

# Early life conditions and precipitation influence the performance of widespread understorey herbs in variable light environments

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## Summary

1. The understorey of tropical forests is heterogeneous across time, and plants that inhabit this layer may exhibit adaptations (e.g. trait plasticity) that enable them to exploit this variability to their advantage. We tested the hypothesis that two widespread understorey herbs would perform equally well in a variable as in a constant environment, using a 2-year shade-house experiment.

2. We measured demographic traits (growth and survival), a physiological trait (maximum photosynthetic capacity), and life-history traits (leaf life span and biomass allocation) of *Heliconia tortuosa* and *Calathea crotalifera*. We investigated how these traits were affected by light availability at the seedling stage, precipitation, and whether individuals experienced a constant or variable light environment.

3. Whether or not a variable environment was favourable for plants depended upon precipitation and the environment in which individuals started life. At low precipitation, plants in a variable light environment grew more than those in a constant environment, but only when individuals had lived as seedlings in low light. At high precipitation, plants in a constant environment grew more than those in a variable environment, regardless of early conditions. Survival was lower in a variable environment at low precipitation, and more so at high precipitation. Photosynthetic capacity was lower for individuals in a variable environment than in a constant environment when they had lived in high light as seedlings.

4. *Calathea* grew faster and survived more poorly than *Heliconia*, independently of the treatments. *Calathea* grew more at high than low precipitation while *Heliconia* grew more at low than high precipitation. Leaf life span and biomass allocation did not differ among treatments, although *Calathea* had a significantly greater proportion of its biomass above-ground vs. that of *Heliconia*.

5. **Synthesis.** Environmental variability had a neutral or positive effect on biomass allocation, photosynthetic capacity, and leaf life span for these species. Survival was the only trait that was always lower in a variable environment. The effect of environmental variability was dependent on early life conditions as well as precipitation, suggesting that generalist species may experience high fitness as forest environments become more variable by maintaining high growth at the expense of survival.

**Key-words:** *Calathea*, *Heliconia*, photosynthetic capacity, plant development and life-history traits, plasticity, relative growth rate, survival

## Introduction

Light in tropical rain forests is a spatially heterogeneous and temporally variable resource, the availability of which fluctuates with the opening and closing of gaps in the tree canopy (Chazdon & Fetcher 1984). The presence of canopy gaps also influences soil moisture in the surrounding microhabitat (Camargo & Kapos 1995; Denslow, Ellison & Sanford

1998); gaps have higher soil moisture and temperature than the adjacent forest understorey (Denslow, Ellison & Sanford 1998). The availability of light and moisture has been shown to influence demographic, morphological, physiological and functional traits of tropical plants (Kitajima, Mulkey & Wright 1997; Valladares *et al.* 2000; Chazdon, Brenes & Alvarado 2005). Therefore, the need to capture and efficiently use light and moisture as they fluctuate should promote high trait plasticity for plants restricted to the forest understorey.

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In the forest understorey, species vary in their degree of shade tolerance and in the manner in which they respond to environmental variability. Shade-tolerant species are those that require little light to survive (Valladares & Niinemets 2008), while shade-intolerant species perform best in bright environments. Shade-intolerant gap species have been found to have greater plasticity in leaf production and photosynthetic capacity than shade-tolerant species (Lei & Lechowicz 1990; Kubiske & Pregitzer 1996). In contrast, shade-tolerant species have been found to be more plastic than shade-intolerant species in specific leaf mass, leaf display and leaf nitrogen concentration (Lei & Lechowicz 1990; Kubiske & Pregitzer 1996). The majority of rain forest tree species have intermediate shade requirements (hereafter, moderately shade-tolerant), while few species exist at the extremes (Wright *et al.* 2003). For these generalist species, environmental variability should have a less detrimental effect on their performance than for either shade-tolerant or shade-intolerant species with more restricted ranges. Maintaining high fitness as the environment changes may be achieved by high trait plasticity, allowing generalists to fully exploit ephemerally abundant resources while also having the capability to persist and thrive in more commonly occurring low-resource conditions.

Acclimation to changing light levels may be achieved via changes (i) in whole plant structure, such as leaf life span, biomass allocation and self-shading, (ii) leaf morphology, such as regulation of stomatal density, mesophyll layer thickness and chlorophyll content, and (iii) leaf biochemistry, such as functioning of proteins within the photosynthetic apparatus (Demmig-Adams & Adams 1992; Valladares & Niinemets 2008). Photosynthetic capacity, chlorophyll content and stomatal conductance, have also been shown to exhibit plasticity in response to changing light conditions (Valladares *et al.* 2002; Walters 2005; Portes *et al.* 2010).

When resources are abundant, previous studies of tropical tree seedlings have shown that the ability to acclimate to unexpected future conditions is greater than when resources are limited (Valladares *et al.* 2002). While the ability to acclimate quickly may be beneficial on short time-scales, the long-term effects could be negative, if the positive effects of acclimating are outweighed by the accompanying high costs. For example, survival could be reduced when environments shift from resource-rich to resource-poor when organisms use resources to make machinery that is more suited to the new environment, but is more costly to produce and maintain (Chazdon *et al.* 1996).

The primary objective of this study was to test the effects of environmental variability on the demographic performance and trait responses of two moderately shade-tolerant generalists. We measured demographic performance (growth and survival), a physiological trait (photosynthetic capacity) and life-history traits (leaf life span and biomass allocation). These physiological and life-history traits were selected because previous studies have determined that they exhibit plasticity (Huante & Rincón 1998; Valladares *et al.* 2000), and because they can directly influence growth and survival (Kitajima 1994; Huante & Rincón 1998). Increasing photosynthetic

capacity should increase potential carbon gain when respiration is held constant, following the light response curve equation model (Thornley 1976), which may increase fitness by increasing growth rates. Similarly, when light is limiting, increasing allocation to above-ground biomass (leaves, stems, etc.) increases light capture, while increasing allocation to below-ground biomass increases absorption of moisture and nutrients when they become limiting (Alvarez-Buylla & Martinez Ramos 1992). Lastly, understorey species have been shown to increase the life span of their leaves when light becomes limiting (Kitajima *et al.* 2012). Therefore, longer lived leaves should increase fitness in low-light environments.

We sought to answer four research questions: (i) Are demographic performance, physiological traits and life history traits, influenced by the availability of light? (ii) If light does influence these response variables, do early life conditions influence future performance? Here, we are asking whether the responses differ when individuals move from shaded (resource-poor environments) to bright (resource-rich environments) environments vs. the opposite (resource-rich to resource-poor). (iii) Does precipitation influence the manner in which these species respond to variable light environments? We tested for an effect of precipitation because canopy gaps are known to directly influence temperature and soil moisture availability in rain forests (Denslow 1987), and few experimental studies (Sack & Grubb 2002; Sack 2004) have tested for interactions among precipitation and light availability, on plant performance and trait plasticity. Lastly, (iv) Do differences in morphology alter the manner in which two co-occurring herbs respond to environmental variability?

The study species are two understorey, perennial herbs, *Calathea crotalifera* and *Heliconia tortuosa*. Due to their wide distribution in the rain forest, these species may be considered as moderately shade-tolerant habitat generalists. We tested these two species because, although they are functionally similar and occur in similar environments, they differ in their morphology in ways that are likely to result in subtle differences in their ability to tolerate environmental variability. Both species reproduce sexually and asexually via clonal shoots, but *Calathea* ramets branch close to the ground, resulting in lower self-shading than occurs in *Heliconia* (A. Westerband, personal observation). Furthermore, *Calathea* leaves possess a pulvinus, which is a thickening at the base that regulates light capture throughout the day. Thus, *Calathea* may be less responsive to environmental variability than *Heliconia* due to its greater ability to regulate light capture. A previous study concluded that *Calathea* was more shade-tolerant than *Heliconia* (Westerband & Horvitz 2015), because it survived better in low light and required less light to grow than *Heliconia*.

We tested three hypotheses with regard to the effects of environmental variability on demographic performance: (i) *Calathea* will grow and survive equally well in constant as in variable environments; (ii) *Heliconia* will grow more and survive better in high light than in low light; (iii) Precipitation will have similar effects on the growth and survival of both species in variable environments. We tested three hypotheses

with regard to the effects of environmental variability on physiological and life-history traits: (i) For *Calathea*, photosynthetic capacity, biomass allocation and leaf life span will respond similarly in constant as in variable environments; (ii) For *Heliconia*, mean photosynthetic capacity and leaf life span will be higher for plants that move from high to low light than for those that move from low to high light; (iii) Precipitation will have similar effects on the physiological and life-history traits of both species in variable environments. If we found these species to be negatively influenced by environmental variability, it would suggest a low capacity to acclimate to changes in the environment, unexpected for widely distributed species.

## Materials and methods

### STUDY SPECIES

*Heliconia tortuosa* (Order Zingiberales: Family Heliconiaceae) is a perennial, herbaceous understorey monocot that exhibits rhizomatous growth, with ramets 1–3 m tall. *Heliconia* reproduces sexually via seeds and asexually via clonal shoots (Appendix S1, Supporting Information). *Calathea crotalifera* (Order Zingiberales: Family Marantaceae) is a perennial, herbaceous understorey monocot that is also rhizomatous, with ramets 1–3 m tall (Appendix S2). *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 understorey plants at our study site, they appear to be moderately shade-tolerant (they occupy a large range of light environments, including both large gaps and closed canopy understorey), and they reach large enough sizes to compete with tree saplings and other herbs for light, making them likely contributors to 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 a mid-elevation premontane tropical rain forest, and receives approximately 4 m of annual rainfall. There is a slight reduction in precipitation from December to April (but no pronounced dry season) and mean diurnal temperature over the year ranges from 13 °C to 26 °C.

Soils at the field site are volcanic in origin and moderately acidic (mean pH of 5.6 ± 0.26) (Sandoval & Mata 2014). Soil types include Inceptisols, Andisols and Ultisols. The soil texture ranges from sandy loam to loamy sand. To obtain soil for our shadehouse experiments, we dug a 4 × 4 m soil pit at a depth of c. 10 cm in selectively logged forest. We include soil data for six replicate sites ≤ 1 km from this pit (Appendix S3). The soil excavated from this pit was sieved to remove large debris and mixed with an organic fertilizer produced at the field station.

### SEEDLING SAMPLING DESIGN

In July 2013, 1186 seedlings (614 *Calathea* and 572 *Heliconia*) were collected over a 4-week period and transplanted into a shadehouse immediately. We used seedlings rather than collect and germinate

seeds because previous studies have found evidence of dormancy in *Heliconia* (Bruna 1999). By collecting seedlings of similar size, we limited the variability due to differences in light availability during the earliest life stages. We only collected seedlings that had the seed-coat still attached to the radicle, with one stem and less than four leaves, so that their sizes were similarly distributed. We do not have data on the size distributions of the seedlings at the time of collection, however, the size distributions at the onset of the experiment (60 days after seedlings were collected) can be found in Appendix S4. These results reflect how rapidly individuals grew within the shadehouse. The median sizes were 15.7 and 11.7 cm<sup>2</sup> for *Calathea* and *Heliconia* respectively. Plants were transferred to 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

Our experiment was conducted in a shadehouse, a structure that is more commonly used in the tropics than greenhouses, because shadehouses maintain ambient temperatures using shade cloth, rather than glass. The shadehouse is not an experimental unit, rather it is an architectural structure akin to a greenhouse (approximate dimensions of 15 m × 10 m × 10 m). Within the shadehouse, we conducted our experiment as a split-plot design, where light at the seedling stage was fixed at either low or high light (factor 1, two levels) and plants in each light treatment were randomly assigned to high or low precipitation (factor 2, two levels) and to a variable or constant light environment (factor 3, two levels) (experimental design and sample sizes in Table 1). Thus, the three factors, each with two levels, resulted in a total of eight treatment groups. Because this experiment was conducted using a split-plot design, there is only one replicate per light treatment in each block. 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 traits (growth and survival) and each of the physiological and life-history traits (leaf life span, 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 three times during the course of the 2-year experiment (Appendix S5). We haphazardly shifted the location of individuals within the treatments every 2 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 shade cloth to simulate high-light and low-light forest environments, respectively. The maximum observed PAR in the high-light treatment corresponds to 7% canopy openness (A. Westerband, unpublished data), and only 5% of individuals of our study species in natural populations at our site are found in spots with higher openness than this level. The maximum observed PAR in the low-light treatment corresponded to 2% openness and half

**Table 1.** Experimental design. N represents sample size at onset of experiment. There is a slight reduction in precipitation from December to April, therefore we denote this period as the dry season, although it is not pronounced (see Materials and methods)

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

\*Denotes a change in the treatment after the first year (see Materials and methods).

of the individuals of our study species in natural populations at our site are found in spots this shady or shadier. Thus, the light levels in our experiment mimic the range of conditions encountered by our study species in natural populations. Individuals assigned to the variable environment treatment were switched between light treatments every 6 months. We switched plants between light treatments once every 6 months to reflect conditions that might be expected in the field. The amount of light in the understorey can indeed change rapidly. In a separate earlier field experiment, one of us (CCH) measured changes in the availability of light in the understorey over a 2-year period at two tropical wet forest sites. Within 7 months, the mean light at the study points that were initially chosen to be high, medium and low light declined by 24%, 25% and 21%, respectively, in one of the forests and by 55%, 32% and 19% in the other forest. By the end of the experiment, 24 months, it was seen to be 17%, 20% and 23% of initial light, respectively, at the first forest and 18%, 20% and 17% at the second forest (C. Horvitz, unpublished data). The quantity of light was estimated by indirect site factor, which is highly correlated with PAR, from hemispherical fish-eye canopy photographs (Whitmore *et al.* 1993). Our study differs from earlier greenhouse studies that simulate environmental change by switching plants once (between light environments) throughout the experiment, are typically conducted during the seedling stage, and are primarily focused on trees. In contrast, in this study, we continually changed the environment and tracked responses from the seedling stage to the pre-reproductive adult stage using understorey herbs.

#### PRECIPITATION TREATMENT

We studied the interactive effects of light and precipitation because gaps in the tree canopy have been shown to influence moisture availability (Denslow 1987; Denslow, Ellison & Sanford 1998), and both light and moisture are known to influence the vital rates of tropical plants (Kitajima, Mulkey & Wright 1997; Valladares *et al.* 2000; Chazdon, Brenes & Alvarado 2005). Our aim was to induce drought stress by inducing mid-day wilting and we achieved this effect by manipulating precipitation levels. Precipitation was manipulated for plants in the low precipitation treatment by excluding natural rainfall using clear plastic sheeting placed below the shade cloth 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 to two times a week. This change occurred after 6 months and 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 and maintain mid-day wilting varied with plant size. We did not measure soil moisture in our pots, thus our precipitation treatments do not describe soil water availability quantitatively, but describe levels of watering. 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 subjected to different environmental conditions, we measured PAR, relative humidity and ambient temperature in all treatments during the summer of 2014. In July, four quantum sensors (Apogee Instruments, Inc., Logan, UT, USA) attached to a Campbell data logger (Campbell Scientific, Inc., Logan, UT, USA) were installed in the low-light treatment for 10 days and then switched to the high-light treatment 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 low light, where they remained for 27 days, with the exception of the sensor in the low-light, high-precipitation treatment, which only logged 5 days after switching because of battery failure. Temperature, relative humidity, and PAR for each treatment are found in Table 2 and described in Results. We tested for differences between treatments using ANOVA. We tested for pairwise differences in the distributions of PAR between treatments using two-sample Kolmogorov–Smirnov tests due to the nonparametric distribution of these values.

#### 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 & 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, 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, above-ground tissue at each census. Therefore, individuals with green stems but no leaves were considered alive, although they had size zero at the time



**Table 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) $\pm$ SD [range]	Mean relative humidity (%) $\pm$ SD [range]	Max PAR ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )
1	High	No	Low	20.8 $\pm$ 2.4 [16.5–33]	98.1 $\pm$ 6.6 [56–104.5]	684
2	High	Yes	Low	20.6 $\pm$ 2 [16.5–28]	99.5 $\pm$ 5.0 [69.5–105.5]	220
3	High	No	High	20.5 $\pm$ 2.5 [16.5–32.5]	99.6 $\pm$ 6.4 [62.5–105.5]	511
4	High	Yes	High	20.4 $\pm$ 2.2 [16.5–29.5]	100.1 $\pm$ 5.8 [16.5–29.5]	405
5	Low	No	Low	20.6 $\pm$ 2 [16.5–28]	99.5 $\pm$ 5.0 [69.5–105.5]	220
6	Low	Yes	Low	20.8 $\pm$ 2.4 [16.5–33]	98.1 $\pm$ 6.6 [56–104.5]	684
7	Low	No	High	20.4 $\pm$ 2.2 [16.5–29.5]	100.1 $\pm$ 5.8 [16.5–29.5]	405
8	Low	Yes	High	20.5 $\pm$ 2.5 [16.5–32.5]	99.6 $\pm$ 6.4 [62.5–105.5]	511

of census. During the experiment, only one individual reached reproductive maturity and produced an inflorescence.

#### PHOTOSYNTHETIC PERFORMANCE AND LEAF LIFE SPAN

We estimated maximum photosynthetic capacity ( $A_{\text{max}}$ ) in 363 randomly chosen individuals (165 *Calathea* and 198 *Heliconia*) using a LiCOR 6400 (Li-Cor, Lincoln, NE, USA) in 2014 and 2015. Across all photosynthesis measurements,  $\text{CO}_2$  concentration was  $400 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , leaf temperature was  $25 \pm 2^\circ\text{C}$  and average relative humidity was  $58 \pm 8\%$ . Only mature leaves were used, and were selected to have little or no evidence of senescence or herbivory, and maximum exposure to sunlight compared to other leaves within the individual. This was done to minimize variability within individuals following Cornelissen *et al.* (2003). Increasing  $A_{\text{max}}$  should increase potential carbon gain if respiration and efficiency remain constant (Percy *et al.* 1987), and should thus positively influence plant performance.  $A_{\text{max}}$  was measured every 6 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*). For each individual, we counted the initial number of leaves, the number of leaves produced, and the number of leaves that died monthly, for up to 14 months. Leaf life span was calculated as the inverse of the rate of leaf mortality (Wright, Westoby & Reich 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 below-ground biomass was measured for 227 individuals. We sampled seven *Calathea* that started in low light, switched between light environments and experienced drought, and 10 *Heliconia* that started in low light, remained in low light and experienced drought. For the other 14 treatment groups, we sampled 15 individuals. Plants were removed from their pots, roots were washed to remove all soil, and plants were dried in an oven ( $70^\circ\text{C}$  for 48 h) before separating above- and below-ground tissues and weighing the tissues on an electronic balance. Above-ground biomass is defined as all living leaves and stems; below-ground biomass includes roots and rhizomes. We then estimated the ratio of above-ground biomass to total biomass.

#### STATISTICAL ANALYSES

To determine the main effects of the 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 was log transformed to achieve normality and was modelled using a generalized linear mixed-effects 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 RGR (dependent variable) using ANOVA and found no significant effect ( $P > 0.05$ ).

To determine the effects of the treatments on leaf life span, 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 life span. We determined that the photosynthetic rates did not deviate significantly from normality using QQ plots (Quinn *et al.* 2002), and therefore used ANOVA to examine differences in photosynthesis among our treatments. We tested effects of environmental variability, initial light environment, precipitation and species.

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

## Results

#### ABIOTIC CONDITIONS

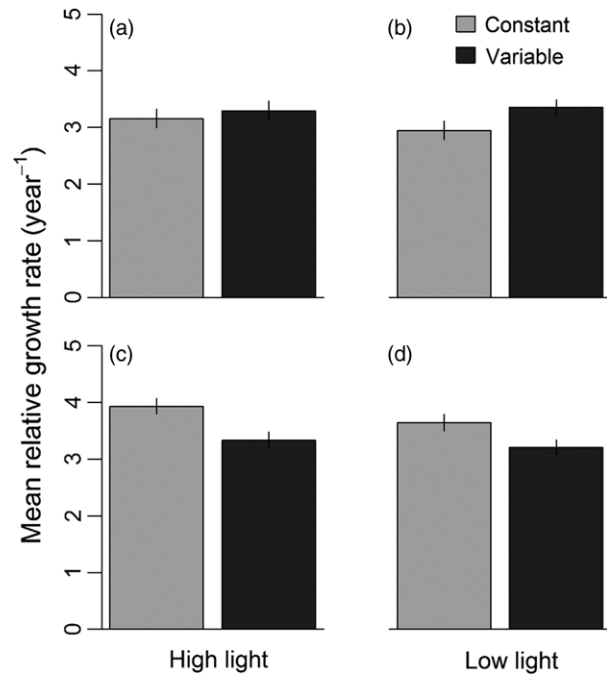
The shade cloth and watering treatments affected the abiotic environment in intentional and unintentional ways. On the high-light side of the shadehouse, humidity was significantly lower in the low-precipitation treatments ( $P < 0.0001$ ) and temperature was significantly greater ( $P < 0.0001$ ). On the low-light side, humidity was significantly lower in the low-precipitation treatments ( $P < 0.0001$ ) and temperature was significantly greater ( $P < 0.0001$ ). The low precipitation treatments had significantly lower PAR values (a more positively skewed distribution) than the high-precipitation treatments on

the high-light side and the low-light side ( $P < 0.0001$  for all four two-way comparisons of PAR sensors). The high-light side had higher PAR than the low-light side in both precipitation treatments ( $P < 0.0001$  for all comparisons). Unexpectedly, the distributions of PAR for the two sensors within each precipitation treatment also differed significantly ( $P < 0.02$ ), although differences between the means within the light treatments were not as large as differences between the means of the high-light vs. low-light side. Because we moved plants within each treatment every 2 weeks, differences within treatments should not confound our results, because the differences between the precipitation treatments and between the light treatments were statistically significant.

#### DEMOGRAPHIC TRAITS

##### No species differences

Mean RGR and survival were significantly influenced by different combinations of the independent variables: species, initial light environment, environmental variability later in life and precipitation. Relative growth rate was significantly higher for individuals exposed to high light as seedlings than for those exposed to low light, and significantly lower for individuals in high than in low precipitation (Table 3, Fig. 1). Under low and high precipitation, individuals that started in high light (Fig. 1a and c) grew more rapidly than those that started in low light (Fig. 1b and d), and the effect was amplified with high precipitation. The effect of being in a variable light environment was significantly influenced by precipitation and initial light environment (a three-way interaction) (Table 3, Fig. 1). In low precipitation (Fig. 1a and b), plants in a variable light environment grew more when individuals were exposed to low light as seedlings (Fig. 1b) but environmental variability had no influence on growth when individuals were exposed to high light as seedlings (Fig. 1a). In high precipitation (Fig. 1c and d), a constant light environment resulted in slightly higher growth whether individuals started in low or high light. Individuals that started in low light had



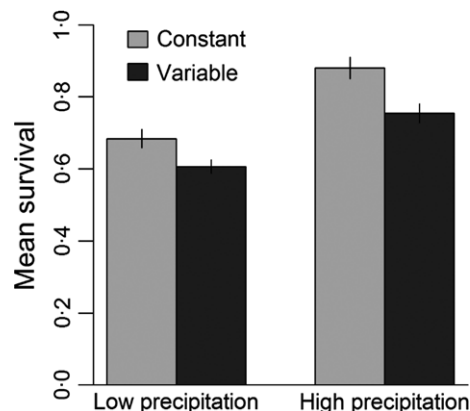
**Fig. 1.** Relative growth rate. The effects of precipitation, initial light environment and environmental variability and their interaction on mean relative growth rate (per year). (a, b) are low precipitation; (c, d) are high precipitation; (a, c) high initial light; and (b, d) are low initial light. 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  $\pm$  1 SE.

significantly lower survival than individuals that started in high light (data not shown). Individuals in the high-precipitation treatment had significantly higher survival than individuals in low precipitation (Table 3, Fig. 2). The effect of environmental variability on survival was significantly influenced by precipitation (a two-way interaction) (Table 3, Fig. 2). 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

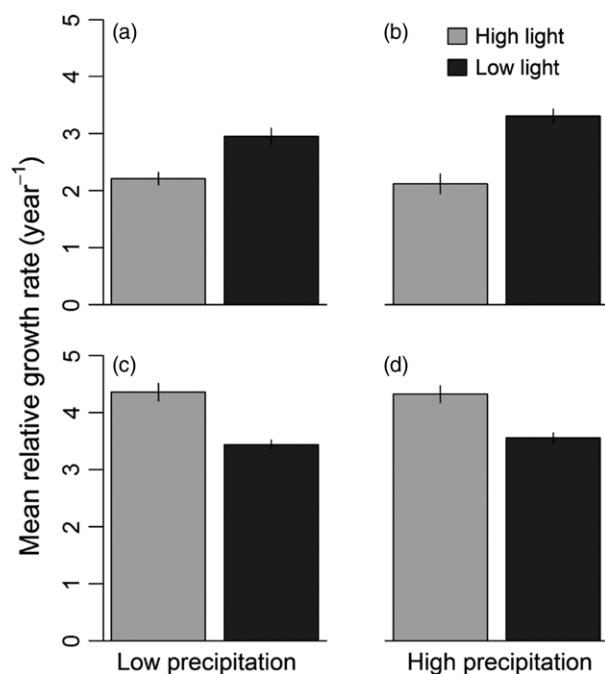
**Table 3.** Effects of species, precipitation, initial light environment and environmental variability on demographic and functional traits for two species, *Calathea crotalifera* and *Heliconia tortuosa*. Of all possible main effects and interactions, only statistically significant effects are shown (no four-way interactions)

	Significant main effects	Significant two-way interactions	Significant three-way interactions
Demographic trait			
Relative growth rate	Initial light*** Precipitation*** Species**	Initial light $\times$ precipitation** Precipitation $\times$ species**	Initial light $\times$ precipitation $\times$ species* Initial light $\times$ precipitation $\times$ variability*
Survival	Initial light*** Precipitation** Species***	Precipitation $\times$ variability**	
Physiological or life-history trait			
Above-ground: total biomass	Species*		
Photosynthetic capacity	Initial light* Precipitation*	Initial light $\times$ variability <sup>†</sup>	

Asterisks indicate significance level: <sup>†</sup> $P < 0.1$ , \* $P < 0.05$ , \*\* $P < 0.001$ , \*\*\* $P < 0.0001$ .



**Fig. 2.** Survival. The effects of precipitation and environmental variability on the probability of survival (on a scale of 0–1). 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  $\pm$  1 SE.



**Fig. 3.** Relative growth rate. The effects of species, precipitation and light and their interaction on the mean relative growth rate (per year) 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  $\pm$  1 SE.

the effect was greater for high precipitation than for low precipitation (Table 3, Fig. 2).

#### Species differences

Relative growth rate was significantly higher in *Heliconia* than *Calathea* (Table 3, Fig. 3). There was a significant difference between the species in terms of the effect of precipitation on RGR; *Calathea* grew more in low precipitation than high precipitation while *Heliconia* grew slightly more

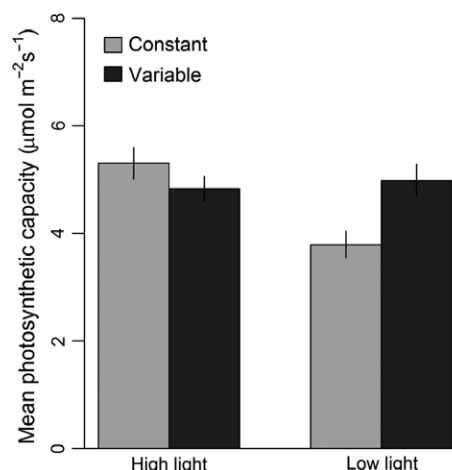
in high than low precipitation (Table 3, Fig. 3). Initial light conditions also influenced the interaction between precipitation and species (a three-way interaction, Table 3). For *Calathea*, plants exposed to high light as seedlings grew more than those exposed to low light, but the effect of initial light availability was significantly greater for plants in low precipitation than in high precipitation (Fig. 3a and b). For *Heliconia*, plants exposed to high light grew more than those exposed to low light and were not strongly influenced by precipitation (Fig. 3c and d). Survival was significantly higher in *Heliconia* than *Calathea* (data not shown), and there were no two- or three-way interactions that included species.

#### PHYSIOLOGICAL AND LIFE-HISTORY TRAITS

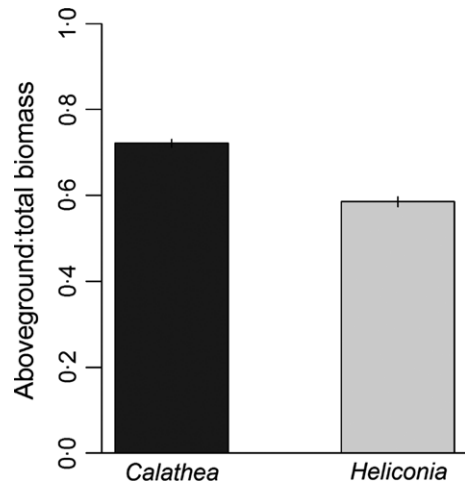
##### No species differences

Leaf life span did not differ significantly due to the treatments and did not differ by species (data not shown). Leaf life span 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 mean life span for *Calathea* was 1.8 months ( $\pm$  0.08) and the mean for *Heliconia* was 1.6 ( $\pm$  0.05) months.

Photosynthetic capacity was significantly higher for individuals that started in high light than those that started in low light (Table 3, Fig. 4). Photosynthetic capacity was also significantly lower for individuals in low precipitation than those in high precipitation (data not shown). There was a marginally significant interaction between environmental variability and initial light environment (Table 3, Fig. 4). 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 light environment than a constant light environment (Table 3, Fig. 4).



**Fig. 4.** Photosynthetic capacity. The effects of initial light environment and environmental variability and their interaction on photosynthetic capacity ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). There were no significant differences between the species (*Calathea* and *Heliconia*), therefore they were combined. Bars represent mean photosynthetic capacity  $\pm$  1 SE.



**Fig. 5.** Biomass. The ratio of above-ground to total biomass for *Calathea* and *Heliconia*. None of the treatments had any statistically significant effect on this ratio. Bars represent mean biomass  $\pm$  1 SE.

### Species differences

Above-ground 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 above-ground biomass than *Heliconia* (Table 3, Fig. 5).

## Discussion

### DEMOGRAPHIC TRAITS

We tested whether two widely distributed species that inhabit temporally variable environments would perform equally well in an experimentally varied environment vs. a constant environment. One underlying assumption is that species that inhabit heterogeneous and variable environments should achieve high fitness by having highly plastic traits (Alpert & Simms 2002), where plasticity is defined as the ability to respond to a change in the environment. Thus, we did not test whether traits were plastic or not, and instead measured trait responses and fitness components in variable vs. constant environments. We also sought to understand the persistent effects of acclimation to resource availability at early life stages on performance later in life, and to ascertain how light and precipitation interact to influence performance.

For both species, plants exposed to high light as seedlings grew more than plants exposed to low light, supporting our hypothesis that high light early in life improves performance in a variable light environment. Plants moved from high to low light grew more than those that remained in constant low light. These results differ from those of Yamashita, Koike & Ishida (2002) who found that when pioneer tree seedlings were moved from high to low light, they grew less than those in constant low light. Discrepancies between these studies are likely due to differences in life history (pioneer trees vs. understorey herbs). Additionally, Martinez-Garza & Howe (2005) found that leaf traits of non-pioneer tropical trees

changed with ontogeny in response to current environmental conditions, and reflected expected future conditions. Because herbs never reach the tree canopy, early life conditions should more strongly influence future performance than expected future conditions (which are highly similar for herbs), and explains why individuals exposed to high light early in life had such high growth rates, even when light availability diminished.

Previous studies have found that interactions between light and moisture affect RGRs and allocation strategies of herbs and tree seedlings (Canham *et al.* 1996; Baruch, Pattison & Goldstein 2000). We simulated drought-like conditions by manipulating precipitation levels over a long period of time, and found that *Calathea* exposed to high light as seedlings grew more than those exposed to low light (whether they moved between light environments or not) but the effect was greater for plants in low than high precipitation. This result demonstrates that early life acclimation to high light is most beneficial for plant growth under low precipitation. If low precipitation is stressful for *Calathea*, high light early in life may have ameliorated any negative effects of moving to low light, and produced an overcompensation in growth. Overcompensation would remove treatment effects due to environmental variability. However, because *Calathea* grew more in low than high precipitation, low precipitation is not likely to be stressful (stress is defined as a decrease in acclimation potential or a condition that decreases carbon gain, following Muraoka *et al.* 2002). In contrast, *Heliconia* exposed to high light as seedlings grew more than those exposed to shade, and the effect was not influenced by precipitation. Even though *Heliconia* grew most 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 under high and low precipitation. Thus, it is possible that when plants acclimated to high light, they produced carbohydrate reserves that allowed them to persist through stressful conditions later in life. Sack & Grubb (2002) found no interaction between moisture and irradiance in seedlings of three woody species.

When precipitation was low, individuals in variable environments grew more when exposed to low light as seedlings but grew equally well when exposed to high light as seedlings. When precipitation was high, environmental variability always decreased growth. Thus, our results refute our hypothesis that these species would perform equally well in variable vs. constant environments, and refutes our hypothesis that early life acclimation to high light would increase performance in a variable light environment, and this was true for both precipitation levels. We offer three potential explanations. First, plants exposed to high light and high precipitation may have grown more below-ground biomass early in the experiment. Because we only measured biomass at the end of the study, we cannot address any treatment effect on biomass allocation that would have occurred during early life stages. Second, for plants in high precipitation, photosynthetic acclimation to high light may have induced high maintenance costs. Future environmental variability would then be stressful for plants acclimated to high light because periods of



darkness might have resulted in insufficient carbon gains to offset respiratory costs (Chazdon *et al.* 1996). Third, plants acclimated to high light may store carbohydrates, as is common in other perennials (Landa *et al.* 1992). Storage would diminish growth initially, while promoting growth once light becomes scarce, buffering growth during stressful periods. Determining which of these potential explanations is correct would have required destructive excavation of individuals over the course of the experiment (which would have required much larger initial sample sizes).

Survival was higher for *Heliconia* than for *Calathea*, but high light early in life decreased survival, which may be evidence that metabolic costs associated with acclimation to high light reduced performance later in life. Increasing precipitation increased survival, which supports our hypothesis, but environmental variability decreased survival, and more so when precipitation was high. This was unexpected, given our prediction that these widely occurring species would perform equally well in variable environments and more so when moisture was abundant. These results instead suggest that environmental variability may be stressful for understory species and high precipitation amplifies its negative effects on survival. 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 their environment, but survival is less plastic than growth. Individuals that remained in a constant environment survived more but grew equally well (unless precipitation was high) compared to those in a variable environment. Because we did not record exactly when individuals died, we cannot account for potential treatment effects on survival at the onset of the experiment.

#### PHYSIOLOGICAL AND LIFE-HISTORY TRAITS

Leaf longevity correlates negatively with resource availability. Long-lived leaves tend to have lower photosynthetic rates, be better defended against biotic enemies, and exhibit more resilience to extreme environments than short-lived leaves (Chabot & Hicks 1982; Reich, Walters & Ellsworth 1992). Temporal heterogeneity in light for spring understory herbs in temperate deciduous forests follows a pattern that is quite different from understory herbs in tropical evergreen forests. In the former, there is an annual cycle of leafing out and canopy closure that determines light availability, whereas for understory herbaceous species in evergreen forests, gaps of different sizes can form at any time above them, when branches or trees fall. Furthermore, the duration of these gaps depends on their size; large gaps remain open longer while small gaps close rapidly. Abiotic conditions are known to influence leaf life span. When light becomes limited, many plant species have been shown to produce durable, long-lived leaves (Chabot & Hicks 1982; Valladares *et al.* 2000; Kitajima *et al.* 2012), allowing individuals to recoup the resources invested in leaf construction. Short-lived leaves should have higher photosynthetic rates (or lower construction costs) than long-lived leaves (Chabot & Hicks 1982). In evergreen tropical forests, leaf life span in high light ranges from 2 months to 1 year, while life span for understory

plants (in low light) may be up to 5 years (Coley 1983; Bazzaz 1984). Long-lived leaves may thus experience several alternations of light and dark from the time they are formed until they fall. We found no evidence that environmental variability decreased leaf life span. Despite changing environments, leaves of both species lived on average 1.6–1.8 months, no worse than in constant high or low light. The lack of a treatment effect resulted from the high degree of variability in leaf life span. In this study, leaf life span does not appear to explain the observed influence of environmental variability in light on growth and survival, despite its importance for light capture. Additional insight could be achieved by tracking the ages of senescing leaves to determine whether new leaves or old leaves abscised first. Previous studies have shown that hydraulic conductance (and therefore failure) is correlated with leaf life span (Simonin, Limm & Dawson 2012) where plants that retain their leaves would have a reduced capacity to conduct water to those leaves, concurrent with a reduction in transpiration rates (Maseda & Fernandez 2006). Thus, the plants in our study may be producing leaves as quickly as they drop old leaves (with low hydraulic conductance), resulting in no net effect of light on leaf life span.

Comparing with other species, the leaves of our study species would be considered short-lived leaves, and would be expected to have high photosynthetic rates and dark respiration, as has been estimated for species with similarly short-lived leaves (<2 months) (Reich *et al.* 1998). However, leaf life span did not reflect photosynthetic capacity for our study species, suggesting that the two rates are not as tightly linked for understory herbs as has been documented for trees.

Individuals initially exposed to high light and moved to low light had lower photosynthetic capacity than individuals that remained in high light. In contrast, individuals exposed to low light and moved to high light had the same photosynthetic capacity as individuals that remained in low light. These results support our hypothesis that photosynthetic acclimation during early life influences photosynthesis later in life. For individuals acclimated to low light during early stages, alternating between environments did not influence their photosynthetic rates, and is evidence of low plasticity. Conversely, individuals acclimated to high light not only maintained their ability to use high light but also maintained the ability to decrease their photosynthetic rates in low light. Our results demonstrate that photosynthesis is plastic and can be induced by favourable abiotic conditions during earlier life stages, as has been demonstrated for tropical trees (Martinez-Garza & Howe 2005). Additionally, we found that photosynthetic capacity was high when initial light was high and was higher when precipitation was high than when precipitation was low, supporting our hypothesis that high precipitation is more beneficial than low precipitation. When soil moisture is low, stomatal closure reduces photosynthetic rates for plants even under periods of high light (Muraoka *et al.* 1997).

When moisture and nutrients are plentiful, plants should invest resources in above-ground biomass to capture light, and when moisture and nutrients are limiting, they should increase root production (Alvarez-Buylla & Martinez Ramos

1992). We found no differences in resource allocation with increasing environmental variability, indicating low sensitivity to environmental change. Therefore, biomass allocation does not appear to contribute significantly to the observed effects of environmental variability on growth or survival. A treatment effect on above-ground growth but not biomass ratio may also indicate a lack of trade-offs between above and below-ground biomass, or that our study species are storing carbohydrates. We found evidence that *Calathea* allocates more resources to above-ground biomass than *Heliconia*, which is likely due to differences in their morphology (individual *Calathea* exhibit more branching among ramets than individual *Heliconia*).

Species comparisons revealed that despite the presence of a pulvinus on the leaves of *Calathea*, and despite reduced self-shading in *Calathea* compared to *Heliconia*, the species responded similarly to environmental variability when the effect of precipitation was ignored. We hypothesized that *Calathea* would be less sensitive to environmental variability than *Heliconia*, due to its greater ability to regulate light capture (with a pulvinus). Our results instead demonstrate that despite differences in the physical ability to regulate light capture, *Heliconia* is equally well suited for these environments as *Calathea*. Relevant traits that we did not measure which could enhance *Heliconia*'s performance include leaf thickness, leaf nitrogen content and specific leaf area. Precipitation did have a stronger negative effect on *Calathea* than on *Heliconia*, suggesting that *Calathea* may be less drought tolerant than *Heliconia*.

It is important to note that our precipitation treatments may not have fully mimicked drought (despite observed wilting), and may thus not fully capture the interactions between light and moisture that may influence the vital rates of forest species. Because we did not quantify soil water content, we cannot quantitatively describe the amount of available water in our study. Furthermore, we did not quantify soil nutrient availability, which is correlated with soil moisture (Wardle 1992) and influences plant size and reproductive output for a closely related species, *Calathea micans* (Le Corff 1993).

## Conclusions

Our controlled experiment revealed that imposing variability in the light environment of two widely distributed habitat generalists has generally neutral or positive effects on performance (with the exception of survival), and the direction of the effect depends on early life light conditions as well as precipitation. Early life light availability appears to persistently affect later life performance for understorey herbs, as has been documented for tropical tree seedlings, and may be most strongly influenced by the ability to adjust photosynthetic capacity. We found no evidence of plasticity in leaf life span or biomass allocation, contrary to previous studies of tropical tree seedlings. Our results suggest that widespread understorey herbs are able to maintain high growth as their environment changes, but at the expense of a reduction in survival. Because this experiment was not long enough for

individuals to reach reproductive maturity, determining whether these responses are adaptive or not is out of the scope of this study. However, we speculate that a growth-survival trade-off may increase fitness for these herbs if the surviving individuals reproduce more as a consequence of their increased size and photosynthetic capacity. Indeed, Westerband & Horvitz (2015) found that the probability of reproducing increased with plant size for both species.

## Authors' contributions

Both authors designed the experiment. A.W. collected the data (with the exception of an earlier dataset that measured the availability of light in the understorey over a 2-year period at two tropical wet forest sites—C.C.H.) and conducted the analyses. The manuscript was written by A.W. with numerous edits and revisions by C.C.H.

## Acknowledgements

We thank the Vaughn Jordan Foundation for their generous grant, which was used to construct the shadehouse at Las Cruces Biological Station. We also thank the Organization for Tropical Studies for summer fellowships awarded to A.W., and the University of Miami, Department of Biology for various grants. Finally, we thank Álamo Matarrita for overseeing the shadehouse experiment from February 2013 to October 2015 and for helpful suggestions from two anonymous reviewers.

## Data accessibility

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.bj28m> (Westerband & Horvitz 2017).

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Received 3 August 2016; accepted 15 February 2017

Handling Editor: Frank Gilliam

## Supporting Information

Details of electronic Supporting Information are provided below.

**Appendix S1.** *Heliconia tortuosa* in a study plot at Las Cruces Biological Station, San Vito, Costa Rica. Photo credit: Theresa Bersin.

**Appendix S2.** *Calathea crotalifera* in a study plot at Las Cruces Biological Station, San Vito, Costa Rica. Pictured with field assistant, Jose Delgado.

**Appendix S3.** Soil nutrients and texture at six sites  $\leq 1$  km away from site of soil collection. See Materials and methods for detailed description of study site and soil collection methods.

**Appendix S4.** Size distributions of plants at the onset of experiment.

**Appendix S5.** Dates of experiment.