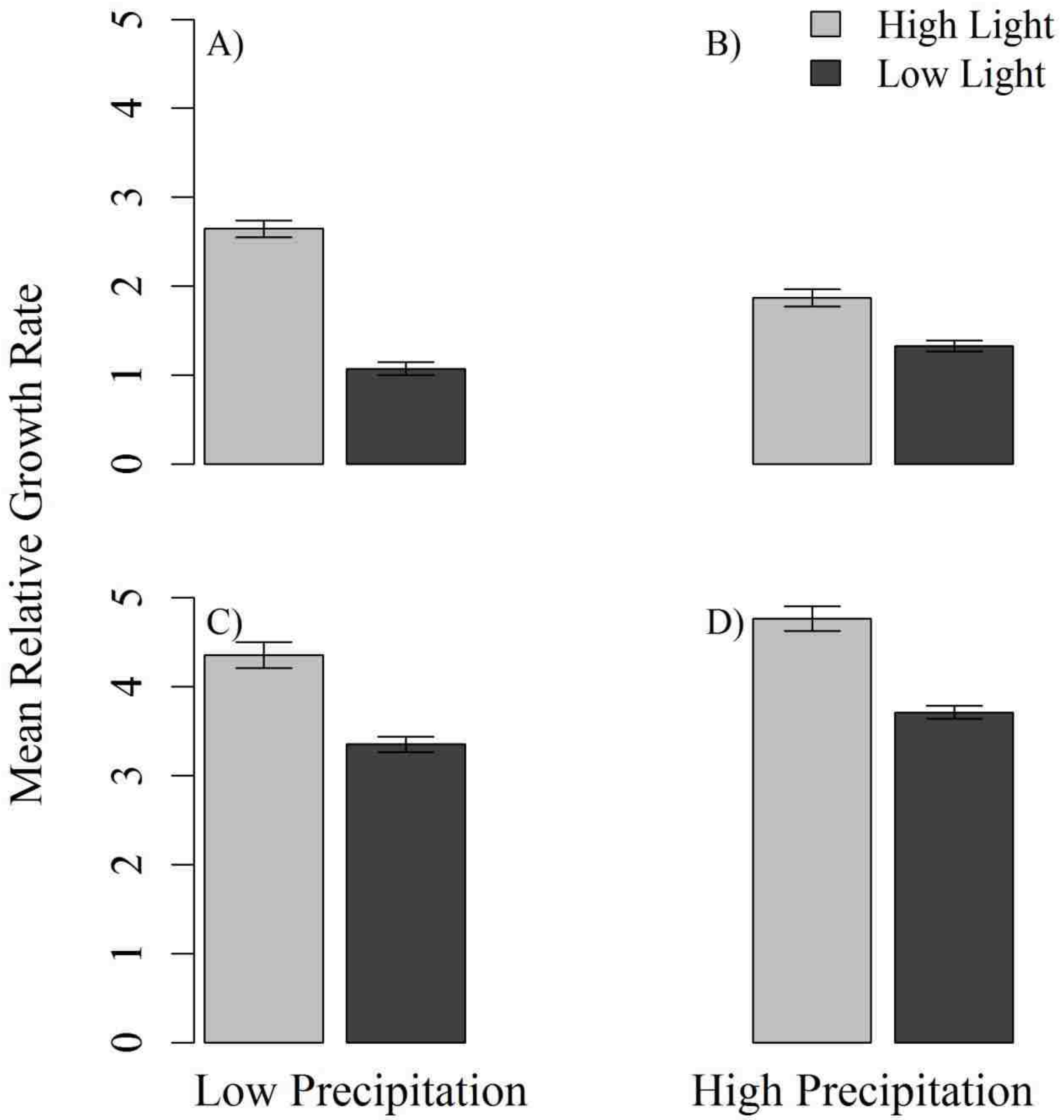

Figure 4.2 The effects of precipitation on the mean relative growth rate (leaf area yr^{-1}) for *Calathea* and *Heliconia*. A, B) are *Calathea*; C, D) are *Heliconia*; A, C) are low precipitation; B, D) are high precipitation. Bars represent mean growth rate ± 1 standard error.

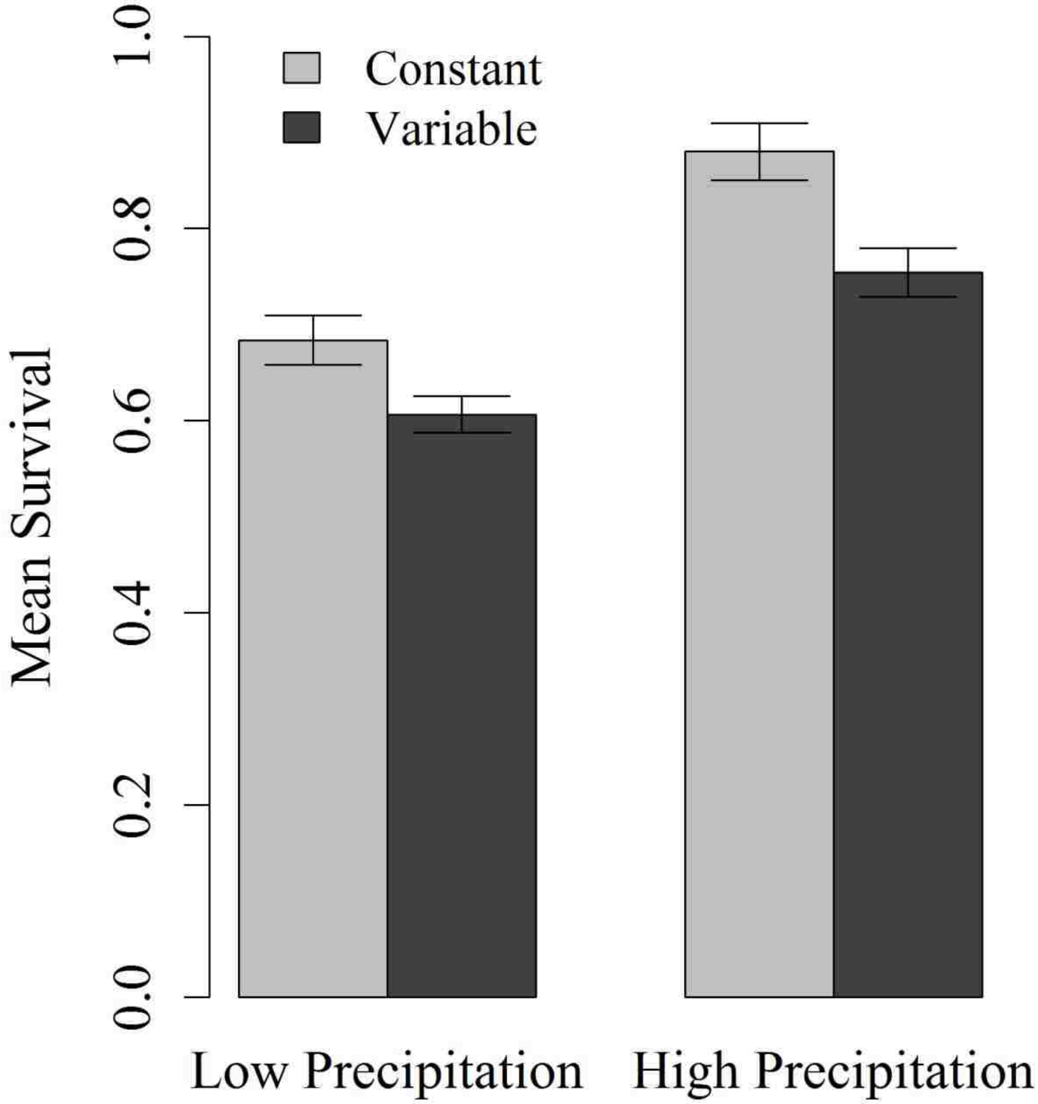

Figure 4.3 The effects of precipitation and environmental variability on the probability of survival (on a scale of 0 to 1). There was a significant difference between the species (*Calathea* and *Heliconia*), but not a three-way interaction, therefore the species were combined. Bars represent mean survival ± 1 standard error.

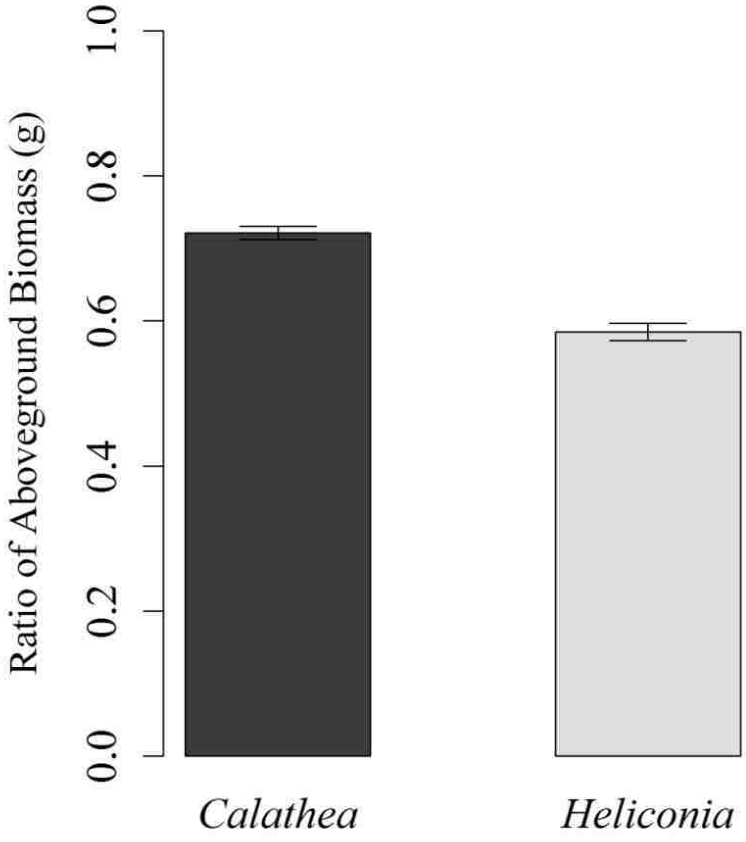

Figure 4.4 The ratio of aboveground to total biomass (grams) for *Calathea* and *Heliconia*. None of the treatments had any statistically significant effect on this ratio. Bars represent mean biomass ± 1 standard error.

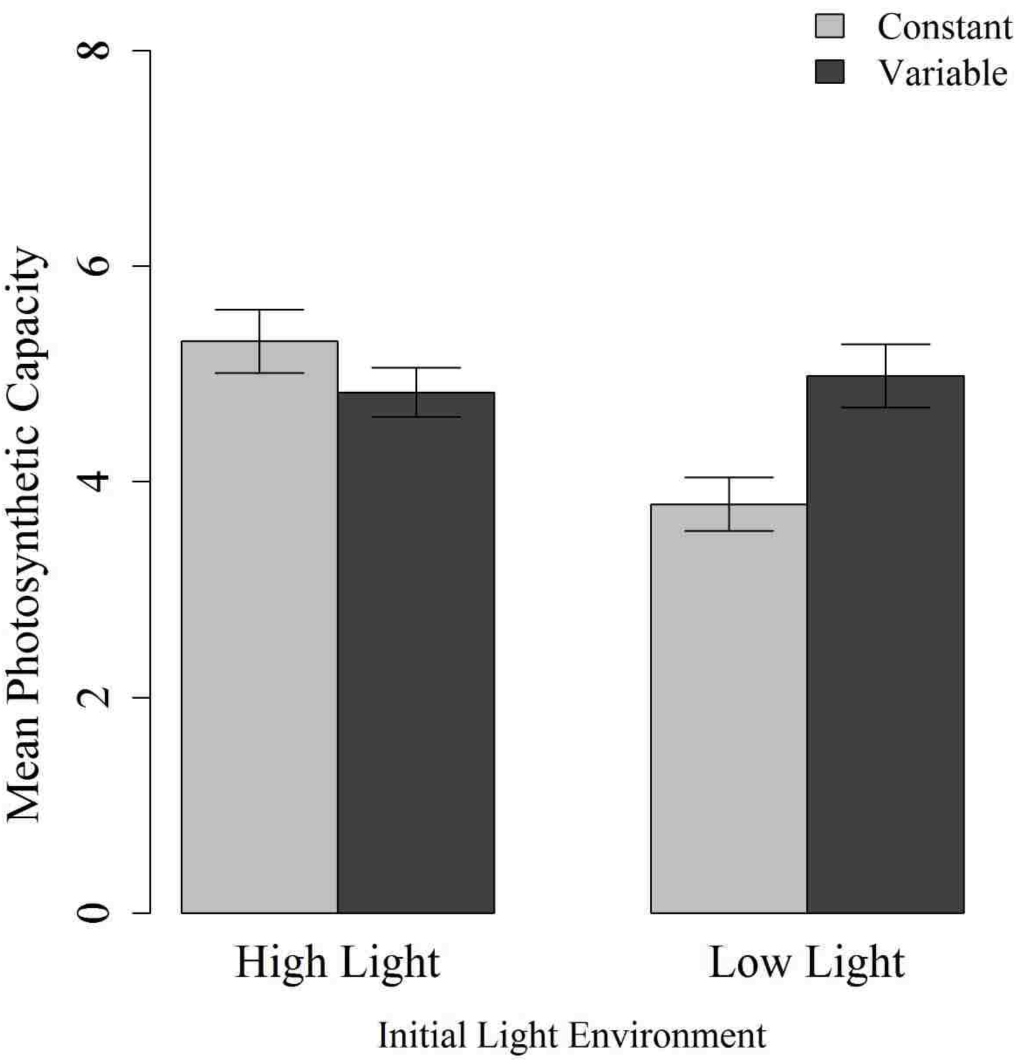

Figure 4.5 The effects of initial light environment and environmental variability on photosynthetic capacity (µmol m^{-2} s^{-1}). There were no significant differences between the species (*Calathea* and *Heliconia*), therefore they were combined. Bars represent mean photosynthetic capacity ± 1 standard error.

Chapter V: Photosynthetic rates influence the population dynamics of herbs in stochastic light environments

Overview

Random temporal variation in light from gaps in the tree canopy strongly influence the population dynamics of understory plants. From 2012-2015, we estimated the size-specific demographic rates of two herbs, *Calathea crotalifera* and *Heliconia tortuosa*, and monitored canopy openness during four annual censuses. We estimated maximum photosynthetic capacity (A_{max}) for a subset of individuals (N=39) during three censuses, and modelled future size as a linear function of current size, canopy openness, and A_{max}. We then estimated the population growth rates in deterministic (λ) and stochastic light environments (λ_S), using Integral Projection Models. As light availability increased, λ increased for *Calathea* but decreased for *Heliconia*, and increasing A_{max} had no effect on λ for *Calathea* but increased λ for *Heliconia* in low light. As A_{max} increased, λ_S increased for *Heliconia*, but not *Calathea*. We also calculated the proportional sensitivity of λ_S to changes in: the mean and variance of the vital rates, the variance of the vital rates, and to environment-specific (β) values of vital rates; E^S, $E^{S\sigma}$, and $E^S{}_\beta$, respectively. E^S, $E^{S\sigma}$, and $E^S{}_\beta$ differed due to changes in A_{max} for *Heliconia* but were unaffected by A_{max} for *Calathea*. For *Heliconia*, the sensitivity of λ_S to intermediate- and large-sized individuals was greatest when light was low, and λ_S became more sensitive to seeds and seedlings with increasing light. For *Calathea*, the sensitivity of λ_S to intermediate-sized individuals was greatest in high light, which means that events that affect these vital rates in high light have more impact on overall fitness than events that affect these vital rates in shady environments. In other words there is (potential for) stronger selection by events affecting large individuals that happen when plants are in high light than when they are in low light. The lack of sensitivity to A_{max} may indicate that *Calathea* is more shade tolerant than *Heliconia* and A_{max} dependent elasticities may reflect the potential carbon gain of individuals of various sizes. We conclude that photosynthetic physiology can have large consequences for the population dynamics of plants in both deterministic and random light environments.

Background

In the understory of tropical forests, the availability of resources is highly heterogeneous and temporally dynamic (Denslow 1987). Light is the key resource which limits rates of growth, survival, and reproduction in these environments (vital rates) (Denslow et al. 1990, Westerband and Horvitz 2015). Because vital rates are strongly influenced by the availability of light, random temporal variations in resource availability should have strong consequences for the fates of plant populations in tropical rainforests. Thus, to better understand how plant fitness is influenced by temporal changes in the environment, and how photosynthetic rates influence population dynamics, we estimate the population growth rates of two herbs over a range of photosynthetic rates in both single environments (λ) and stochastic light environments (λ_S), using Integral Projection Models (IPM). IPMs are discrete-time structured population models that allow demographic rates to be modelled as functions of discrete and continuous variables (e.g. age, height, weight)(Rees and Ellner 2009). We also evaluate the proportional sensitivity, or elasticity, of λ_S to perturbations of the mean and variance of the vital rates (E^S), and perturbations of only the variance in vital rates ($E^{S\sigma}$) over all light environments (Tuljapurkar et al. 2003). While E^S describes the elasticity of λ_S to a 1% change in the vital rates in every state of the environment, λ_S may respond differently to perturbations in vital rates, depending on the environment. This type of elasticity is known as the environment-specific elasticity E^S_β (Caswell 2005, Horvitz et al. 2010). The entry $e_{i,j,\beta}$ in each elasticity matrix is the percent change in λ_S produced by a 1% change in the *ij*th vital rate when the population is in environmental state β (Caswell 2005, Horvitz et al. 2010).

Previous IPMs and matrix models for forest species have successfully incorporated environmental stochasticity with regards to changes in light availability (Pascarella and Horvitz 1998, Metcalf et al. 2009). However, one area of study that is lacking in these IPMs (and population models in general) is the inclusion of physiological responses to the environment. To address this shortcoming, we model growth rates of plants as functions of photosynthetic rates, allowing us to evaluate the effects of increasing photosynthetic rates on the population dynamics of co-occurring plant species in random light environments.

Plants adapted to shaded environments have been shown to possess different suites of morphological and physiological traits than plants adapted to high light. For example, plants adapted to shade tend to possess small thin leaves, are small statured and grow slowly, have low respiration rates, a low capacity to use high light, are subject to photoinhibition (a reduction in the net photosynthetic rate under high light), and are highly efficient in how they use small quantities of light (Valladares and Niinemets 2008). Conversely, plants adapted to high light often have large thick leaves, grow quickly, have high respiration rates and a high capacity to use high light, but are inefficient in how they use light (Valladares and Niinemets 2008).

In most ecological studies, adaptation to shade is synonymous with shade tolerance, defined as the minimum amount of light necessary for survival (Valladares and Niinemets 2008). However, we argue that there is a need to distinguish between the ability to tolerate and survive under very low light (shade-tolerant), and the inability to withstand high light because of photoinhibition (shade-adapted), the latter of which we have coined as light intolerance (Westerband and Horvitz 2015). Species that are highly shade-adapted should experience higher fitness in shady environments than bright (sunny) environments, while species that are shade-intolerant should experience higher fitness in bright environments than shady environments. Species that fit these syndromes would be considered habitat specialists, in the sense that their ecological breadths of distribution are restricted. Conversely, species that are highly shade-tolerant may possess the ability to withstand long periods of shade and wait for gaps to open, resulting in a much wider distribution. For habitat generalists, increasing their capacity to use resources should have little effect on their fitness because they have the ability to maintain fitness in resource-poor environments and maximize their fitness under favorable conditions (Sultan 2001). For habitat specialists, small changes in their ability to capture and utilize resources should have a larger effect on their fitness compared to generalists.

The range of environments in which plants establish and persist is determined by how their vital rates respond to the environment, and is regulated by physiological and morphological adaptations to the environment. Changes in gas exchange rates, such as stomatal conductance, can influence net photosynthesis and carbon gain (Santiago et al. 2004). Previous studies have found that wood anatomy and hydraulic conductance of stems directly influences relative growth rates and survival rates (Poorter et al. 2010). In this study, we focus on the maximum photosynthetic capacity (A_{max}), defined as the highest amount of net photosynthesis (A, gas exchange per unit leaf area) at saturating light levels. Previous studies have shown that shade-tolerant species have less variability in their photosynthetic capacity than shade-intolerant species, when exposed to a range of light levels (Straussdebenedetti and Bazzaz 1991) although some studies have contradicted these findings (Kitajima 1994). In addition, shade-tolerant species have lower A_{max} and lower relative growth rates in both low and high light compared to shade-intolerant species (Kitajima 1994, Walters and Reich 1999).

Changes in A_{max} may influence fitness in various ways. Under favorable environments, increasing A_{max} may increase the production of carbohydrates, which may be used towards growth, to construct reproductive structures, or make secondary compounds to ward off herbivores (Kitajima et al. 2012). For the purposes of investigating the effect of changing A_{max} on fitness, we evaluate population models at different levels of A_{max} while maintaining photosynthetic efficiency and respiration constant. While such a scenario may be uncommon in nature, given that photosynthetic efficiency and the maximum photosynthetic capacity are inversely related, our model represents a simple method of incorporating physiological parameters into a population model. Our assumption is that individuals with high A_{max} should experience a higher net carbon gain in a given light environment than individuals with low A_{max}. Pearcy et al. (1987) found that individuals with high A_{max} have a higher net carbon gain than individuals with low A_{max} values when respiration remains constant. We focus on the effects of A_{max} on growth, and hold A_{max} constant to model survival and reproduction.

Our study species are two locally coexisting perennial herbs, *Calathea crotalifera* and *Heliconia tortuosa*. These species inhabit a wide range of environments at our study site and a previous study described both as being moderately to highly shade tolerant (Westerband and Horvitz 2015). We tested the hypothesis that A_{max} would be lower for *Calathea* than for *Heliconia* and *Calathea.* We also tested the hypothesis that *Calathea* would have a narrower range of A_{max} values over the observed light environments. This hypothesis arises from the results of a previous study, which described the effects of light availability on the vital rates of both species (Westerband and Horvitz 2015). Additionally, we tested five hypotheses with regard to the effects of A_{max} on the deterministic population growth rate, λ, and the stochastic population growth rate, λ_S, for our study species (Table 1).

1) The population growth rate in a constant high light environment should be lower than the population growth rate in a constant shady environment, if these species are both adapted to shade.

2) The population growth rate of *Calathea* should decrease with increasing light levels more so than the population growth rate of *Heliconia*, due to photoinhibition.

3) When light is scarce, increasing A_{max} should have a greater impact on fitness in high light environments than low light environments. This results from the shape of the light response curve, which describes the amount of net photosynthesis with increasing light availability (Figure 5.1). When light is scarce, increasing A_{max} while maintaining all other light response parameters constant has little effect on net photosynthesis, but when light is abundant, increasing A_{max} results in greater net photosynthesis.

4) If our study species are shade-adapted (narrow breadth of distribution), their fitness in temporally variable environments will be highly sensitive to A_{max}. Conversely, if our study species are shade-tolerant (wide breadth of distribution), increasing their capacity to use light (A_{max}) should have little influence on fitness in temporally variable environments.

We predict that the sensitivity of λ_S to changes in A_{max} will increase with increasing light availability ($E^S{}_\beta$). We use the term sensitivity in a colloquial sense, except when discussing the sensitivities of λ_S and λ. Although we did not measure the distributions of our species at our study site, we consider shade-tolerant species to be habitat generalists and shade-intolerant species to be specialists, because shade-tolerant species persist in a wider range of light environments than shade-intolerant species.

Methods

STUDY SYSTEM— Two species considered moderately shade tolerant were chosen for this study; no quantitative assessment of their abilities to tolerate low light were previously made (Berry and Kress 1991). These study species were chosen because they are among the most common understory plants at our study site, they occupy a large range of light environments (including under large gaps and completely closed canopies), and they reach large enough sizes (up to 3 m tall) to compete with tree saplings and other herbaceous species for light, making them likely contributors to the process of forest succession in our plots.

Heliconia tortuosa is a perennial, herbaceous understory monocot that exhibits rhizomatous growth, and ramets grow 1-2 m tall. Individuals reproduce sexually via seeds, and asexually via clonal shoots that are connected by subterranean stems called rhizomes, and can spread laterally to form clumps. Inflorescences are characterized by bright red floral bracts (Linhart 1973) and bright yellow flowers are produced in these bracts resulting in blue fruits that are held in the bract until the ramet falls to the ground, dispersing the fruit. Each fruit produces two to three seeds. *Calathea crotalifera* is a perennial, herbaceous understory monocot that is rhizomatous, and ramets grow 1-3 m tall. Inflorescences possess yellow, erect floral bracts (reminiscent of a rattlesnake's rattle) that grow up to 25 cm long. *Calathea* reproduces sexually and asexually and several clonal shoots arise from a sympodially branched rhizome near the ground (Grime 1977), resulting in greater spatial spread among leaves on a ramet, compared to *Heliconia*. *Calathea* flowers are yellow-white and produce two to three seed capsules containing one dark blue seed surrounded by white flesh, and do not persist on the inflorescence. *Heliconia* is hummingbird-pollinated whereas *Calathea* is pollinated by bees.

This study was conducted at the Las Cruces Biological Station, located 1200 m above sea level (8° 47' 7" N, 82° 57' 32" W) in Coto Brus county, southern Costa Rica. This region is designated as mid-elevation premontane forest and receives approximately 4 m of annual rainfall. There is a dry season from January to March and mean diurnal temperature over the year is between 13 and 26°C. Our study sites were located in primary, secondary, and selectively logged forest, within the station, although we do not focus on these distinctions of logging history in the current analyses. A more detailed description of the collection of demographic data is described in Westerband and Horvitz (2015). We tagged and monitored 1278 individual plants (482 *Calathea crotalifera* and

796 *Heliconia tortuosa*) starting in 2012, following the fates of the survivors over four annual censuses in June 2012-2015. For each individual for each annual census, areas of individual leaves were summed to give total leaf area per plant, used here as a metric of size. The probability of reproducing was determined by the presence or absence of inflorescences, and reproductive output was calculated as the number of inflorescences per individual. Seedling recruitment was also recorded in our study plots at each census and the sizes of individuals were recorded to obtain the mean and variance of seedling size. Survival was determined by the presence or absence of individuals at the next annual census.

We also measured canopy openness over each surviving plant at each census on a scale of 1 to 25, using a rapid assessment technique known as the canopy scope (Brown et al. 2000). The highest observed canopy openness was approximately 30% (canopy score of 25) and the lowest was 1% (canopy score of 1)(Brown et al. 2000). At our study site, canopy scores were strongly and positively correlated with the amount of photosynthetically active radiation in μmol m^{-2} s^{-1} (*rho*=0.72, p<0.001) measured with a quantum sensor on a LI-6400 (Li-Cor, Lincoln, NE, USA). Using the distribution of canopy scores at our study sites, we categorized five light environments: low, medium, medium high, high, and very high, which correspond to canopy scores of 1, 4, 7, 11, and 20, respectively. We chose to evaluate the regression equations used to construct models of population dynamics of our species with these canopy scores rather than the entire range of light scores to simplify our analyses. Although canopy scores ranged from 1 to 25, the positively skewed distribution of canopy openness scores in our sample in our sample suggest that distinguishing more levels at the low end of the scale would capture more about the variation experienced by our populations (which are generally found most often in the shade) than distributing the levels of interest across the full range at equal intervals (Appendix 16). Differences between species were evaluated using a Wilcoxon-Mann Whitney U test and a Kolmogorov-Smirnov test.

SEED AND SEEDLING DATA— The probability of seeds germinating in high light (canopy score ≥10) or low light (canopy score of 1) was estimated by placing 30 wire mesh boxes containing ten seeds in high light and 30 boxes in low light, at our study site. Half the boxes contained *Calathea* seeds and half contained *Heliconia* seeds (a total of 600 seeds planted). The boxes were filled with forest soil and remained in each light environment for three months, August-October 2015. The boxes were checked weekly for signs of germination. After three months, we retrieved the boxes and collected seeds that had not germinated during the study period. These seeds were moistened overnight and cut longitudinally through the embryonic axis before being completely immersed in a 1% solution of tetrazolium chloride for 8-16 hours. We examined the embryo for red coloration. Embryos that had discoloration or necrosis in more than 50% of the embryonic structure were considered not viable (Parker 1953). 64 seeds were destroyed due to waterlogging (46 *Calathea*, 18 *Heliconia*), and were removed from the analysis.

The three month observation period was not sufficient to capture true germination probabilities over a full year, but the results of this experiment could be used to estimate the relative probability of seeds staying alive (as seeds or seedlings) in low and high light. Seeds that did not germinate but were alive based on the tetrazolium assay were classified as dormant. We used two relevant studies for estimates of germination probabilities in low and high light (more details below). To determine the number of fruit per inflorescence, we counted the number of fruit present on an inflorescence for individuals in the forest plots during the summer of 2014 (78 *Calathea*, 36 *Heliconia*), and averaged our estimates per individual, then averaged the estimates of all individuals to obtain values of 23 and 37 for *Calathea* and *Heliconia*, respectively. Because we only observed reproductive individuals over the course of a few weeks and the reproductive season is longer than our observation period, these values underestimate the number of fruit produced per inflorescence over one year. To obtain the number of seeds per fruit, we dissected fruit of *Heliconia* and observed *Calathea* fruit in the forest plots. We observed *Heliconia* producing 2-3 seeds per fruit, therefore we set the number of seeds per fruit to 2.5 in our model. For *Calathea*, we were not able to count the seeds per fruit because they do not persist on the inflorescence, but Gargiullo et al. (2008) describe *Calathea* as containing three seeds per fruit, which we use in our model.

To calculate the number of *Heliconia tortuosa* seedlings in low light that are expected to be alive after 1 year, we divided the mean proportion of *Heliconia acuminata* seeds placed on the ground in a continuous forest that germinated after one year (Bruna 1999), by the proportion of living seeds after one year. The proportion of living seeds after one year was calculated as the number of seeds living after one year divided by the total number of seeds planted in the seed germination experiment described above, resulting in 26% of seedlings being alive after one year. To calculate the number of *Heliconia tortuosa* seedlings in high light that were alive after one year, we divided the upper limit of the standard error of the mean proportion of germinated *Heliconia acuminata* seeds placed on the ground in a continuous forest (Bruna 1999), by the proportion of living seeds in high light, which we calculated from our seed germination experiment, resulting in 33% (0.33) of seedlings being alive after one year. For *Calathea crotalifera*, we used seed germination probabilities in low and high light for *Calathea lutea*, from Horvitz et al. (2002). We divided these probabilities by the proportion of living seeds in low and high light that we estimated from our seed germination experiment, resulting in 14% and 95% of seedlings being alive after one year in low and high light, respectively. Seeds will either be alive as seeds or as seedlings.

PHYSIOLOGICAL ESTIMATES— We estimated maximum photosynthetic capacity (A_{max}) for 39 individuals in June and July 2013 (n=18 for *Heliconia*, n=21 for *Calathea*), 40 individuals in 2014 (n=20 for *Heliconia*, n=20 for *Calathea*), and 31 individuals in 2015 (n=12 for *Heliconia*, n=19 for *Calathea*). Individuals were chosen haphazardly among study plots, to represent a range of plant sizes. Four individuals were added to the study in 2014 to replace those that died, but none were added in 2015. A_{max} was measured in the forest plots by estimating rates of gas exchange ($\mu mol^{-2}s^{-1}$), using a portable gas exchange system (LI-6400; Li-Cor, Lincoln, NE, USA) and constructing a photosynthesis light response curve, that shows how the rate of net photosynthesis (A) responds to light. To construct the curves, leaves were exposed to a gradient of eight light levels from 0 to 1000 μmol PAR m^{-2} s^{-1} (starting at high light and decreasing to zero) and we measured the rate of exchange of CO_2 and H_2O from the leaf at each light level. The asymptote of the curve measures A_{max}. On one leaf per individual, we measured a photosynthetic light response curve between 0900 and 1100 hours to minimize any confounding effects of sampling during the hottest hours of the day. Across all photosynthesis measurements, CO_2 concentration was 400 μmol m^{-2} s^{-1}, leaf temperature was 25°C±2, and average relative humidity was 58%±8. Only mature leaves were used, and were selected to have little or no damage (evidence of senescence or herbivory) and maximum exposure to sunlight.

We fit the estimates of gas exchange per unit time to the rectangular hyperbola model (Equation 1) (Thornley 1976) using nonlinear least squares regression. The rectangular hyperbola model of photosynthesis has three parameters:

$$Net\ Photosynthesis = \frac{alpha \times A_{max} \times I}{alpha \times I + A_{max}} - R_d \qquad (1)$$

assimilation rate at saturating light (A_{max}, μmol CO_2 m^{-2} s^{-1}), the assimilation rate when no light was present (dark respiration, R_d, μmol CO_2 m^{-2} s^{-1}), and the quantum efficiency of the photosystems (α, alpha). *I* represents the light intensity (μmol PAR m^{-2} s^{-1}).

We eliminated three outlier A_{max} values for *Calathea*, which ranged from 10 to 12 μmol CO_2 m^{-2} s^{-}1. The elimination of these outliers resulted in a normal distribution of values. No outliers were eliminated for *Heliconia*, and this variable was normally distributed. A student's t-test was used to determine whether there were any significant differences in A_{max} between the species. We also tested for significant correlations between canopy openness at time *t* and A_{max} for both species, using Spearman Rank Correlation analyses. We determined the 25th, 50th, and 75th percentile of the A_{max} values for each species, and designated these levels as low, medium, and high A_{max} values. We evaluated the population growth rates at each of these A_{max} values for both species (see *Integral Projection Model*), which correspond to 5, 6, and 7 μmol CO_2 m^{-2} s^{-1} for *Calathea*, and 5, 7, and 8 μmol CO_2 m^{-2} s^{-1} for *Heliconia* (Appendix 16).

VITAL RATES— Growth was statistically modelled as total leaf area at time *t*+1 versus total leaf area at time *t*, and was modelled using data from the individuals that had A_{max} estimates (N=39, N=40, and N=31 in 2013, 2014, and 2015, see *Physiological estimates*). To estimate growth, we used a regression model with three continuous explanatory variables, plant size (total leaf area), canopy openness, and A_{max} (Equation 2). The species were modelled separately. There were 42 nested models derived from the full model. We estimated the importance of each variable, and all interactions among variables using model averaging (Appendix 20) (Burnham and Anderson 2002). We calculated the values of all model coefficients in the average model and evaluated the model at a canopy score of 1 and 10, to understand how light and A_{max} interact to influence growth (Appendix 18, Appendix 19). The model coefficients from the average model were then used to evaluate an Integral Projection Model at each of five canopy openness levels and three different A_{max} levels; each IPM describes the effects of size at *t* on size at *t*+1 for each combination of canopy openness with A_{max}.

$$Size_{t+1} = x_0 + x_1 Size_t + x_2 Canopy\ Openness_t + x_3 A_{maxt} + x_4 Size_t\ Canopy\ Openness_t + x_5 Size_t\ A_{maxt} + x_6 Canopy\ Openness_t\ A_{maxt} + x_7 Size_t CanopyOpenness_t A_{maxt} \qquad (2)$$

We evaluated the effect of three continuous variables, size, canopy openness, and A_{max}, and all their interactions, on survival and the probability of reproduction using logistic regression models, for the 482 *Calathea* and 796 *Heliconia* that we tracked from 2012 to 2015. Therefore, in the survival and reproduction models, A_{max} was not known for all individuals and was held constant in the models. The species were modelled separately. The survival model with all the main effects and the interactions was

$$Logit(probability\ of\ survival) = x_0 + x_1 Size_t + x_2 Canopy\ Openness_t + x_3 A_{maxt} + x_5 Size_t\ Canopy\ Openness_t + x_6 Size_t A_{maxt} + x_7 Canopy\ Openness_t A_{maxt} + x_8 Size_t CanopyOpenness_t A_{maxt} \quad (3)$$

Inflorescence production was estimated using Poisson models, where the model with all the main effects and the interactions was

$$Log(Number\ of\ inflorescences) = x_0 + x_1 Size_t + x_2 Canopy\ Openness_t + x_3 A_{maxt} + x_5 Size_t\ Canopy\ Openness_t + x_6 Size_t A_{maxt} + x_7 Canopy\ Openness_t A_{maxt} + x_8 Size_t CanopyOpenness_t A_{maxt} \quad (4)$$

When the vital rates were evaluated over different A_{max} levels, the parameters in each model were held constant.

INTEGRAL PROJECTION MODEL— The parameter values used in our IPM can be found in Table 2. We used the vital rates to construct an IPM for each species and estimated the deterministic population growth rate in each of five light environments: low light, medium light, medium high light, high light, and very high light. The canopy openness scores corresponding to these environments are 1-3 for low light, 4-6 medium light, 7-10 medium high light, 11-19 high light, and >20 very high light. The maximum observed canopy score was 25. We repeated this procedure for each of three levels of A_{max} for each species, as described earlier: low, medium, and high, resulting in 15 λ for each species. Each λ is calculated as the dominant eigenvalue of a matrix used to approximate the dynamics of a particular size-structured IPM, the parameter values of which are determined by the regression equations evaluated at particular levels of canopy openness and A_{max}. This protocol assumes that the combinations of canopy openness and A_{max} that were tested can and do occur and are independent of each other (although this was not true for *Calathea,* see *Results*).

We also estimated λ_S, which describes the population growth rate in stochastic environments (Tuljapurkar et al. 2003). The stochastic population growth rate was estimated with a 100,000 time steps simulation sequence (not counting 2,000 time steps to eliminate the transients). Using this method, each state of the environment is represented by a distinct integral projection model and probability rules determine which model is chosen at each time step. The probability rules arise from a Markov chain model of the light dynamics, which was constructed using the observed transitions of individuals among categories of canopy openness. We analyzed the stochastic dynamics of environment-dependent integral projection models by incorporating the environment-specific IPMs into a model that includes light.

Size at $t+1$ was determined by size at t, light, and A_{max}, using the coefficients of the average model. In the general form of an IPM, the projection kernel is $K(y, x) = p(y, x) + f(y, x)$, where p represents survival and growth from size x to size y and f represents the production of size y offspring by size x reproductive individuals. In our model, p is replaced by $p(y, x, j, A_{max})$, which represents transitions of an individual of size x to size y as a function of survival, s, and growth, g, in light environment j for a given A_{max}: $p(y, x, j, A_{max}) = s(x, j, A_{max}) \times g(y, x, j, A_{max})$. $s(x, j, A_{max})$ represents the probability of survival of an individual of size x in light environment j. $g(y, x, j, A_{max})$ represents growth of individuals of size x to size y in environment j. The $f(y, x, j, A_{max})$ kernel describes the per-capita production of individuals of size y in the next census by reproductive individuals of size x and light environment j. f(y, x, j, A_{max}) is calculated by multiplying: the probability of reproducing, reproductive output, the number of fruit per inflorescence, the number of seeds per fruit, probability of a seed living to the next census, and the probability of seedling survival. All parameters depend on the environment, with the exception of fruit per inflorescence and seeds per fruit. We note that A_{max} is held constant for s and f, and varies for g because we were unable to estimate the effect of A_{max} on survival and reproduction in our sample of individuals due to the very low rates of death and reproduction.

Individuals produced by f(y, x, j, A_{max}) were distributed among future size classes using the mean and variance of seedling recruits, based on our annual census data. Individuals were distributed among future size classes using the standard deviation of the growth model with the lowest AIC, from the set of 42 nested models used in the model averaging. These models are shown in Appendix 22.

The state of a size-structured population at time *t* is described by n(x, t). Therefore, to project the population forward we would use

$$n(y, t+1)=\int_{L}^{U} K(y, x,j)n(x,t)$$

Where L and U are the lower and upper bounds of the range of plant sizes and j represents the environmental state. We do not model the projected population size in this study and instead focus on the population growth rate and its sensitivity to perturbations in the matrix elements.

We calculated the proportional sensitivity, hereafter elasticity, of λ_S to changes in the mean and variance of vital rates (E^S), for low and high A_{max} values. E^S is achieved by perturbing the vital rate in every habitat state by an equal amount, which has no net effect on variance. We also analyzed the effects of perturbations in only the variance of vital rates ($E^{S\sigma}$). Finally, we calculated the environment-specific elasticity of λ_S, $E^S{}_\beta$, which describes the percent change in λ_S produced by a 1% perturbation in the *ij*th life-history transition rate when the population is in environmental state β. All statistical analyses were conducted using the program R v. 3.0.2 (R Core Team, Vienna, Austria, http://www.R-project.org/).

Results

The long-term equilibrium frequency of environments (derived from the environmental transition matrix, **c**) is 0.83, 0.13, 0.03, 0.006, and 0.001, meaning that 83% of the observed light environments will fall into the low light category and less than 1% will correspond to very high light.

Photosynthetic capacity (A_{max}) did not differ significantly between the species ($p=0.15$). The mean A_{max} for *Calathea* was 6.1±0.22 μmol CO_2 m^{-2} s^{-1} and the mean for *Heliconia* was 6.6±0.31 μmol CO_2 m^{-2} s^{-1} (not shown). Although the A_{max} values had similar distributions (Appendix 17), the median and 75th percentile of A_{max} were greater for *Heliconia* than *Calathea* (not shown). *Heliconia* also had a larger range of A_{max} (3.1 to 11.7 μmol CO_2 m^{-2} s^{-1}) than *Calathea* (2.3 to 10.2 μmol CO_2 m^{-2} s^{-1}).

The canopy openness scores for plants that were used to estimate photosynthetic rates ranged from 1 to 10 for both species, and the canopy scores were significantly different between species (Appendix 15, Wilcoxon $p=0.01$), where *Heliconia* occurred in slightly brighter environments than *Calathea* (mean 3.04 versus 2.55). A Kolmogorov-Smirnov test indicated no significant differences in the distributions of canopy openness scores for the two species (p=0.08). The canopy openness scores were positively skewed for both species (Appendix 15). Canopy openness scores at time *t* were significantly correlated with A_{max} for *Calathea* (*rho*=0.38, p=0.004) but not *Heliconia* (*rho*=0.05, p=0.73). The canopy openness scores for all plants that were tagged in the plots (used to estimate the parameters of the survival and reproduction models) ranged from 1 to 25 for *Calathea* and 1 to 21 for *Heliconia* and were significantly different between species (Appendix 16, Wilcoxon p=0.008), where *Calathea* occurred in slightly brighter environments than *Heliconia* (mean 2.96 versus 2.48). The canopy openness scores were positively skewed for both species (Appendix 16).

Model averaging revealed that size was the most important single parameter influencing future size for *Calathea*, while light was the most important parameter that influenced future size for *Heliconia* (Appendix 20). The current size by light interaction was the most important interaction that influenced future size for *Heliconia*, and its importance was high (0.84) (Appendix 20). For *Calathea*, all two-way interactions were equally important and the importance values were low (0.21-0.24) (Appendix 20). The importance of the three-way interaction (between current size, light, and photosynthetic capacity) was low for both species (0.02 for *Calathea* and 0.16 for *Heliconia*, not shown). Current size has a positive effect on future size for both species (Appendix 21). The influence of current size on future size was greater in *Calathea* than *Heliconia*. The parameter values for light and A_{max} were very low for *Calathea*. For *Heliconia*, light had a strong negative effect on future size while A_{max} had a moderately strong, positive effect on future size. Increasing A_{max} had no effect on growth for *Calathea* in low or high light (Appendix 18). Increasing A_{max} increased growth for Heliconia in both low and high light, and the effect was more pronounced for small individuals. The effect of A_{max} differed only slightly with increasing light, but there was more evidence of shrinkage with increasing light (Appendix 19). The parameter values associated with the two-way interactions were very low for *Calathea* (all values $<|0.01|$) (Appendix 21). The value of the size by light interaction was the largest two-way interaction for *Heliconia* (0.18), while the remaining two interactions were very low ($<|0.05|$) (Appendix 21). The parameter values associated with the three-way interaction were very low for both species ($<|0.005|$, not shown).

The deterministic population growth rates (λ) ranged from 1.28 to 1.7 for *Calathea* and from 0.25 to 1.48 for *Heliconia*. λ for *Calathea* increased slightly with increasing light (Figure 5.2A), while λ for *Heliconia* decreased with increasing light (Figure 5.2B). Increasing A_{max} increased λ for *Heliconia* but only in low and medium light; increasing A_{max} had no effect on λ when light availability was high. In contrast, λ for *Calathea* were unaffected by changes in A_{max} across all light environments.

The stochastic population growth rates (λ_S) ranged from 1.293 to 1.297 for *Calathea* and from 1.11 to 1.41 for *Heliconia*. λ_S differed between species due to the effects of increasing A_{max} (Figure 5.3). The λ_S for *Calathea* were unaffected by increasing A_{max} (Figure 5.3A), whereas increasing A_{max} increased λ_S for *Heliconia* (Figure 5.3B). The elasticity of λ_S to perturbations in the vital rates over all environments (E^S) was influenced by A_{max} for *Heliconia* (Figure 5.4) but was unaffected by changes in A_{max} for *Calathea* (Figure 5.5). For *Heliconia*, increasing A_{max} resulted in a greater E^S to growth and stasis (i.e., survival without change in size) of small- to intermediate-sized individuals (stasis is on the diagonal of Figure 5.4A and5.4B). There was also slightly greater sensitivity to reproduction of large individuals when A_{max} was high than when it was low (upper right corner of Figure 5.4A and 5.4B). For *Calathea* with both low (Figure 5.5A) and high A_{max} (Figure 5.5B), λ_S was most sensitive to stasis and reproduction. Compared to *Heliconia*, λ_S for *Calathea* was much less sensitive to stasis and there was less sensitivity overall. The elasticity of λ_S to increased variability in the vital rates ($E^{S\sigma}$) was also affected by changes in A_{max} for *Heliconia* (Figure 5.6), but was unaffected by A_{max} for *Calathea* (Figure 5.7). For *Heliconia* with low A_{max} (Figure 5.6A), λ_S was most sensitive to increased variability in stasis and growth of small- and intermediate-sized individuals, while λ_S was most sensitive to increased variability in stasis and growth of small individuals and to reproduction, when *Heliconia* had high A_{max}. For *Calathea* with low and high A_{max}, λ_S was most sensitive to increased variability in vital rates associated with reproduction. Compared to *Heliconia*, λ_S for *Calathea* was much less sensitive to increased variability in the vital rates. Overall, both species had negative elasticities when variability increased, which would reduce λ_S but *Calathea* was far less sensitive to the increased variability than *Heliconia*.

The elasticity of λ_S with respect to vital rate perturbations in different light environments (environment-specific elasticity, $E^S{}_\beta$) also differed significantly due to changes in A_{max} for *Heliconia* (Figure 5.8), and was unaffected by changes in A_{max} for *Calathea* (Figure 5.9). For *Heliconia* with low A_{max} in low light (Figure 5.8A), λ_S was most sensitive to perturbations in intermediate sized individuals (Figure 5.10A) and more broadly, to elements below the diagonal (Figure 5.11A). As light increased (Figure 5.8B), sensitivity shifted primarily to reproduction and secondarily to small and large individuals (Figure 5.10A, 5.11A). For *Heliconia* with high A_{max} in low light (Figure

5.8C), λ_S was most sensitive to perturbations in large individuals (Figure 5.10A) and growth (elements below the diagonal)(Figure 5.11A). As light increased (Figure 5.8D), λ_S became more sensitive to perturbations in small individuals and less sensitive to seeds and seedlings.

For *Calathea* with low A_{max} in low light (Figure 5.9A), λ_S was most sensitive to seeds and seedlings (Figure 5.10A) and more broadly, to growth (Figure 5.11B). As light increased (Figure 5.9B), sensitivity shifted to intermediate-sized individuals (Figure 5.10B) and to growth (Figure 5.11B). Changing A_{max} had little effect on the environment-specific elasticities of λ_S (Figure 5.10B and 5.11B); the effect of increasing light was the same for *Calathea* with low A_{max} as it was for *Calathea* with high A_{max}.

In summary, *Calathea* λ_S was most sensitive to perturbations in intermediate-sized individuals under high light, and changing A_{max} had little effect on this relationship. When light availability was low, elasticities were more widely distributed among the size classes, but λ_S was much more sensitive to seeds and seedlings. In contrast, *Heliconia* λ_S was sensitive to intermediate- and large-sized individuals when light availability was low, and became much more sensitive to seeds and seedlings as light availability increased. Changing A_{max} had much more of an effect on elasticity of *Heliconia* when light was abundant than when light was scarce.

Discussion

The maximum photosynthetic capacities (A_{max}) of our study species did not differ significantly over the range of light environments in which we sampled, and their rates were similar to those of shade tolerant and moderately shade tolerant *Heliconia* (Rundel et al. 1998). These results support our hypothesis that these two co-occurring and functionally similar species possess similar photosynthetic rates. These results also refute our hypothesis that *Calathea* would have significantly lower A_{max} than *Heliconia*. As shade tolerance increases, the range of photosynthetic capacities in both low and high light should decrease (Straussdebenedetti and Bazzaz 1991). Despite having similar distributions, the median and 75th percentile of A_{max} were greater for *Heliconia* than *Calathea*, as was the range of A_{max}. Thus, *Calathea* has a narrower range of responses than *Heliconia*, which supports our hypothesis that *Calathea* is more shade tolerant, despite the lack of a significant difference in the mean A_{max} between species.

Model averaging revealed that current size was the most important predictor of future plant size for *Calathea*, while light availability (canopy openness) was the most important predictor for *Heliconia*. Current size positively influenced future size for both species, which agrees with previous studies (Westerband and Horvitz 2015). Increasing light negatively influenced growth for *Heliconia*, which suggests that *Heliconia* is light intolerant, or shade-adapted, while increasing light had a weak, positive effect on *Calathea*, suggesting that *Calathea* is less shade-adapted than *Heliconia* and may be able to grow within a larger range of light environments than *Heliconia*. A companion study determined that *Calathea* was more shade tolerant than *Heliconia*, and found evidence of shrinkage for large individuals in high light (Westerband and Horvitz 2015). Thus, the contradictory result that light negatively influences *Heliconia* growth may result from the interaction between plant size and light, which we do not describe in this study, despite its high importance in the average growth model. For *Calathea*, A_{max} had little effect on future size, whereas increasing A_{max} had a positive effect on growth for *Heliconia*. These results suggest that *Calathea* is a shade tolerant to moderately shade tolerant generalist because increasing its photosynthetic rates has little effect on its growth according to our model, whereas *Heliconia* growth is more sensitive to changes in A_{max}, suggesting that *Heliconia* requires a high photosynthetic capacity to persist in the environments we studied, and is more likely to be a habitat specialist.

Similar to the importance values of the factors (size, light, and A_{max}), the interactions between the factors differed with regards to their effect on future size. For *Heliconia*, the size by light interaction was the most important predictor of future size, and it was highly important, whereas the two-way interactions were all equally important for *Calathea*, and they had low importance values. The results for *Heliconia* agree with a previous study by Westerband and Horvitz (2015) while the lack of strong interactions between size, light, and A_{max} for *Calathea*, demonstrate that plant size is the most important predictor of future size for this widespread herb. The three-way interaction was not important for either species, indicating that the influence of light availability on future size is equally influenced by current size for all levels of A_{max}. In summary, the results of the model averaging demonstrate that growth is regulated by different factors for these co-occurring species and that photosynthetic responses to the light environment directly influence future growth. Comparative studies on the physiology and demography of co-occurring forest species have demonstrated large differences in the ability to capture and utilize light (Mulkey et al. 1991, Mulkey et al. 1993), which may promote co-existence among species.

The effects of increasing light and A_{max} on the deterministic population growth rates (λ) differed between species. Increasing light positively influenced λ for *Calathea*, refuting our hypothesis that *Calathea* is highly shade-adapted and should therefore be negatively influenced by light, while λ decreased (from population growth to shrinkage) with increasing light for *Heliconia*, as we hypothesized would occur for a shade tolerant species. We also found that increasing A_{max} increased *λ* for *Heliconia* but only in low and medium light, and had no effect on λ when light availability was high. These results reflect a two-way interaction between light and A_{max} on future growth, and demonstrate that when forest light availability is low, increasing the capacity to use light has a positive effect on population growth rates for some understory herbs. These results were contrary to our hypothesis that increasing A_{max} would increase net photosynthesis and therefore increase fitness in high light but have little effect on fitness in low light. Although in low light, a small increase in A_{max} does not have as large of an effect on net photosynthesis as in high light, a small increase in net photosynthesis in low light appears to have a greater positive influence on fitness than it does in high light. In contrast to *Heliconia*, *λ* for *Calathea* were unaffected by changes in A_{max} across all light environments, and *λ* was always above 1. These results again suggest that *Calathea* is adapted to occupy a large range of light environments (a generalist) and demonstrates species-specific differences in the sensitivity of the deterministic population growth rate to A_{max}. Thus, the higher sensitivity of *λ* for *Heliconia* than for *Calathea* supports our hypothesis that *Heliconia* is less shade-adapted than *Calathea*. To occupy a large range of environments, habitat generalists should have high plasticity in their traits, where plasticity is defined as the ability to change a trait in response to the environment. Changing a trait response should therefore have little effect on overall fitness of a generalist, if they are able to adjust other traits to maintain fitness when conditions are poor, or maximize fitness when conditions are favorable (Sultan 2001). Thus, *Calathea* may adjust other physiological light response parameters, or adjust their morphology to compensate for changes in A_{max}, resulting in low sensitivity (in a colloquial sense) of fitness to photosynthetic capacity, A_{max}.

The stochastic population growth rates of our study species also reflected the influence of A_{max} on growth and supported our hypothesis that *Calathea* would be less sensitive to changes in A_{max} than *Heliconia*. For *Calathea*, λ_S was unaffected by changes in A_{max}, while λ_S for *Heliconia* increased with increasing A_{max}. These results arise directly from the effect of A_{max} on the deterministic population growth rates; increasing A_{max} positively influenced the deterministic population growth rates in low light, and low light environments were the most commonly observed environments in the stochastic model. Thus, for *Heliconia*, increasing the capacity to use light increases the population growth rate in random light environments, but has no effect on population growth for *Calathea*. Metcalf et al. (2009) studied the demographic rates of tropical trees in random light environments, and demonstrated that the probability of individuals reaching the tree canopy increases when they start in the light, versus starting in the dark. Because high light availability has been shown to increase photosynthetic capacity within tropical forest species (Straussdebenedetti and Bazzaz 1991), it is plausible that tree species that started in light had higher A_{max} from a young age, which improved their future growth and survival probabilities in a random light environment.

The elasticity of λ_S with respect to perturbations in the vital rates over all environments (E^S) differed significantly due to changes in A_{max} for *Heliconia* but was unaffected by changes in A_{max} for *Calathea*. For *Heliconia*, increasing A_{max} resulted in an increased elasticity to growth and stasis of small- to intermediate-sized individuals. These results may reflect the importance of increasing A_{max} on potential carbon gain. When A_{max} is low, λ_S may be only weakly sensitive to the growth of photosynthetically active small- and intermediate-sized individuals, because the net carbon gain of these individuals is likely to be low. When A_{max} values are high, individuals of all sizes have a higher net carbon gain than they did when A_{max} was low (provided that respiration rates are unchanged), even in low light. Previous studies have found evidence of ontogenetic changes in gas exchange rates (Kubien et al. 2007), such as increased photosynthetic rates with age, size, or with the transition from pre-reproductive to reproductive (Donovan and Ehleringer 1991, Zotz et al. 2001, Thomas and Winner 2002, Maherali et al. 2009). Because ontogenetic changes in physiological performance influence net carbon gain, they will also directly influence individual plant fitness (Maherali et al. 2009). For *Calathea*, λ_S was most sensitive to reproduction, for all A_{max} values, again indicating that physiological responses to the light environment have no influence on the population growth rates of *Calathea*. Because *Heliconia* is most sensitive to growth and stasis of small and large individuals, our results demonstrate that this perennial herb has experienced strong selection for persistence of large individuals that are highly resource efficient rather than for small individuals with high reproductive rates, i.e., K selection and not r-selection (MacArthur and Wilson 1967). Previous studies have found that trees tend to be more sensitive to survival, while herbs are more sensitive to growth (Silvertown et al. 1993) but *Heliconia* appears to be more similar to trees. In contrast, *Calathea* appears to have experienced stronger selection for increased reproduction than *Heliconia*, which may arise from its ability to persist in a wider range of light environments (due to its shade tolerance). A previous study found that reproductive output in *Calathea* was unaffected by light availability, whereas *Heliconia* reproduction increased with light (Westerband and Horvitz 2015). Therefore, *Calathea* fitness is most strongly influenced by its ability to reproduce equally well across light environments.

An increase in λ_S that is accompanied by an increase in the variance of vital rates can be considered as evidence of selection for vital rate plasticity ($E^{S\sigma}$, Tuljapurkar et al. 2003). $E^{S\sigma}$ also differed by species, and was affected by changes in A_{max} for *Heliconia* but not *Calathea*, reflecting the results of our model averaging. For *Heliconia*, increasing A_{max} increased the sensitivity of λ_S to variability (or plasticity) in stasis and growth of small individuals, and also to reproduction. For *Calathea*, increasing A_{max} had no effect on $E^{S\sigma}$, and λ_S was most sensitive to variability associated with reproduction. The elasticity of λ_S to variability in vital rates is likely to be strongly influenced by A_{max} for shade-intolerant gap species if A_{max} varies widely over a range of light environments, and if A_{max} has a direct influence on vital rates. Short-lived plant species should be more sensitive to variability of vital rates than long-lived species because they have no seed or propagule bank to buffer against the potentially negative impacts of environmental fluctuations (Morris et al. 2008, Villellas et al. 2013). Thus, *Calathea* and *Heliconia* should have similar elasticities, but we found evidence of increased selection for variability in vital rates in *Heliconia* and not *Calathea*, because increasing variability increased the population growth rate. These differences may reflect the degrees of shade tolerance of our study species. A relevant study on *Calathea ovandensis* (Morris et al. 2008) found that it had positive elasticities to increasing variability in vital rates, implying that its long-term growth rates would increase if its environment became more variable. In our study, *Calathea* had weak negative elasticities to reproduction, while *Heliconia* had strong negative elasticities to growth and stasis. Because increased variability may positively influence the growth rates of disturbance-adapted species (Morris et al. 2006), our results provide further evidence that our study species are adapted to persist in low to moderate light environments, rather than disturbed areas of high light, and that *Calathea* may be less plastic than *Heliconia* because of reduced selection for vital rate plasticity.

The environment-specific elasticity (E^S_β) also differed significantly between the two species, and was influenced by changes in A_{max} for *Heliconia* but not *Calathea*, due to the insensitivity of *Calathea*'s growth to A_{max}. *Heliconia* λ_S was sensitive to intermediate- and large-sized individuals when light availability was low, and increasing light availability increased sensitivity to seeds and seedlings. These results suggest that during periods of shade, large individuals have a greater influence on the population growth rate than during periods of high light, but as light availability increases recruitment becomes a more important determinant of the population growth rate. Studies on closely related species of *Calathea* have found similar sensitivities to reproduction and recruitment in deterministic and random environments (Horvitz and Schemske 1995, Horvitz et al. 2010). Changing A_{max} had much more of an effect on elasticity of *Heliconia* when light was abundant than when light was scarce, and increasing A_{max} shifted the sensitivity to larger plants. These results suggest that increasing photosynthetic capacity increases the importance of large plants to the population growth rate.

E^S_β was unaffected by A_{max} for *Calathea*, which reflects the results of our model averaging. *Calathea* λ_S was most sensitive to perturbations in intermediate-sized individuals under high light, and changing A_{max} did not effect this relationship. When light was low, elasticities were more widely distributed among size classes, but λ_S was more sensitive to seeds and seedlings. In summary, *Calathea*'s stochastic population growth rate was unaffected by changes in photosynthetic rates within each environmental state but became less sensitive to reproduction as light availability increased. In contrast, *Heliconia*'s stochastic population growth rate was affected by the interaction between A_{max} and light availability and sensitivity to reproduction was greatest under high light.

Because we have estimates of quantum efficiency, respiration rate and light compensation points, a useful analysis would be to compare the effects of each photosynthetic parameter (Equation 1) on the population dynamics of our study species. Baltzer and Thomas (2007) determined that dark respiration was the strongest determinant of whole plant light requirements in tropical tree saplings. We also do not estimate net photosynthesis or carbon gain in this study, and relevant studies have used models such as the Yplant model to determine the effect of leaf arrangement and self-shading on net carbon gain (Pearcy and Yang 1996), which is likely to differ between our species because of differences in their morphology (see Westerband and Horvitz 2015). Once carbon gain is estimated, we could determine how the fitness of our study species are influenced by net photosynthesis rather than the individual parameters of the light response curve (A_{max}, alpha, LCP, and R_d). Another limitation of this study is that A_{max} was correlated with light availability for *Calathea*, but not *Heliconia*, although we assumed independence in our analysis for the purposes of species comparisons.

CONCLUSIONS—In summary, we demonstrate that light and maximum photosynthetic capacity regulate the population dynamics of two co-occurring understory herbs in distinct ways. The deterministic and stochastic population growth rates indicate that *Calathea* is less affected by changes in light and photosynthetic capacity than *Heliconia*. Although increasing light decreased the population growth rate for *Heliconia*, *Heliconia* had a larger range of A_{max} than *Calathea*, and its population growth rate responded positively to increasing A_{max}. Therefore, we conclude that *Calathea* is more shade-tolerant than *Heliconia*, and is likely able to persist in a wider range of environments. Our elasticity analyses supported these findings and demonstrated differences in the sensitivity of population growth to changes in photosynthetic capacity. The contributions of large versus small individuals to population growth changed with A_{max}, which may result from differences in their potential carbon gain. Thus, we are implying that carbon gain within individual plants can influence population growth rates. The results of this study support a previous study of the same species (Westerband and Horvitz 2015) and provide novel insight into the mechanisms that regulate the population dynamics of organisms in resource-limited and dynamic environments.

Table 5.1 Hypothesized relationships between photosynthetic capacity (A_{max}) and population dynamics of plants with different degrees of shade tolerance.

Syndrome	**Trait**
Highly shade tolerant	Low A_{max} A_{max} has narrow range Increasing light decreases λ λ is not sensitive to A_{max} λ_S is not sensitive to A_{max} E^S is not sensitive to A_{max} $E^{S\sigma}$ is not sensitive to A_{max} $E^S{}_\beta$ is not sensitive to A_{max}
Moderately shade-tolerant	Moderate A_{max} A_{max} has moderate range Increasing light has little effect on λ λ is moderately sensitive to A_{max} λ_S is moderately sensitive to A_{max} E^S is sensitive to A_{max} $E^{S\sigma}$ is sensitive to A_{max} $E^S{}_\beta$ is sensitive to A_{max} and elasticity is greatest in low light
Shade-intolerant	High A_{max} A_{max} has wide range Increasing light increases λ λ is sensitive to A_{max} λ_S is sensitive to A_{max} E^S is sensitive to A_{max} $E^{S\sigma}$ is sensitive to A_{max} $E^S{}_\beta$ is sensitive to A_{max} and elasticity is greatest in low light

Table 5.2 Parameter values used in the Integral Projection Model.

	Model coefficient	***Calathea***	***Heliconia***
Survival	Intercept	-2.74	-2.05
	size	0.95	0.78
	light	0.07	-0.22
	size × light	-0.02	0.05
Growth	Intercept	0.76	2.6
	size	0.9	0.56
	light	0.03	-1.55
	A_{max}	0.006	0.44
	size × light	-0.001	0.18
	size × A_{max}	0.00045	-0.034
	light × A_{max}	-0.0052	0.014
	size × light × A_{max}	0.00035	-0.0014
St dev of residuals of growth model		1.53	0.71
Smallest observed plant size (log scale)		0.57	0.78
Largest observed plant size (log scale)		11.90	11.07
Reproduction	Intercept	-13.23	-12.55
	size	1.401	1.527
	light	-0.213	0.154
	size × light	0.043	-0.013
Inflorescence production	Intercept	-6.673	-1.009
	size	0.829	0.157
	light	0.067	-0.382
	size × light	-0.007	0.048
Mean number of fruit per inflorescence		23	37
Mean number of seeds per fruit		3	2.5
Mean size of recruits in high light		2.88	2.34
Mean size of recruits in low light		3.08	2.73
St dev of size of recruits in low light		0.54	0.71
St dev of size of recruits in high light		1.4	1.17
Proportion seeds that live from t to t+1 in high light		0.32	0.2
Proportion seeds that live from t to t+1 in low light		0.29	0.15
Proportion seeds alive that germinate and live to t+1 in high light		0.95	0.33
Proportion seeds alive that germinate and live to t+1 in low light		0.14	0.26

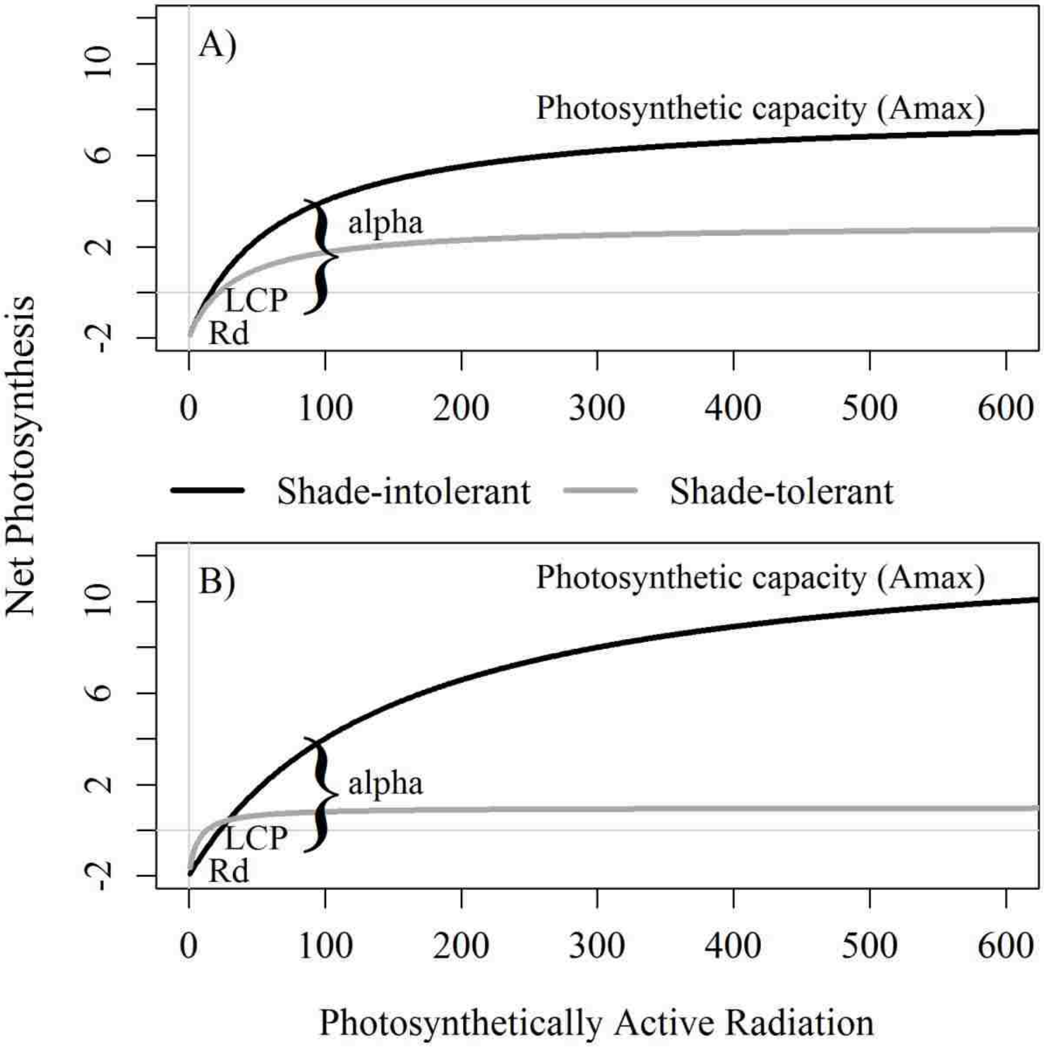

Figure 5.1 Theoretical light response curves for shade-tolerant (dark grey line) and shade-intolerant (black line) plant species. Compared to shade-intolerant species, shade-tolerant species often have low photosynthetic capacity (A_{max}), low respiration (R_d), low light compensation point (LCP), and high photosynthetic efficiency (the initial slope, alpha). In this study, we simulate A) the effect of changing A_{max} while maintaining all other traits constant. In nature, B) increasing A_{max} is often associated with a reduction in alpha, and an increase in R_d and LCP. Light grey vertical line indicates no light and light grey horizontal line indicates zero net photosynthesis.

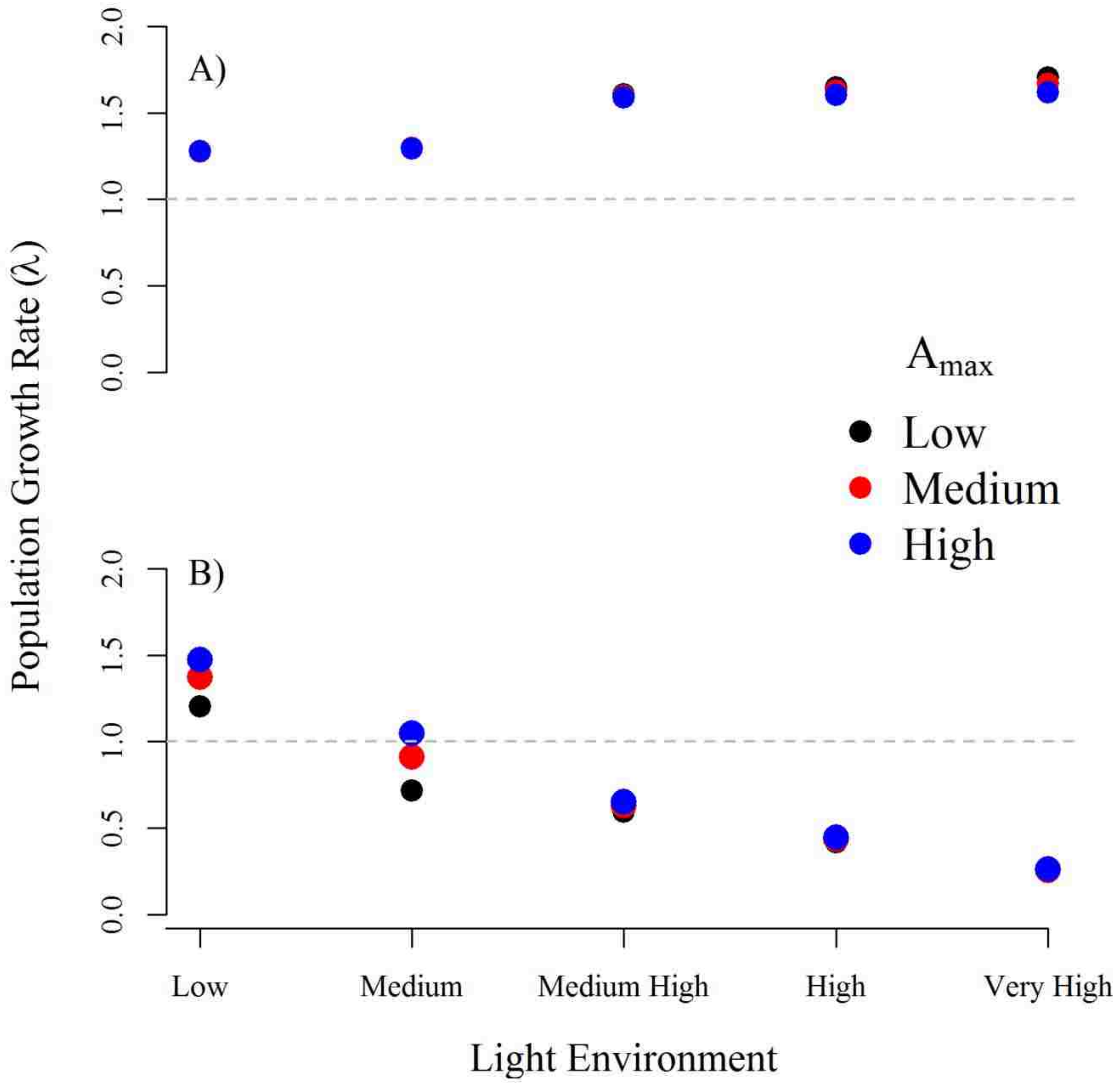

Figure 5.2 Deterministic population growth rate (λ) of A) *Calathea crotalifera* and B) *Heliconia tortuosa*, over a range of light environments and a range of photosynthetic rates (A_{max}). Higher A_{max} is equivalent to a higher photosynthetic capacity.

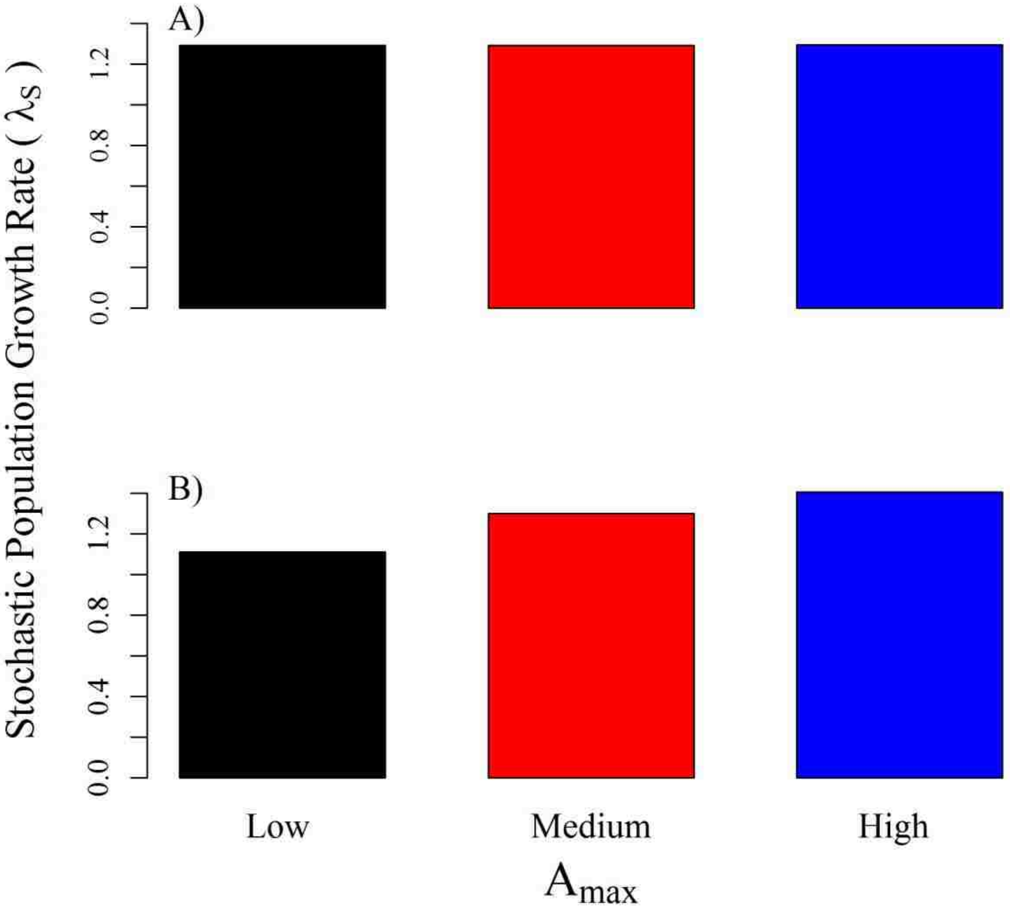

Figure 5.3 Stochastic population growth rate (λ_S) of A) *Calathea crotalifera* and B) *Heliconia tortuosa*, over a range of photosynthetic rates (A_{max}). Higher A_{max} is equivalent to a higher photosynthetic capacity.

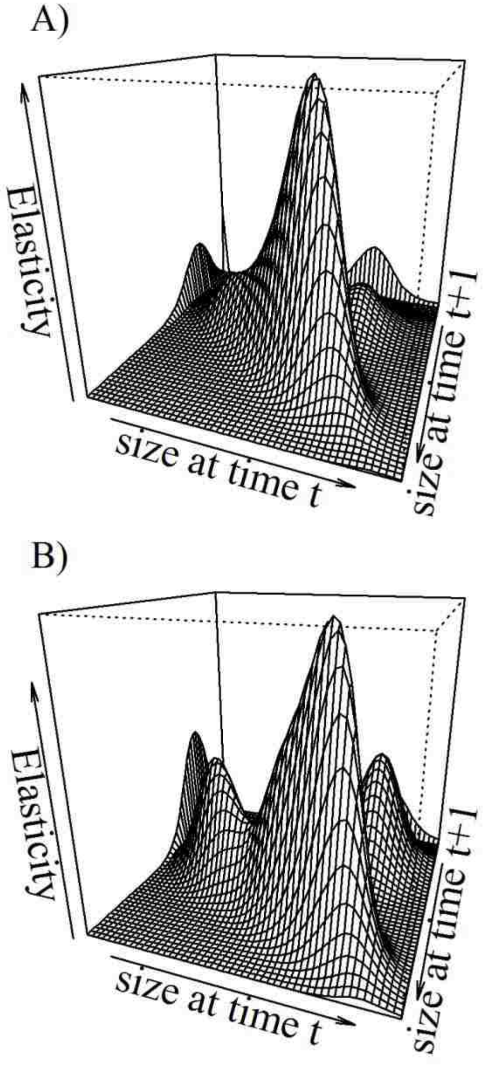

Figure 5.4 Elasticity of λ_S with respect to perturbations in vital rates over all environments (E^S) for *Heliconia tortuosa* with A) low A_{max} and B) high A_{max}.

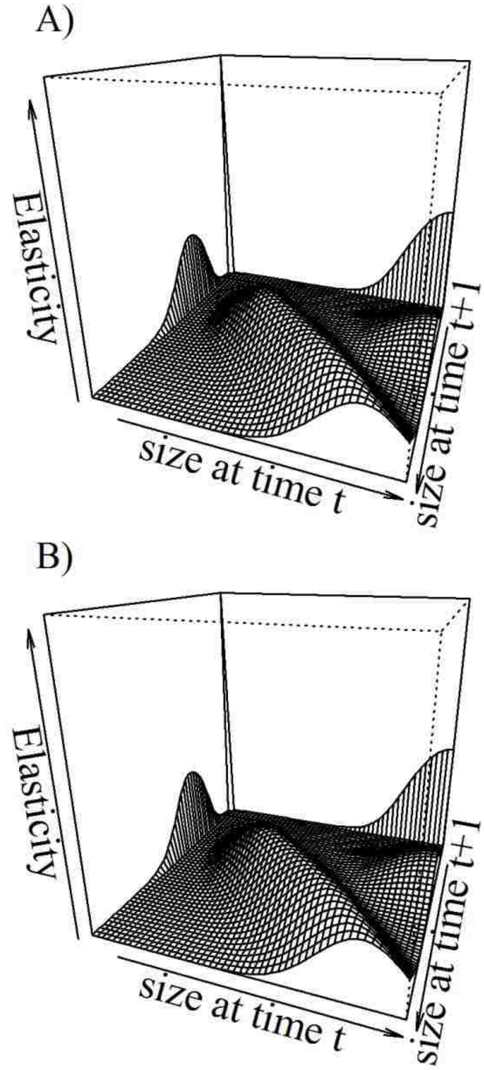

Figure 5.5 Elasticity of λ_S with respect to perturbations in vital rates over all environments (E^S) for *Calathea crotalifera* with A) low A_{max} and B) high A_{max}.

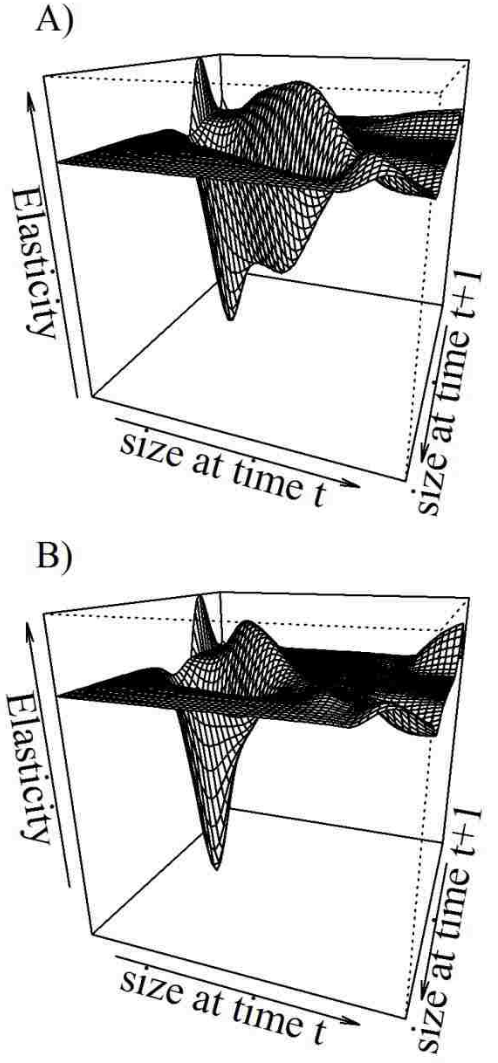

Figure 5.6 Elasticity of λ_S with respect to increased variability in vital rates ($E^{S\sigma}$) for *Heliconia tortuosa* with A) low A_{max} and B) high A_{max}.

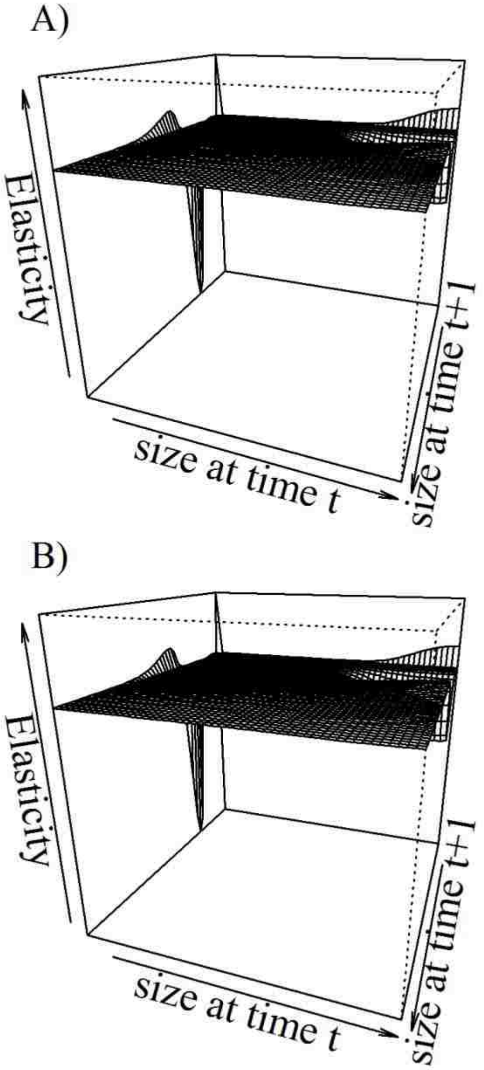

Figure 5.7 Elasticity of λ_S with respect to increased variability in vital rates ($E^{S\sigma}$) for *Calathea crotalifera* with A) low A_{max} and B) high A_{max}.

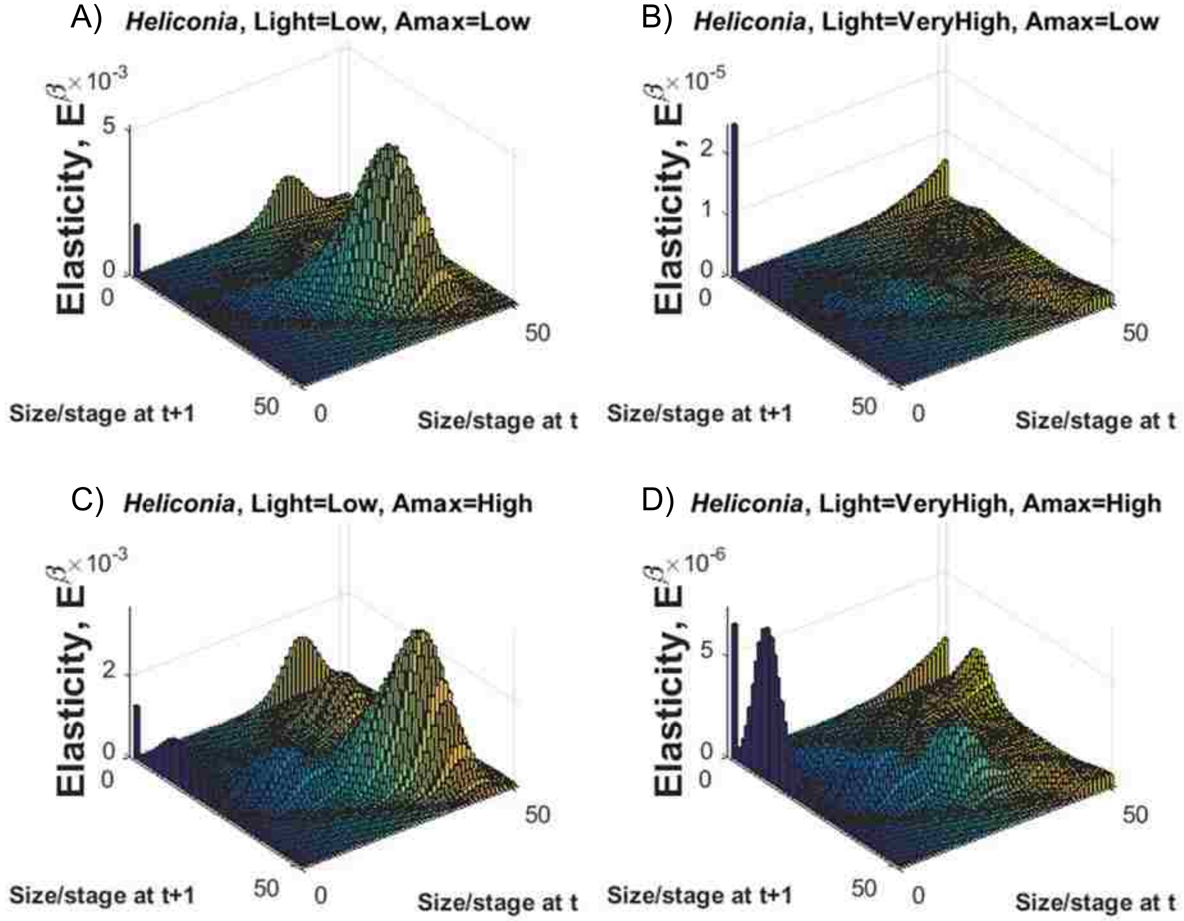

Figure 5.8 Elasticity of λ_S to vital rates in a given environment ($E^S{}_\beta$) for *Heliconia tortuosa*. A) and B) are for *Heliconia* with low A_{max}, C) and D) are for *Heliconia* with high A_{max}. A) and C) are low light and B) and D) are high light.

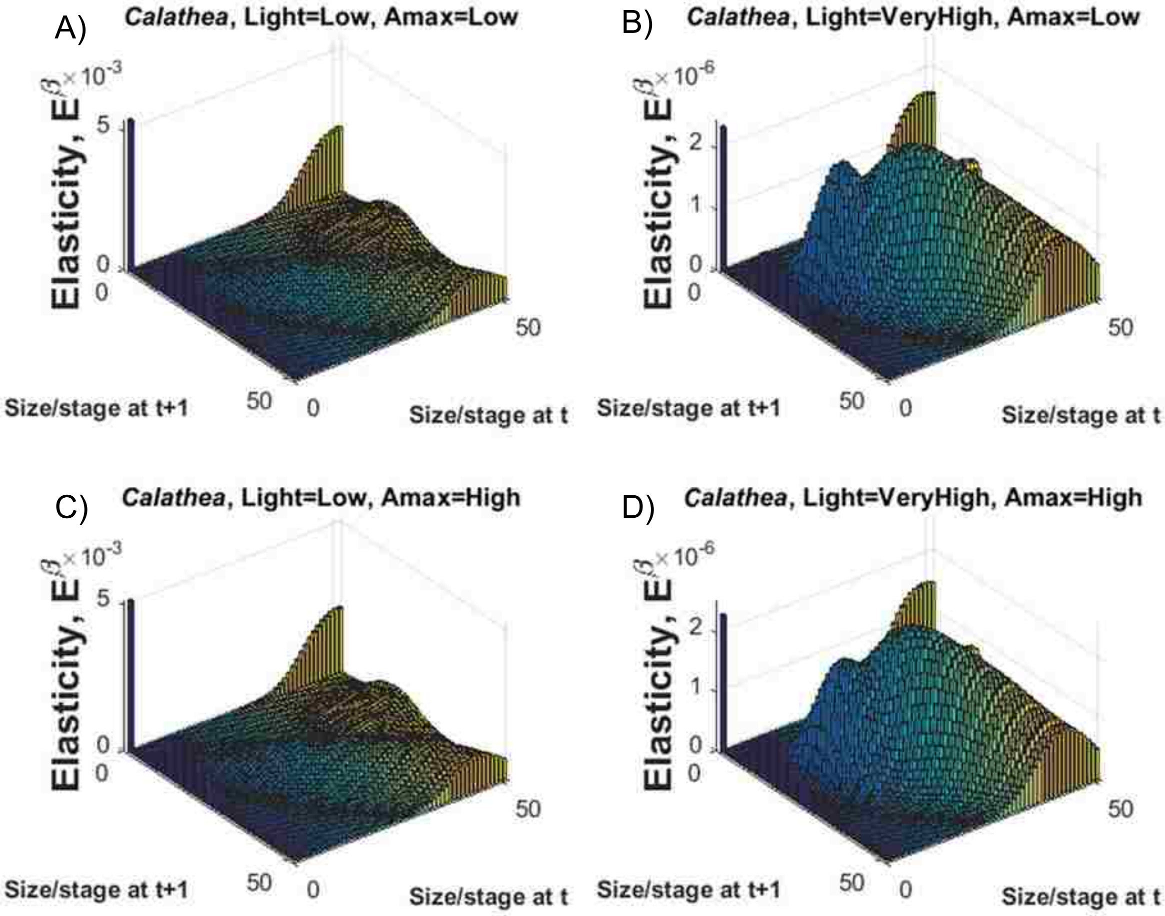

Figure 5.9 Elasticity of λ_S to vital rates in a given environment ($E^S{}_\beta$) for *Calathea crotalifera*. A) and B) are low A_{max}, C) and D) are high A_{max}. A) and C) are low light and B) and D) are high light.

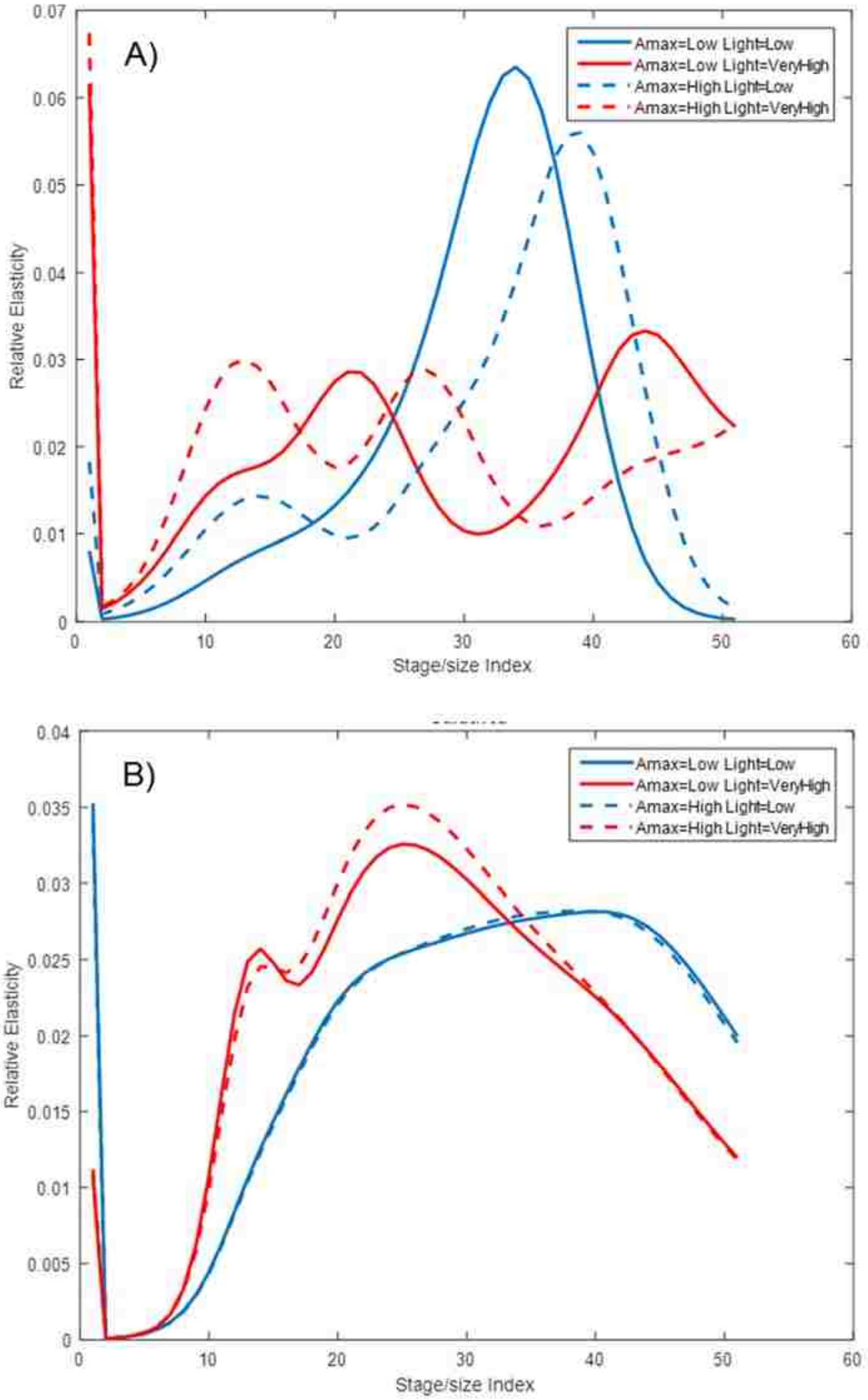

Figure 5.10 Relative elasticity of λ_S to environment-specific perturbations of the vital rates for a given plant size/life stage. A) *Heliconia tortuosa* and B) *Calathea crotalifera*. Blue lines represent low light, red lines represent very high light. Solid lines are for low A_{max}, dashed lines are for high A_{max}.

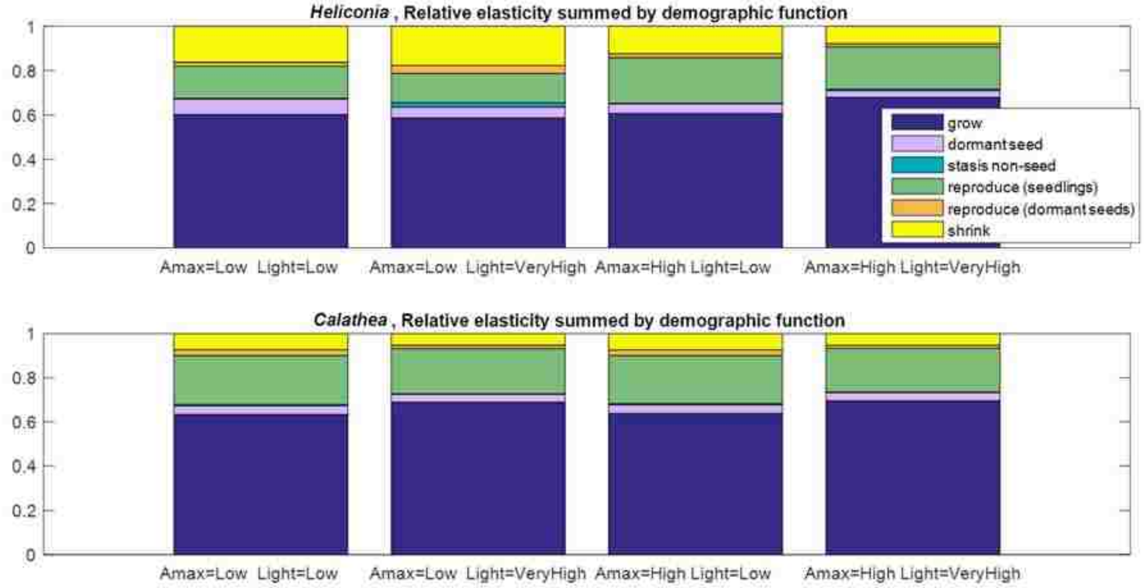

Figure 5.11 Relative elasticities of λS to environment-specific perturbations of the vital rates, for given regions of the matrix. A) *Heliconia tortuosa* and B) *Calathea crotalifera*. Elasticity to elements below represent sensitivity to growth, on the diagonal represents stasis, and above the diagonal indicates shrinkage and reproduction.

Chapter VI: Summary

For understory plants in tropical forests, the availability of light strongly influences their rates of growth, survival, and reproduction, i.e., vital rates (Denslow et al. 1990). Light in these environments is patchy and dynamic because of treefalls that create gaps in the canopy, which slowly close over time. To better understand how light availability influences the population dynamics of plants under the tree canopy, I modelled demographic responses as functions of light availability and physiological responses for two widespread understory herbs, *Calathea crotalifera* and *Heliconia tortuosa* (order Zingiberales). Thus, this dissertation research bridges the gap in translating leaf-level responses to plant population dynamics by incorporating stage-specific morphological and physiological traits into estimation of vital rates.

The goal of this dissertation was to test three primary hypotheses. First, that the vital rates and physiological responses of the study species match what would be expected for shade-adapted species. Second, that the vital rates and physiological responses of one study species, *Calathea*, should more closely match those for shade-adapted species than the second study species, *Heliconia*. Third, that the study species show evidence of having high trait plasticity and have adaptations that maximize their fitness in variable environments. Average lifetime fitness (hereafter, fitness) is synonymous with a population's growth rate for species with overlapping generations (Charlesworth 1974). Trait plasticity is defined as the degree of change in a trait in response to a change in the environment (Alpert and Simms 2002), but, in the context of this study, I consider a species to have high plasticity if environmental variability has a positive effect on its performance. If a species has low trait plasticity, it should have a narrow range of responses, which would result in reduced performance when the environmental conditions change.

Previous studies have found that for species adapted to shade, increasing light should reduce growth and survival, and increase reproduction (Valladares and Niinemets 2008). Physiologically, shade-adapted species should have a low maximum photosynthetic capacity and low rate of respiration, but a high photosynthetic efficiency (Valladares and Niinemets 2008). When plants are adapted to deep shade, exposing them to very bright light can damage their photosynthetic apparatus, in a process known as photoinhibition (Long, Humphries, and Falkowski, 1994; Valladares and Niinemets, 2008). Therefore, the fitness of shade-adapted plants should be high when the environment is shaded and be low when the environment is very bright and sunny. I also hypothesized that when light is scarce, increasing the capacity to use light has little effect on fitness for shade-adapted species but when light is abundant, increasing the capacity to use light should increase fitness.

To test the first hypothesis that the vital rates and physiological responses of the study species match what would be expected for shade-adapted species, I estimated size-specific rates of growth, survival, and reproduction, for *Heliconia* and *Calathea* in a mid-elevation rainforest in Costa Rica. During three annual censuses, I monitored 1278 plants, measuring leaf area, number of inflorescences, and canopy openness (a proxy for light availability). I fitted regression models of all vital rates and evaluated them over a range of light levels. The best fitting models were selected using Akaike's Information Criterion. I found that the vital rates were significantly influenced by size for both species, but not always by light. Increasing light resulted in higher growth and a higher probability of reproduction in both species, but lower survival in one species. These results only partially support my hypothesis that the vital rates of these species would match what is expected for shade-adapted species, because increasing light availability reduced growth in small plants but not large plants.

I then measured rates of gas exchange annually over two years, for 77 plants (a subset of the 1278 individuals described above) to determine whether the physiological responses of these species matched what is expected for shade-adapted species. I estimated four physiological parameters for each individual: maximum photosynthetic capacity (A_{max}), quantum efficiency (alpha), respiration (R_d), and light compensation point (LCP). I found that the relationships among the parameters matched those for shade-adapted species in *Calathea* and not *Heliconia*, which supported my hypothesis.

Lastly, to determine whether increasing light reduced the fitness of both species, as I hypothesized would occur for shade-adapted species, I estimated their population growth rates in static light environments (λ) over a range of photosynthetic values, using Integral Projection Models. As light availability increased, λ increased for *Calathea* but decreased for *Heliconia* (from population growth at low light to diminution), which was contrary to my hypothesis. In summary, I found that the vital rates and physiological responses for *Calathea* more closely matched those for shade-adapted species than for *Heliconia*, but the effect of light on *Calathea*'s fitness did not match what I expect for shade-adapted species. I argue that *Calathea* is more shade tolerant than *Heliconia*, but maintains the ability to live in brighter environments than *Heliconia*.

I tested the second hypothesis that the demographic and physiological responses of *Calathea* would more closely match those for shade-adapted species than *Heliconia*, by comparing the vital rate estimates of the two species and by comparing their physiological responses. This hypothesis arises from the observation that *Calathea* possesses morphological features more commonly observed in shade-adapted species. For example, *Calathea* leaves have a pulvinus, a swelling at the base of the leaf that allows the plant to orient its leaves towards sunlight. *Calathea* also has broader leaves than *Heliconia*, and individual plants have less self-shading among leaves, because the *Calathea* has clonal shoots that arise from a sympodially branched rhizome near the ground (Grime 1977), whereas *Heliconia* shoots begin branching closer to the apex of the individual. Therefore, if *Calathea* is more shade-adapted than *Heliconia*, its demographic and physiological responses should more closely resemble those of shade-adapted species; lower maximum photosynthetic capacity, lower rate of respiration, and higher photosynthetic efficiency than *Heliconia*. Increasing light should more strongly reduce *Calathea*'s growth and survival compared to *Heliconia*, and increasing light should more strongly increase its reproduction compared to *Heliconia*.

The two species did not differ significantly in terms of their mean physiological responses, which was contrary to my hypothesis that *Calathea* is more shade-adapted than *Heliconia*. I then modelled growth for both species as a function of current size, light availability, and the two composite measures of their physiological response parameters. Principal components analysis (PCA) and correlation tests were used to determine relationships among the four parameters. I used model averaging to determine the importance of size, light, and the physiological responses parameters for predicting future size and modelled future size as a function of these variables. I found that the physiological responses of the study species had different effects on growth for the two species; compared to *Calathea* that grew, *Calathea* that diminished in size had either one of two combinations of variables; either high respiration and low efficiency, or, high efficiency and high photosynthetic capacity. Compared to *Heliconia* that grew, *Heliconia* that diminished in size had either one of two combinations of variables; either low respiration and low photosynthetic capacity, or low respiration, low efficiency and low photosynthetic capacity. Thus, these results only partially supported my hypothesis that *Calathea* is more shade-adapted than *Heliconia* because I expected that shade-adapted species would grow fastest when they had low respiration, low photosynthetic capacity, and high photosynthetic efficiency, and neither species matched that combination of variables.

Lastly, I hypothesized that the fitness of *Heliconia* would be more sensitive to changes in the capacity to use light than the fitness of *Calathea*, if *Calathea* is indeed more shade-adapted than *Heliconia*. I used the estimated size-specific vital rates for *Calathea* and *Heliconia*, and estimates of photosynthetic capacity described earlier. Increasing A_{max} had no effect on λ for *Calathea* but increased λ for *Heliconia* in low light, which supported my hypothesis. These results indicate that increasing the ability to use light can positively influence population growth, and therefore fitness, for species that are adapted to a broad range of environments.

I tested the third hypothesis that both species have high trait plasticity in two ways. First, I simulated a variable light environment in a shadehouse experiment and estimated the rates of growth and survival of both species. Second, I measured how sensitive their fitness was to increasing the variability of demographic rates. If increasing variability in demographic rates increases fitness, this is evidence of selection for trait plasticity. In the shadehouse experiment, I measured growth, survival, leaf lifespan, photosynthetic capacity, and biomass allocation of *Heliconia* and *Calathea*, in response to three independent factors: light availability at the seedling stage, precipitation, and whether individuals experienced a constant or a variable light environment. An abundance of light during early life stages should improve performance in a variable environment later in life. Individuals assigned to the variable light environment switched between low and high light every six months. Individuals assigned to constant light remained at either a low (90% shade) or high (60% shade) light level for the entire experiment. Individuals were also assigned to one of two precipitation treatments: constant at low or constant at high precipitation. I used linear regression analyses with mixed effects models to determine the effect of each factor independently and jointly.

Plants in a variable light environment had greater growth than those in a constant light environment when precipitation was low. At low precipitation, a variable light environment increased growth when individuals started in low light and had no influence on growth when individuals started in high light. At high precipitation, a constant light environment resulted in higher growth whether individuals started in low or high light. These results demonstrate that environmental variability does not always have positive effects on performance and may be stressful if plants have low plasticity, i.e., a low capacity to acclimate to light availability. These results also demonstrate that precipitation and light availability interact to influence future growth, as is expected for plants living in the highly heterogeneous forest understory. Survival decreased with increasing environmental variability but more so at high precipitation, and early life conditions had no influence on the relationship. These results demonstrate that survival is less sensitive to early life conditions than growth is, and that survival is also influenced by the joint abundance of water and light.

Photosynthetic capacity (A_{max}) was lower for individuals in a variable light environment, when they had lived in high light as seedlings, but was unaffected by environmental variability when they had lived in low light as seedlings. These results may suggest that for the study species, high light early in life is stressful (i.e., they experience photoinhibition) resulting in the reduced ability to cope with changes in resource availability later in life. It is important to note that the mean A_{max} of plants in forest ($\mu_{Calathea} = 6.1 \pm 1.6$, $\mu_{Heliconia} = 6.7 \pm 2.1$) most closely resembled the mean A_{max} for plants in the high light treatment of the shadehouse experiment ($\mu_{Calathea} = 5.6 \pm 2.6$, $\mu_{Heliconia} = 5.0 \pm 2.8$), whereas plants in the low light treatment ($\mu_{Calathea} = 4.0 \pm 2.4$, $\mu_{Heliconia} = 3.6 \pm 2.0$) had lower A_{max} values. Thus, if we consider that plants in the forest are experiencing environments that switch between light and dark, it is reasonable to conclude that they are experiencing light environments that are more similar to plants in the high light treatment (60% shade) than the low light treatment (90% shade). In the high light treatment, the mean PAR measurement (between 0900 and 1600 hours) was 19.7 $\mu mol\ m^{-2}s^{-1}$, and was 14.4 $\mu mol\ m^{-2}s^{-1}$ in the low light treatment. In comparison, the mean canopy openness score in the forest was 2.66 (corresponding to 293 $\mu mol\ m^{-2}s^{-1}$), while the most commonly observed canopy openness score was 1 (corresponding to 100 $\mu mol\ m^{-2}s^{-1}$). Thus, if we assume that PAR stays constant throughout the daylight hours (which is unlikely) for a given canopy gap, I can conclude that plants in forest are likely to be receiving more light on average than the plants in the shadehouse treatment, but plants in the shadehouse were exposed to a higher maximum amount of light everyday (up to 683.6 μmol $m^{-2}s^{-1}$). In contrast, only a few individuals in the forest were experiencing such high light levels during the observation period. As a result, individuals in the shadehouse experiment grew significantly more than plants in the forest (Figure 6.1A versus 6.1B), even though the mean PAR values were lower in the shadehouse.

Leaf lifespan was not significantly affected by the treatments. *Calathea* invested significantly more resources in aboveground biomass than *Heliconia*, which may increase its ability to capture light. In summary, I found that although these species inhabit highly heterogeneous and variable light environments in nature, they do not exhibit a preference for environmental variability, which was contrary to my hypothesis.

To test the hypothesis that the study species have adaptations that maximize their fitness in variable environments, I estimated fitness in a dynamic light environment using an IPM and measured the effect of changes in photosynthetic capacity on fitness. If a species is adapted to a variable environment, a variable environment should result in higher fitness than a constant environment. Similarly, increasing the physiological capacity to use light should have little influence on the fitness of a species that is adapted to live in a very wide range of environments, but I expected it to have a large effect on a species that is restricted to deep shade or very bright light. In the model, a dynamic light environment is represented by a random sequence of light environments, which I generated using canopy openness scores from the study plots. As photosynthetic capacity increased, λ_S increased for *Heliconia*, but not *Calathea*. These results demonstrate that increasing photosynthetic capacity has a direct positive influence on the least shade tolerant species, *Heliconia* but has no effect on the more shade-tolerant *Calathea*. I emphasize a distinction between the terms shade-adapted and shade-tolerance, which are synonymous in the literature. If we consider a shade-adapted species as one that prefers shaded environments and a shade-tolerant species as one that can tolerate shade but does not prefer shade, the demographic performance of highly shade-tolerant species (*Calathea*) should indeed be less sensitive to changes in their ability to use light than the performance of less shade tolerant species (*Heliconia*).

Lastly, I tested the hypothesis that the study species have adaptations that maximize their fitness in variable environments by estimating the sensitivity of their fitness to perturbations of the vital rates. I also determined the effect of changing photosynthetic capacity on this sensitivity and found that *Calathea* fitness was much more sensitive to photosynthetic capacity than *Heliconia*. Increasing the variability of the vital rates had little effect on the fitness of *Calathea* but increased fitness for *Heliconia*, which is evidence of selection for trait plasticity. *Calathea* showed evidence of selection against plasticity associated with shrinkage of large individuals. For *Calathea*, increasing light increased the sensitivity of fitness to stasis and shrinkage of large individuals. Conversely, for *Heliconia*, increasing A_{max} increased E^{S} to stasis of small individuals and shrinkage of large individuals. Increasing A_{max} increased $E^{S\sigma}$ to stasis of small individuals. For *Heliconia* with low A_{max}, as light increased E^{S}_{β} decreased due to stasis and increased due to shrinkage of large individuals. For *Heliconia* with high A_{max}, as light increased E^{S}_{β} increased due to stasis of large plants, seeds, and seedlings.

These results demonstrate that *Heliconia* is likely to have greater plasticity than *Calathea*, which may be the mechanism that allows it to persist in a wide range of light environments. In contrast, *Calathea* appears to have low plasticity and instead may be able to tolerate a greater range of light levels than *Heliconia*, which allows it to persist over the same range of light environments. Thus, I suggest that these two understory species are able to co-exist in the forest because of differences in how light and their ability to capture light influences fitness.

The sensitivity of fitness to photosynthetic capacity may reflect the potential carbon gain of individuals of various sizes; when light is scarce, the population growth rate is especially sensitive to changes in the size of large plants that produce a greater relative proportion of carbohydrates than do small plants. When light is abundant, the potential carbon gain of large and small plants may be more similar. To fully answer this question would require estimation of net photosynthesis and net carbon gain for individuals of various sizes, and under various canopy openness scores. This could be accomplished by translating canopy openness values to measures of photosynthetically active radiation (PAR). To accomplish this task, I used linear regression to predict PAR as a function of canopy openness and found that a canopy score of 1 was approximately equivalent (R^2=0.65) to 100 µmol m^{-2} s^{-1}. To achieve 1000 µmol m^{-2} s^{-1} would require a moderately large canopy gap, equivalent to a canopy score of 10 (the highest observed value was 25, which would result in 2400 µmol m^{-2} s^{-1}). Thus, in the future, I could substitute canopy openness scores for PAR in my model, although this would require the assumption that PAR remains constant throughout the day.

In summary, I studied adaptation to shade and its demographic consequences for two co-occurring understory herbs. I found ontogenetic differences in the effect of light of vital rates, which is evidence of plasticity in demographic responses. I found that growth is influenced by different combinations of physiological traits and that early life conditions can promote plasticity in both demographic and physiological responses. Finally, I found that changing light conditions have little effect on a species' fitness if it can tolerate a wide range of environments, and has a large effect on the fitness of less shade tolerant species. I also found evidence of selection for plasticity in vital rates for the less shade-tolerant species, *Heliconia*, than the more shade-tolerant *Calathea*. Thus, *Calathea* is able to tolerate both deeper shade and brighter environments than *Heliconia*, despite having a lower plasticity in its vital rates. *Calathea*'s ability to tolerate these environments appears to be facilitated by its greater morphological ability to capture light. In conclusion, physiological responses to light can be used to predict the fates of plant species in temporally variable environments. This is the first study to successfully incorporate leaf-level physiological responses into stage-structured population models and presents a novel method of determining how physiology can influence the population dynamics of plants in both static and dynamic light environments.

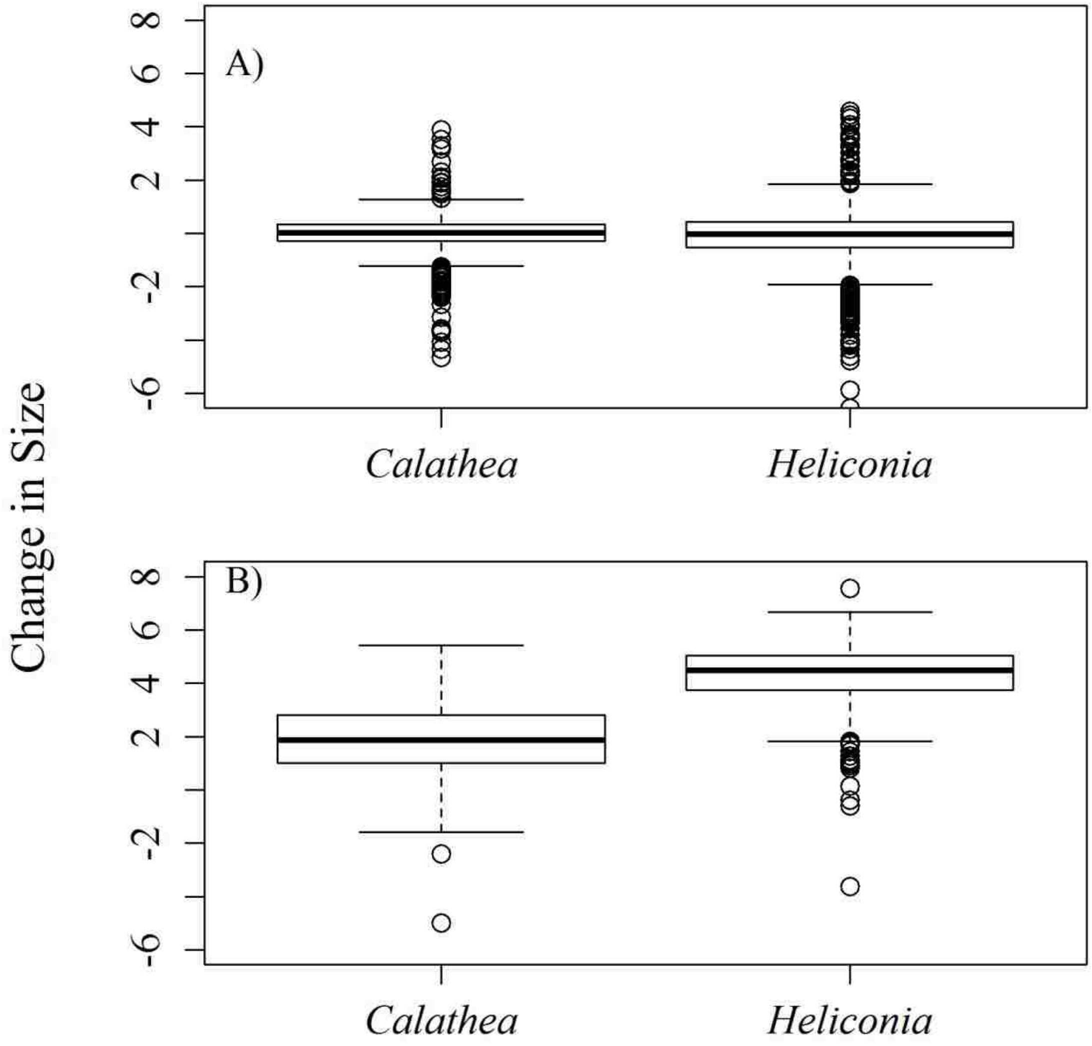

Figure 6.1 Change in plant size (total leaf area) for *Calathea crotalifera* and *Heliconia tortuosa* as measured in the A) forest plots and B) shadehouse experiment.

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Appendices

Appendix 1. Summary of regression analysis for non-reproductive *Calathea crotalifera* above the threshold size at which reproduction was observed (see Appendix 5). Definitions and abbreviations are S (Size = total leaf area) and L (Light = Estimates of light availability based on canopy openness scores). N=304. Grey shading indicates best models selected using AIC. Survival could not be modelled due to low sample size.

		Intercept	Size (S)	Light (L)	Size × Light	R^2	df	ΔAIC
Growth	Size+Light	0.2267	0.9796	0.02057	NA	0.70	4	0
	Size	0.2739	0.9801	NA	NA	0.69	3	0.9864
	Size×Light	-0.0592	1.015	0.1305	-0.0136	0.70	5	1.5286

Appendix 2. Summary of regression analysis for non-reproductive *Heliconia tortuosa* above the threshold size at which reproduction was observed (see Appendix 5). Definitions and abbreviations are S (Size = total leaf area) and L (Light = Estimates of light availability based on canopy openness scores). N=778. Grey shading indicates best models selected using AIC. Survival could not be modelled due to low sample size.

		Intercept	Size (S)	Light (L)	Size × Light	R^2	df	ΔAIC
Growth	Size	0.53105	0.914923	NA	NA	0.47	3	0
	Size+Light	0.52367	0.91199	0.01137	NA	0.47	4	1.5317
	Size×Light	0.67987	0.88856	-0.04961	0.009025	0.47	5	3.3053

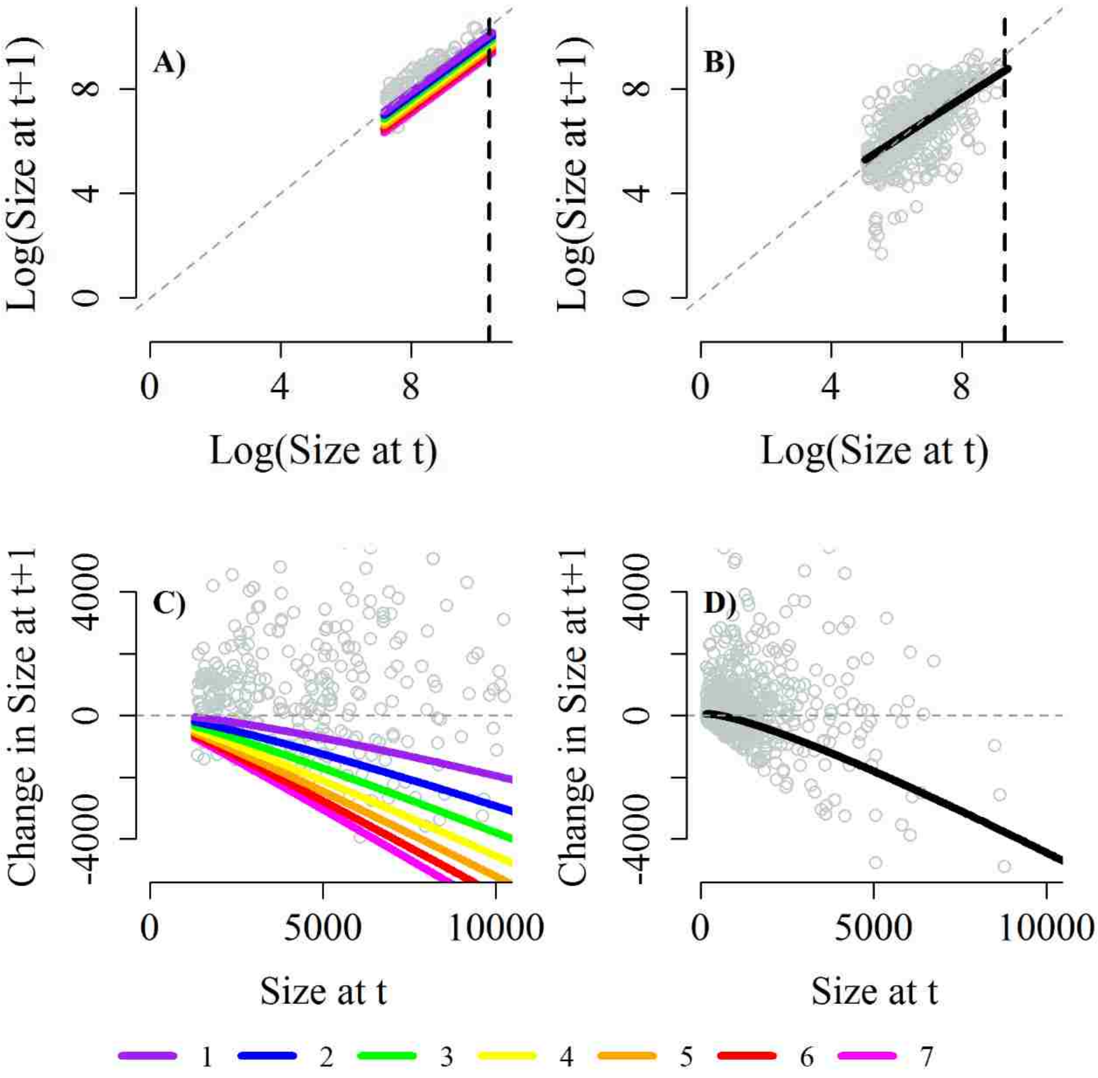
Appendix 3. Summary of regression analysis for reproductive *Calathea crotalifera* (see Appendix 6). Definitions and abbreviations are S (Size = total leaf area) and L (Light = Estimates of light availability based on canopy openness scores). N=222. Grey shading indicates best model selected using AIC. Survival could not be modelled due to low sample size.

		Intercept	Size (S)	Light (L)	Size × Light	R^2	df	ΔAIC
Growth	Size	-0.27195	1.0265	NA	NA	0.8307	3	0
	Size+Light	-0.2710	1.0231	0.0069	NA	0.8318	4	0.5727
	Size×Light	-0.1770	1.0127	-0.0127	0.0021	0.8319	5	2.4544

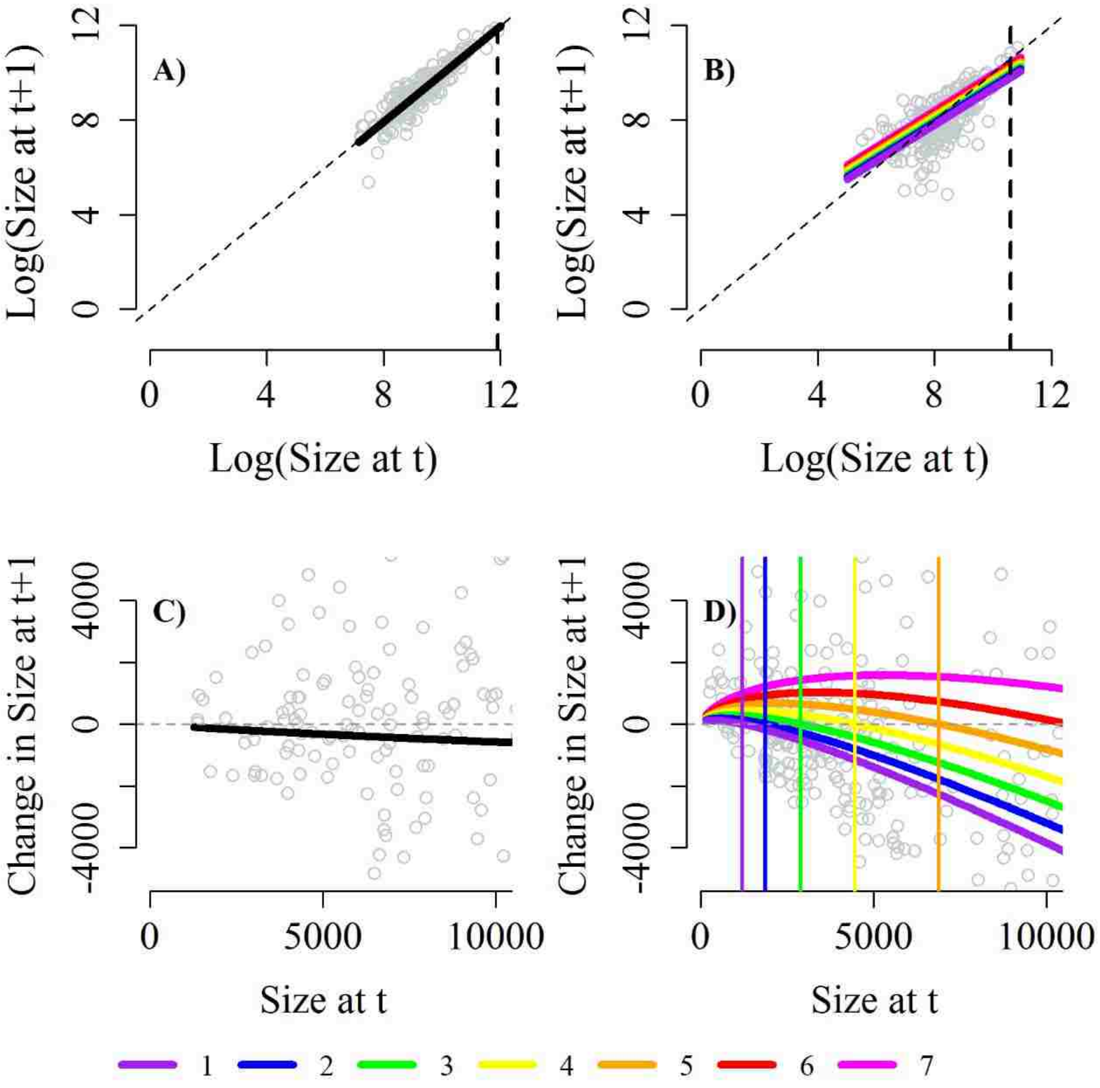
Appendix 4. Summary of regression analysis for reproductive *Heliconia tortuosa* (see Appendix 6). Definitions and abbreviations are S (Size = total leaf area) and L (Light = Estimates of light availability based on canopy openness scores). N=272. Grey shading indicates best model selected using AIC. Survival could not be modelled due to low sample size.

		Intercept	Size (S)	Light (L)	Size × Light	R^2	df	ΔAIC
Growth	Size+Light	1.6912	0.7511	0.05509	NA	0.51725	4	0
	Size×Light	1.5351	0.7698	0.0999	-0.0053	0.5174	5	1.9354
	Size	1.6407	0.7796	NA	NA	0.5020	3	6.5733

Appendix 5. Future size as predicted by current size in nonreproductive individuals above the threshold size at which reproduction was observed in A) *Calathea crotalifera* and B) *Heliconia tortuosa* (1378 cm^2 and 130 cm^2 respectively). Size was log transformed to improve normality. Gray dots in all panels represent all individuals above the threshold size of reproduction. Different colors represent different canopy openness scores. Light gray dashed lines in A) and B) represent identity line (*i.e.,* the line where size at time t+1= size at time t) and black dashed vertical lines indicate largest observed size on log scale. Change in size was calculated by back transforming the log of size (see *Methods*) for C) *Calathea crotalifera* and D) *Heliconia tortuosa*. The largest observed sizes were not plotted in C) and D) because they were outside the scope of the figure. Figures created using regression coefficients from best models in Appendices 1 and 2. N=304 in *Calathea*, and n=778 in *Heliconia*.



Appendix 6. Future size as predicted by current size in reproductive individuals of A) *Calathea crotalifera* and B) *Heliconia tortuosa*. Size was log transformed to improve normality. Gray dots in all panels represent all individuals that were reproductive. Different colors represent different canopy openness scores. Light gray dashed lines in A) and B) represent identity line (*i.e.,* the line where size at time t+1= size at time t) and black dashed vertical lines in A) and B) indicate largest observed size on log scale. Change in size was calculated by back transforming the log of size (see *Methods*) for C) *Calathea crotalifera* and D) *Heliconia tortuosa*. The largest observed sizes were not plotted in C) and D) because they were outside the scope of the figure. Vertical colored lines in C) and D) indicate points at which individuals transition from growing to shrinking (see *Results*). Figures created using regression coefficients from best models in Appendices 3 and 4. N=222 in *Calathea*, and n=272 in *Heliconia*.



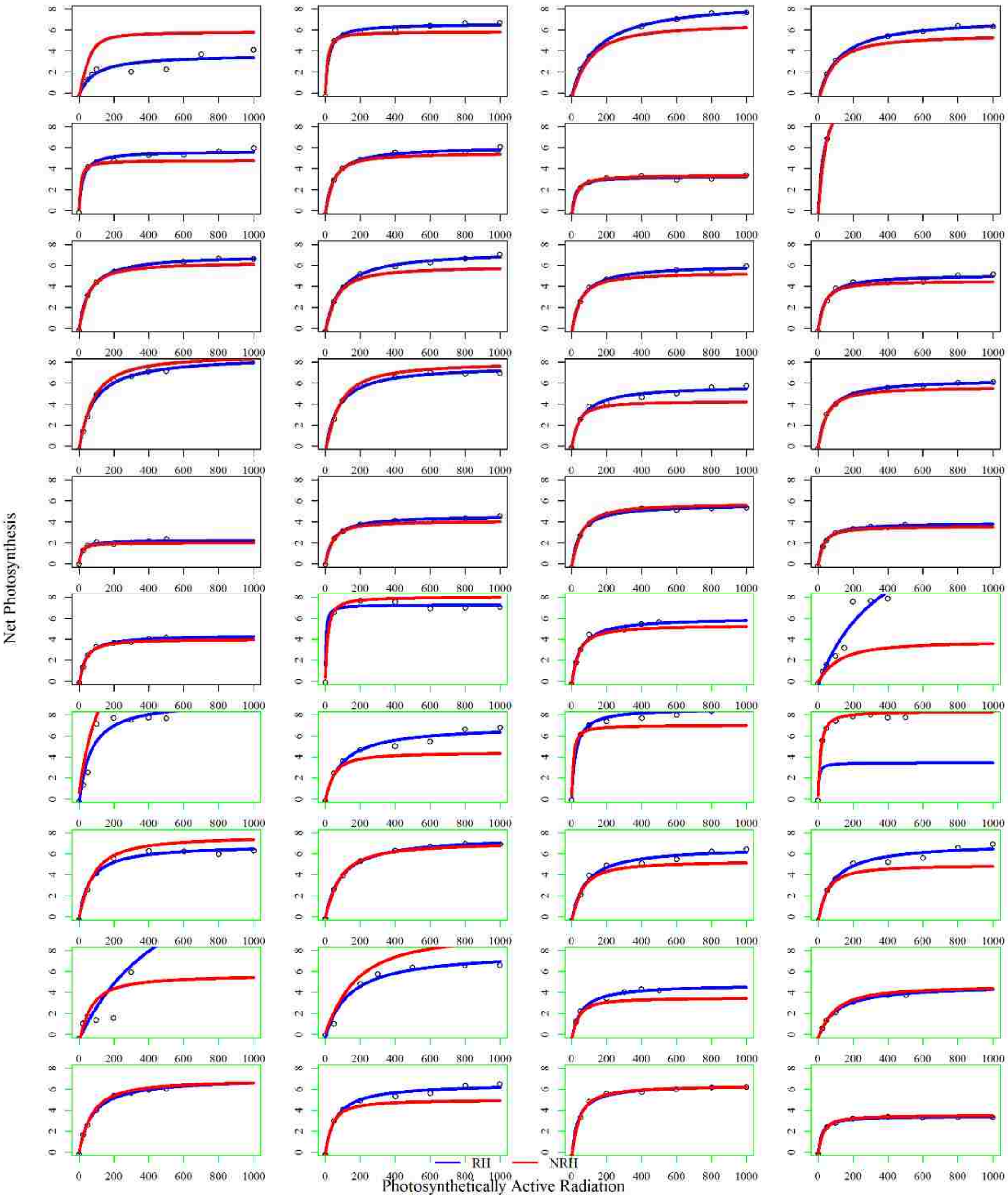
Appendix 7. Effect of increasing light availability on growth in reproductive versus non-reproductive individuals in *Calathea crotalifera* and *Heliconia tortuosa*.

	Reproductive	**Non-reproductive**
Calathea crotalifera	No effect	−
Heliconia tortuosa	+	No effect

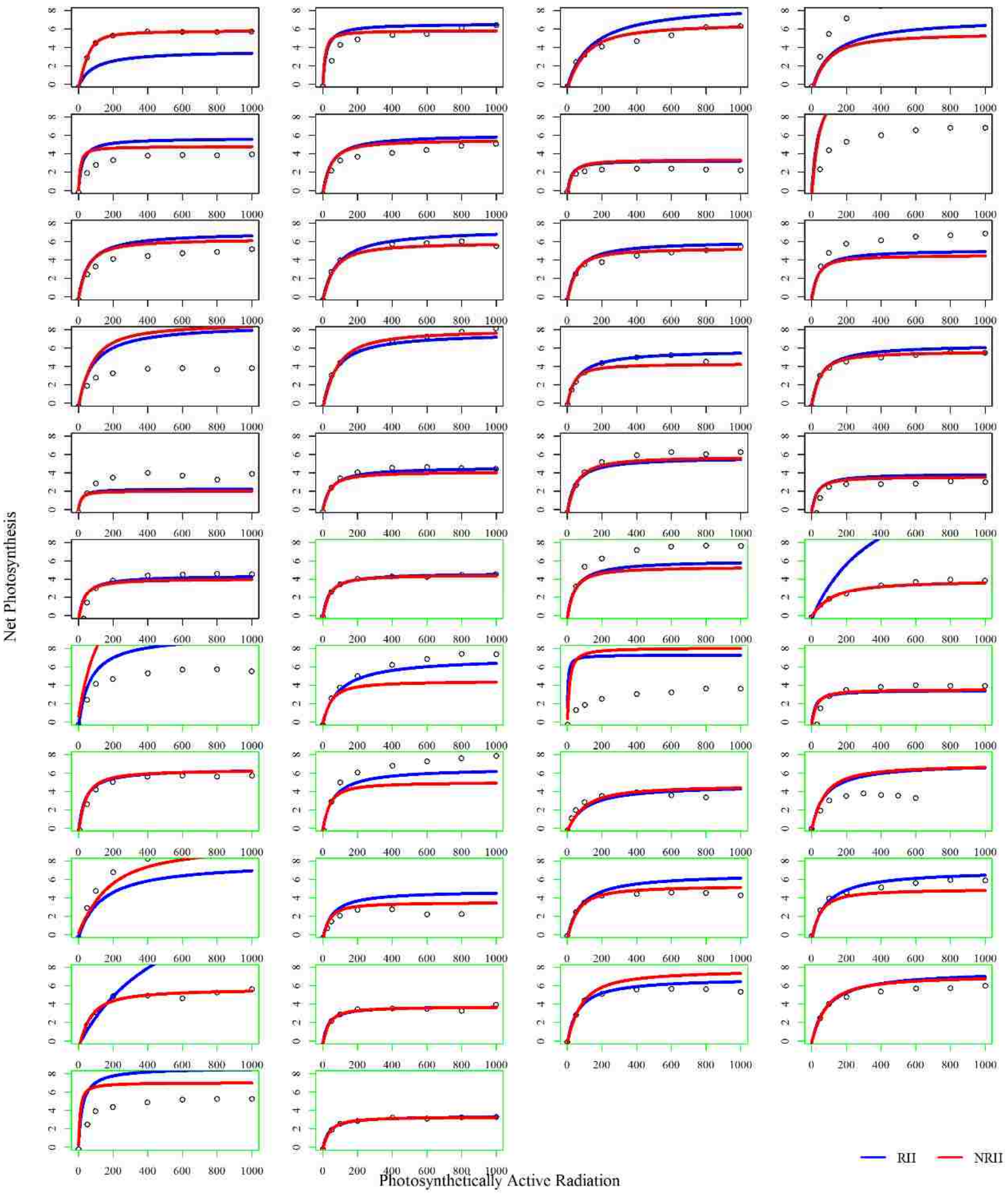
Appendix 8. Intercept and slope coefficients from the linear regression relationship of leaf area (cm^2) as a function of leaf length (cm) for *Heliconia* and *Calathea* at our study site. Leaves were traced onto newspaper in the field and cutouts were scanned using a leaf area meter (LI-3100C, LiCor).

	Intercept	Slope	R^2
Calathea	-1.782	2.195	0.98
Heliconia	-1.182	1.938	0.93

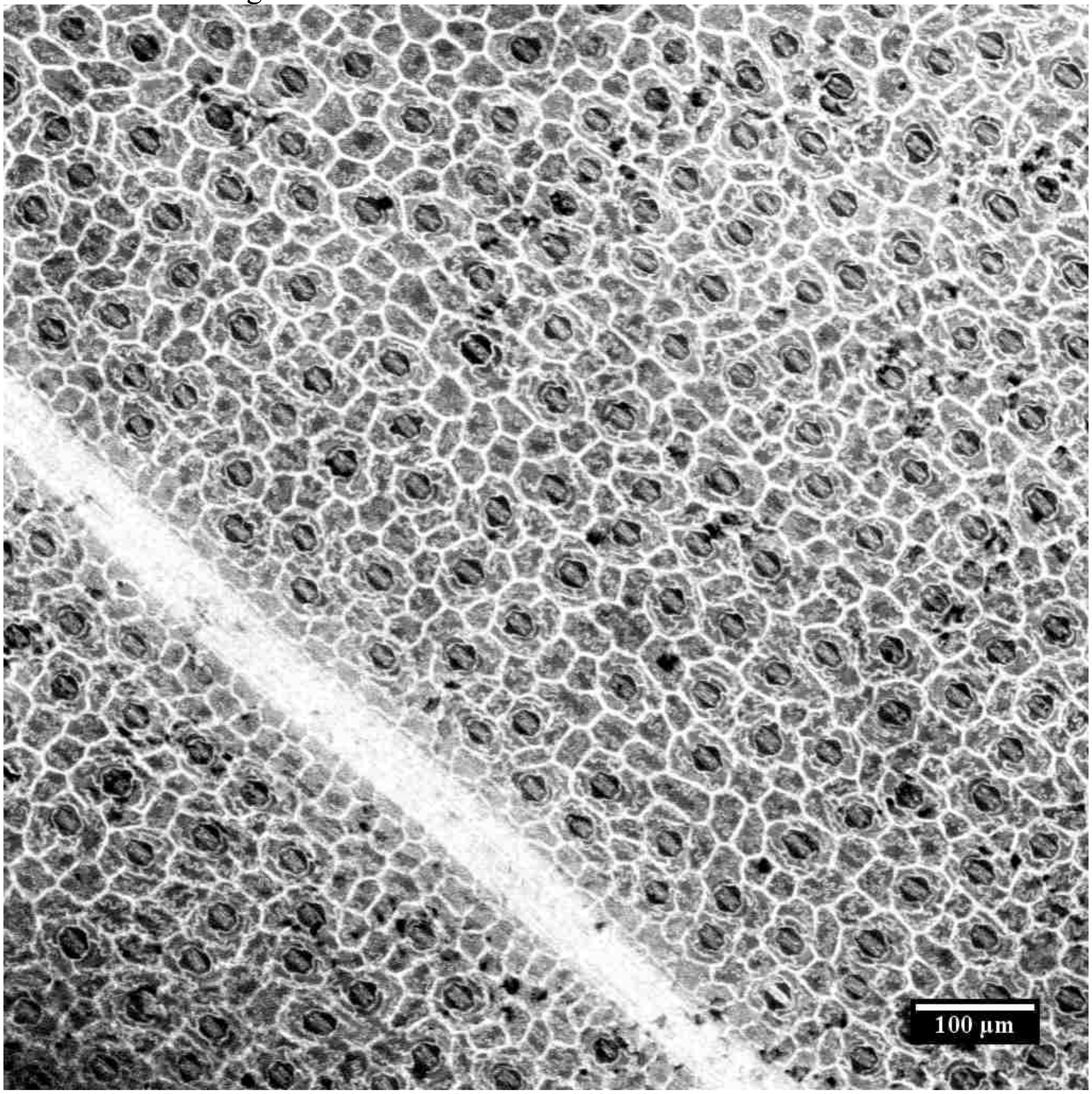
Appendix 9. Light response curves for 40 individuals sampled in 2013. Red lines represent model fits based on the nonrectangular hyperbola, while the blue lines represent model fits based on the rectangular hyperbola. Models were fitted using least squares regression (see *Methods*). Panels with green figure margins are *Heliconia*, those with black margins are *Calathea*.



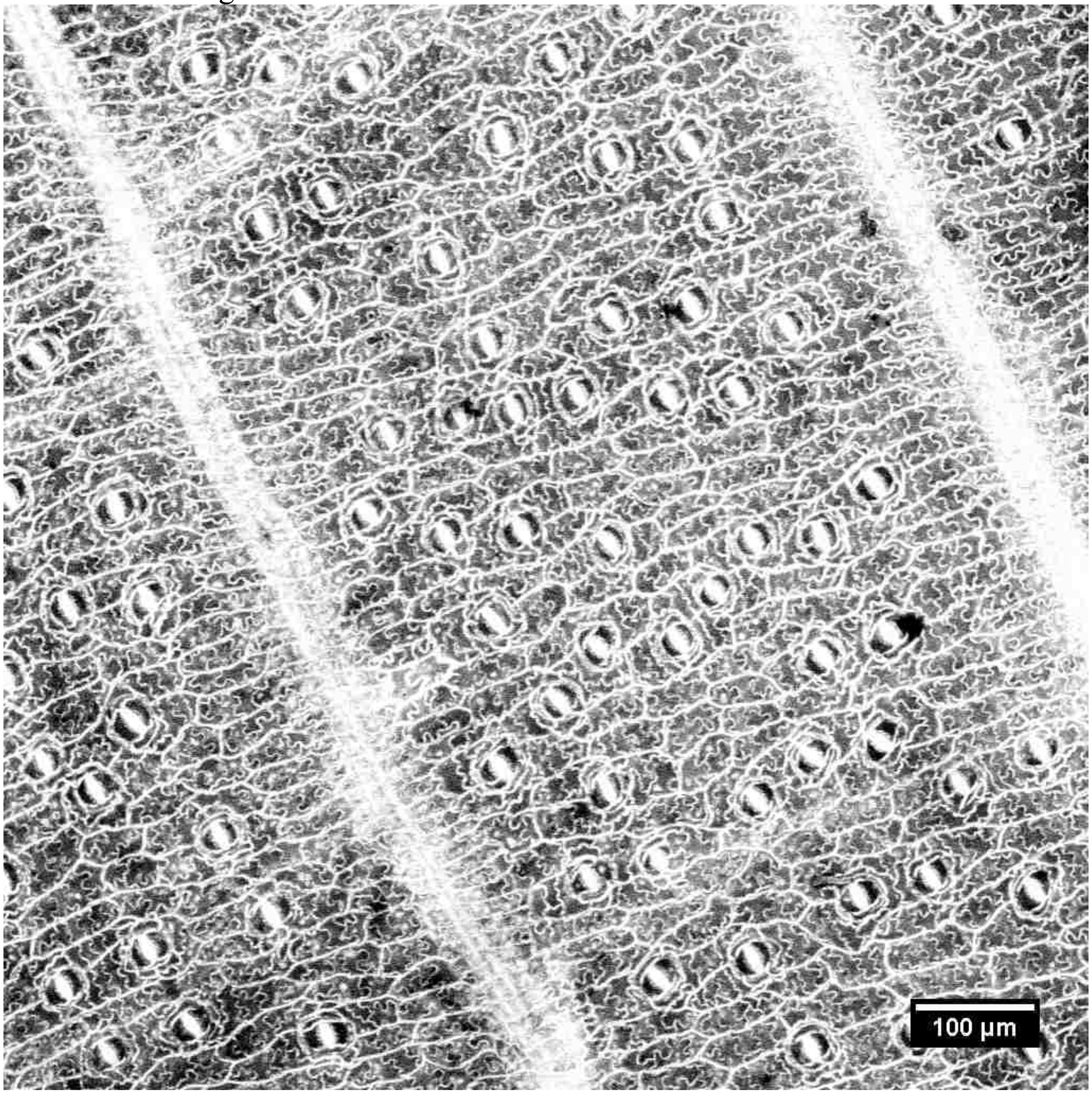
Appendix 10. Light response curves for 39 individuals sampled in 2014. Red lines represent model fits based on the nonrectangular hyperbola, while the blue lines represent model fits based on the rectangular hyperbola. Models were fitted using least squares regression (see *Methods*). Panels with green figure margins are *Heliconia*, those with black margins are *Calathea*.



Appendix 11. Adaxial leaf surface of an adult *Calathea crotalifera* under closed canopy. The image was captured with a confocal microscope, and stomatal size and density were estimated with ImageJ.



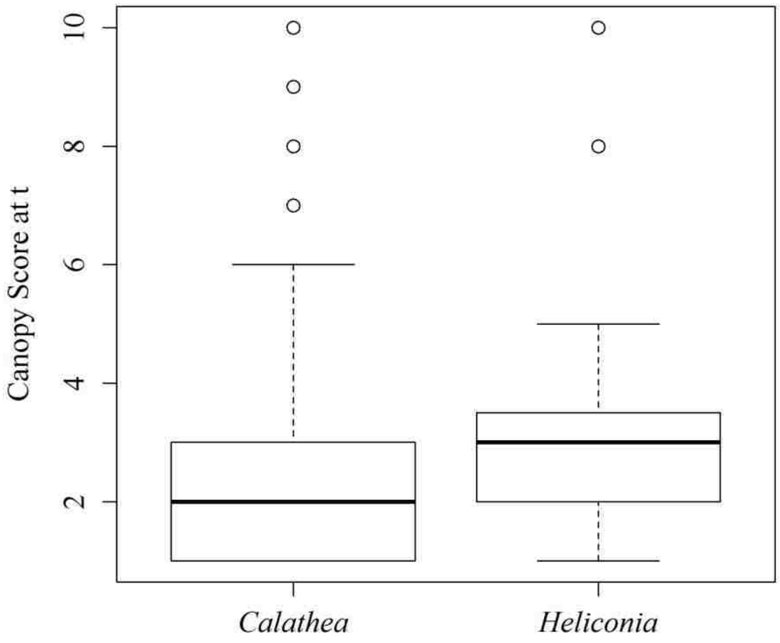
Appendix 12. Adaxial leaf surface of a juvenile *Heliconia tortuosa* under closed canopy. The image was captured using a confocal microscope, and stomatal size and density were estimated with ImageJ.



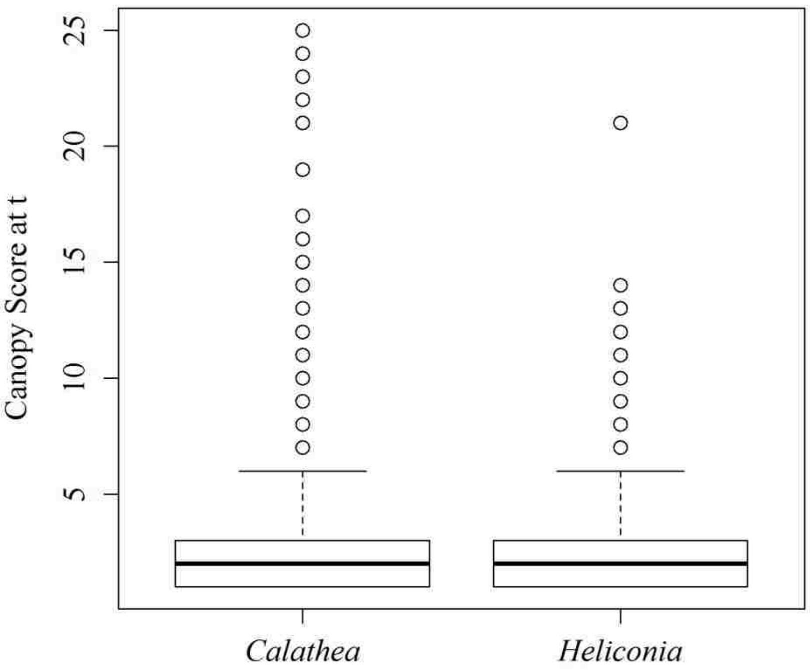
Appendix 13. *Heliconia tortuosa* in a study plot at Las Cruces Biological Station, San Vito, Costa Rica. Photo credit: Theresa Bersin.

Appendix 14. *Calathera crotalifera* in a study plot at Las Cruces Biological Station, San Vito, Costa Rica. Pictured with field assistant, Jose Delgado.

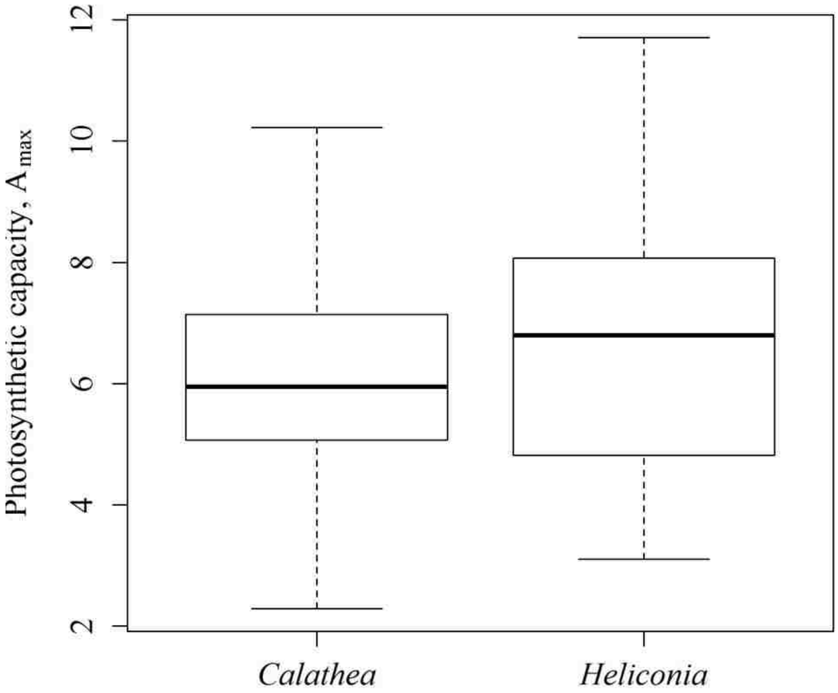
Appendix 15. Canopy openness scores for *Calathea* and *Heliconia* whose photosynthetic rates were estimated and used to model growth. The canopy scores were significantly different from one another (Wilcoxon p=0.01) but both species occurred in very shady environments (low canopy scores indicate low light).



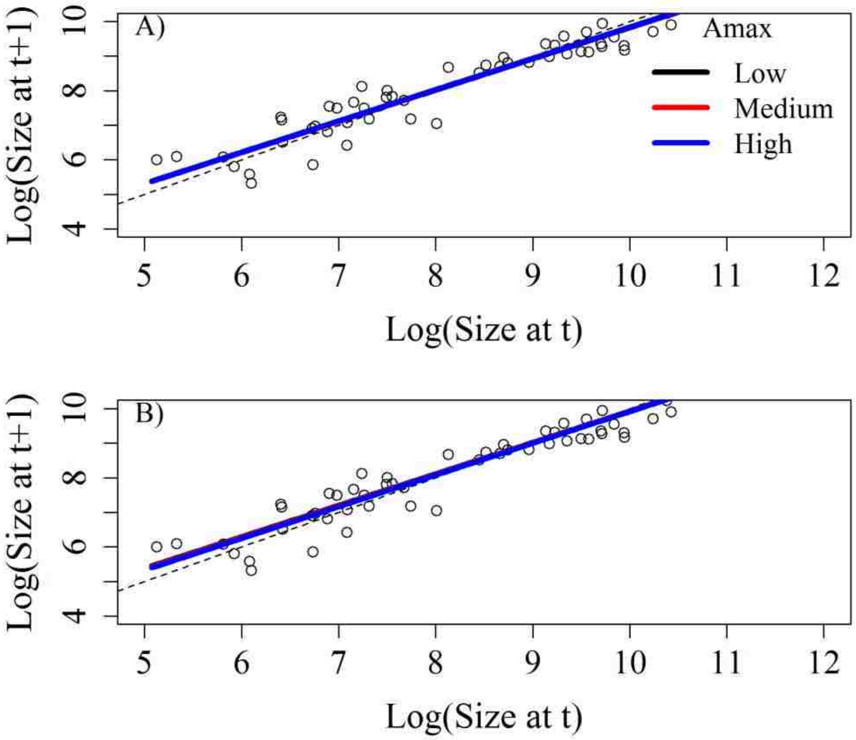
Appendix 16. Canopy openness scores for *Calathea* and *Heliconia* used in our models of survival and reproduction. The canopy scores were significantly different from one another (Wilcoxon p=0.008) but both species occurred in very shady environments (low canopy scores indicate low light).



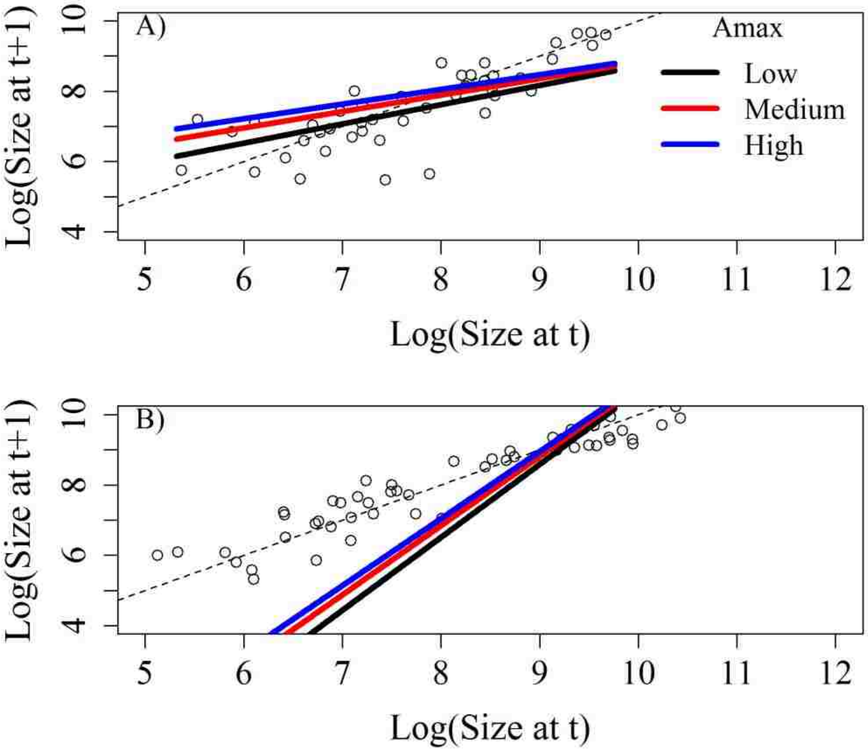
Appendix 17. Photosynthetic capacity (A_{max}) for *Calathea* and *Heliconia*. The species did not differ significantly from one another ($p>0.05$).



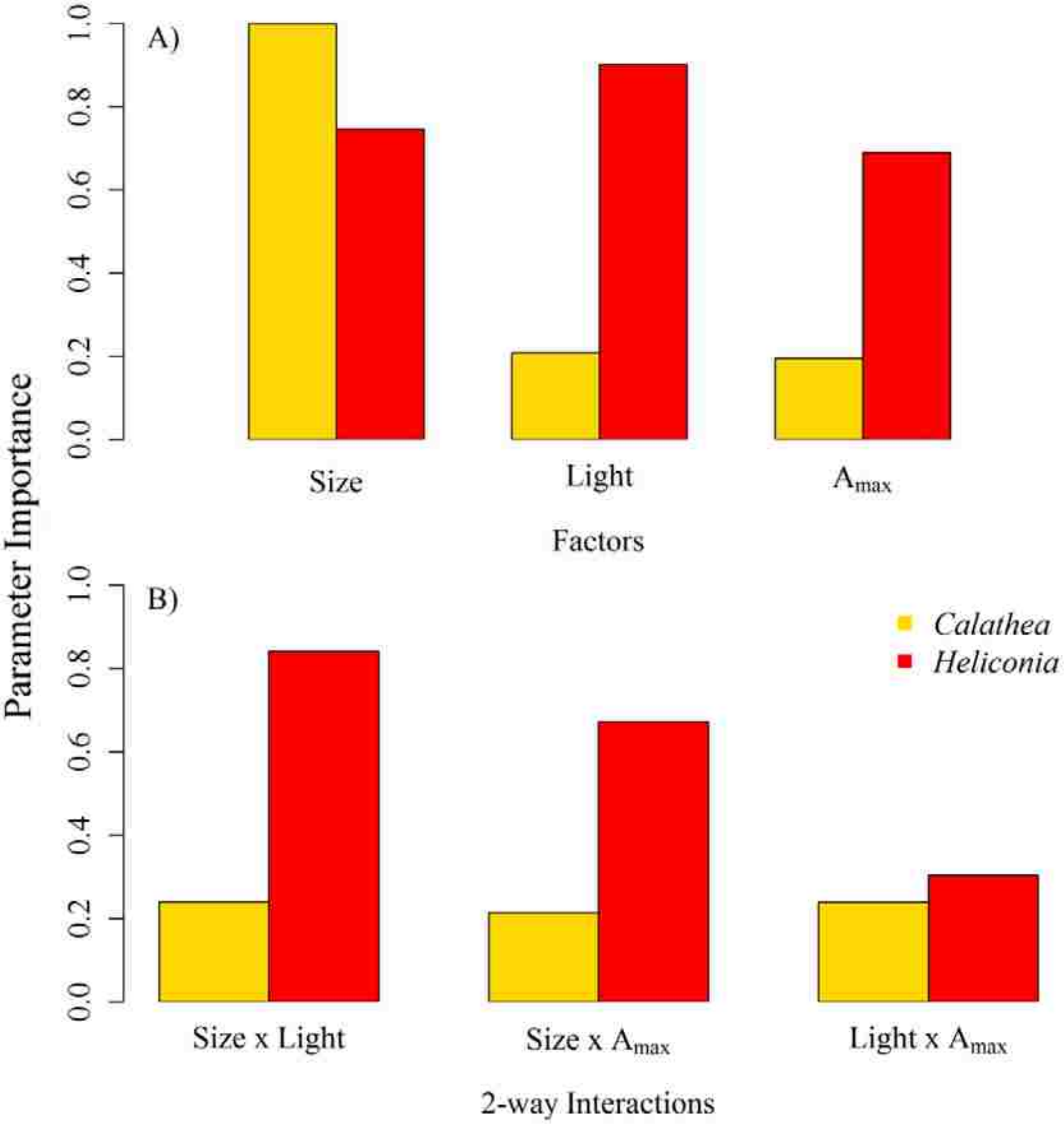
Appendix 18. Future size modelled as a function of current size, light, and A_{max} for *Calathea crotalifera* with a canopy score of A) 1 and B) 10. Colored lines represent values of the A_{max}. Open circles represent data and dashed lines represent identity line. Colored lines below the identity line are diminishing in size, while those above the dashed line are growing.



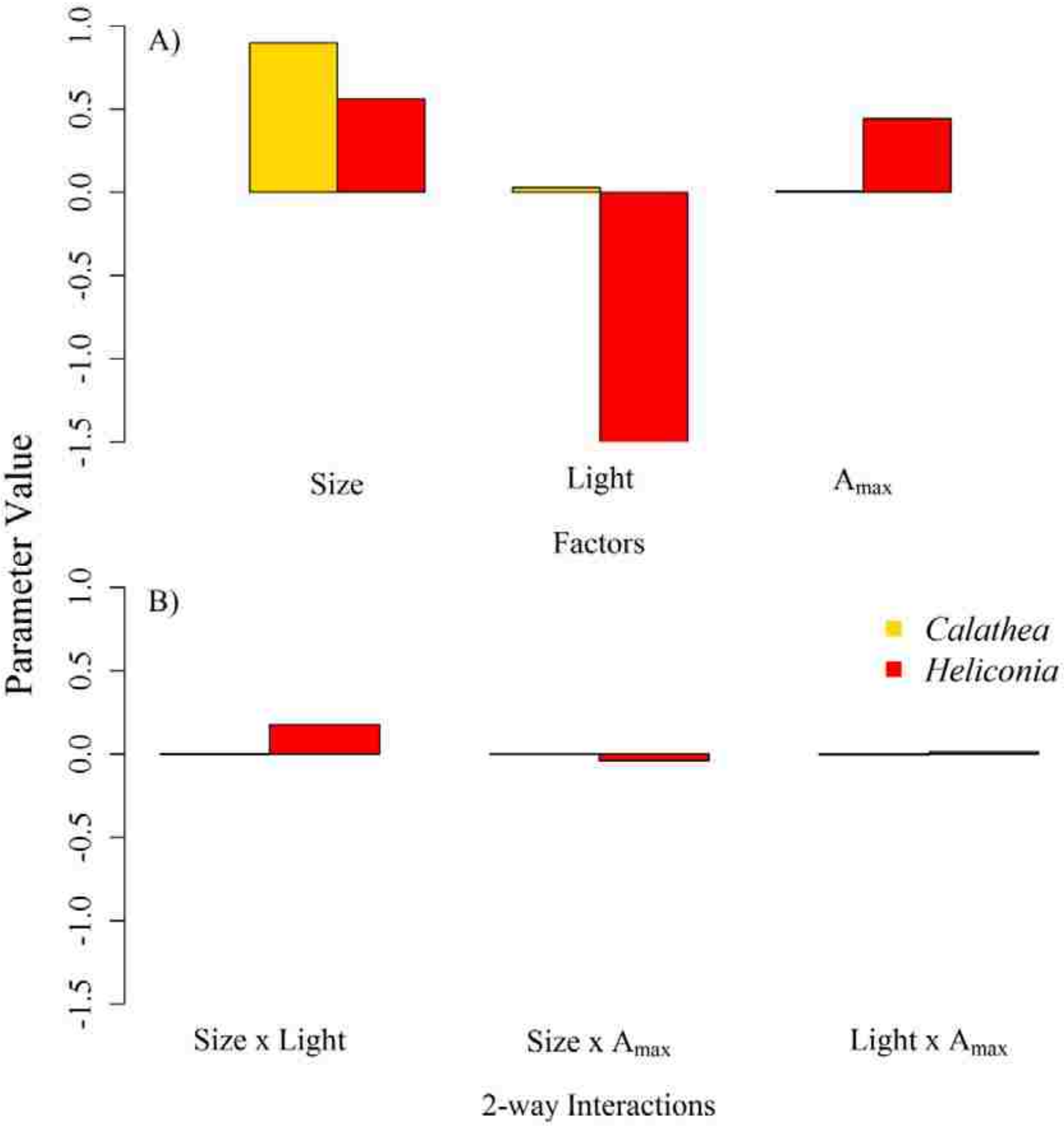
Appendix 19. Future size modelled as a function of current size, light, and A_{max} for *Heliconia tortuosa* with a canopy score of A) 1 and B) 10. Colored lines represent values of the A_{max}. Open circles represent data and dashed lines represent identity line. Colored lines below the identity line are diminishing in size, while those above the dashed line are growing.



Appendix 20. Parameter importance of A) factors and B) two-way interactions between factors, from the “average model” of growth, as determined by Bayesian model averaging. Greater values indicate a variable that is a more important determinant of future size, and importance ranges from zero to one.



Appendix 21. Parameter values from the "average model" of growth, as determined by Bayesian model averaging. Greater values indicate a stronger effect on future size. A) Values of all single factors B) values of all two-way interactions. Values can be found in Table 5.2.



Appendix 22. Growth models with the lowest AIC values for *Calathea* and *Heliconia*. The standard deviations from these models were used in the Integral Projection Models (Table 5.2).

Species	**Model**
Calathea	$Size_{t+1} = x_0 + x_1 Canopy\ Openness_t$
Heliconia	$Size_{t+1} = x_0 + x_1 Size_t + x_2 Canopy\ Openness_t + x_3 A_{maxt} + x_5 Size_t\ Canopy\ Openness_t + x_6 Size_t A_{maxt} + x_8 Canopy\ Openness_t A_{maxt}$