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EFFECTS OF POPULATION SITE AND MATERNAL DROUGHT ON ESTABLISHMENT PHYSIOLOGY IN *IMPATIENS CAPENSIS* MEERB. (BALSAMINACEAE)

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abstract. Populations of *Impatiens capensis* can differentiate across a range of soil moisture conditions. Differences in the plasticity of drought response at both the physiological and morphological level have been documented in populations across the North American range of this species. *Impatiens* populations tend to utilize whichever drought response mechanism will be most helpful in ensuring their survival and persistence in their particular environment. Here, we examine whether populations from a range of moisture environments exhibit tolerance/avoidance strategies in early life-history and whether maternal effects are important to seedling stress responses. Populations from Pennsylvania across a range of three moisture conditions all responded to maternal drought by decreasing stomatal conductance in seedlings; this maternal drought response was ephemeral and only observed during the first few weeks of growth. Moreover, abscisic acid content covaried with this conductance plasticity for two of the three populations. For the population with the greatest amount of soil moisture, abscisic acid sensitivity seemed to be more important for maternal drought response.

Key Words: maternal effects, drought tolerance, ABA, water stress

Drought is a widespread stress that can be particularly important to early life-history and establishment dynamics in plant populations (Lovell et al. 2009). As a result, early stress may play a fundamental role in realized fitness (Donohue 2005; Heschel et al. 2008). Drought escape, desiccation avoidance, drought tolerance, and maternal effects are central mechanisms that impact the capacity of plants to persist in early-season drought environments (Caruso et al. 2006; Ludlow 1989; Riginos et al. 2007; Roach and Wulff 1987).

In order for a plant to survive drought, it must either avoid or tolerate the stress induced by the environment (Heschel and Riginos 2005; McKay et al. 2003). Drought escape involves growing and reproducing in order to avoid drought stress (McKay et al. 2003); escape strategies can include rapid germination, high rates of transpiration, and early reproduction (Heschel and Riginos 2005). In contrast, plants that exhibit drought tolerance or desiccation avoidance tend to delay germination, produce offspring later in the season, and make physiological adjustments to tolerate stress, such as conserving water via increased water-use efficiency (Heschel and Riginos 2005). Generally, ecotypes across a range of species can respond to drought with different combinations of morphological and physiological traits, as well as with combinations of avoidance/tolerance strategies (cf. Bibee et al. 2011; Heschel et al. 2004, 2014).

Carbon assimilation, stomatal conductance (g_{ST}), and stomatal density can play a major role in both drought escape and desiccation avoidance, and plants can better manage drought stress by making adjustments to these physiological and morphological processes. For example, plants can conserve water physiologically and tolerate stress by closing their stomata, resulting in decreased stomatal conductance, reduced carbon assimilation, and desiccation avoidance. This physiological adjustment can represent a trade-off because reduced stomatal conductance can result in lower photosynthate production and therefore decreased growth (Heschel et al. 2014; Maherali et al. 2008). Thus, in order to avoid drought stress, plants might need to waste water in order to assimilate more carbon, reproduce quickly, and escape drought. Morphologically, a plant can prevent excessive water loss by decreasing its stomatal density, but reductions in density can limit the plasticity of traits like stomatal conductance.

Phytohormones provide mechanisms by which plants can respond both physiologically and morphologically to drought stress. For example, abscisic acid (ABA) is a phytohormone that can be involved in both desiccation avoidance and drought escape, as increased levels promote prolonged seed dormancy, delayed flowering time, and the induction of stomatal closure (Bibee et al. 2011; Boggs et al. 2010; Heschel et al. 2014). Trait expression can be influenced by endogenous ABA levels, which can increase with stress. In addition, plant sensitivity to ABA can increase with stress, such that less ABA is needed to elicit a physiological response (Heschel and Hausmann 2001). Moreover, ABA provides an opportunity for maternal growth conditions to impact avoidance and tolerance strategies (Westgate et al. 1996).

Offspring of drought stressed plants may "inherit" certain mechanisms, termed "maternal effects," to tolerate or avoid drought stress. This phenomenon can be attributed to the maternal tissue surrounding developing embryos, and may be caused by the maternal environment, genotype, or a combination of the two factors (Roach and Wulff 1987). These maternal effects have been shown to differ among *Impatiens* *capensis* populations but not at the regional or ecotype level (Riginos et al. 2007); for example, seedlings from a population "locally adapted" to dry conditions responded to maternal drought stress with decreased stomatal conductance, whereas seedlings from a wet site did not respond to maternal drought.

Our study focused on whether offspring of drought-stressed plants from different ecotypes exhibit similar mechanisms to either tolerate or avoid drought stress (i.e., the influence of maternal drought effects on drought escape and desiccation avoidance/tolerance mechanisms). Here, we have experimentally addressed the following questions:

Does maternal treatment (dry or moist) and/or ecological setting (clearing/pond/woods) affect the germination success, carbon assimilation, stomatal conductance, and ABA content of the offspring? If so, do maternal effects weaken or become less pronounced with time?

MATERIALS AND METHODS

Study system. The ability of the facultative wetland annual, *Impatiens capensis* (Jewelweed, Balsaminaceae) to avoid or tolerate stress provides a model for examining how plants deal with drought. *Impatiens capensis* has a contiguous distribution from the East Coast to the Rocky Mountains of the US. Its sensitivity to soil moisture levels is evident in its morphology and propensity for adaptive differentiation (Dudley and Schmitt 1996; Heschel et. al. 2002); populations exhibit distinct physiological and morphological traits that allow for the species to persist across a range of soil moisture environments (Bibee et al. 2011). Moreover, the environment a maternal plant experiences can prepare a seedling for drought stress tolerance/avoidance by altering the expression of these morphological and physiological traits in *Impatiens* populations (Riginos et al. 2007).

Sites and maternal treatments. *Impatiens capensis* seeds were collected from three different sites at Longwood Gardens in southern Pennsylvania (the southeastern part of the range for this species). The sites were defined as clearing, pond, and woodland, and represented the full range of typical *I. capensis* habitats: the clearing site was the driest and consisted of an open meadow with high light levels; the woodland (hereafter referred to as woods) site was heterogeneously dry with an oak-hickory canopy; the pond site was adjacent to standing water and had consistently wet and high light conditions, with potentially drier edge habitats (note: the gradient between the edge and the core of the pond site was not as strong as the moisture differences between the pond, clearing, and woods sites). The three sites were all within one km of each other, but we expected that differences in the timing of chasmogamous flower production would limit cross-pollination (S. Heschel, pers. obs.). Seeds were collected from cleistogamous (self-fertilized) fruits from each of these sites in July, 2012, and cold/dark stratified at 4°C for about three months. Ten lines per site were grown in the Colorado College greenhouse for two months under bright, moist conditions in April–May 2013. Plants were grown in Fertilome soil (Lambert Peat Moss, Inc., QC, Canada) in four-inch-diameter plastic pots and fertilized as needed with Peters NPK (200 ppm). During this period of growth, one cotyledon was removed from each of 8 maternal lines per site for stomatal density assessment (see below). In June 2013, these maternal plants were subjected to either dry or moist conditions (four replicates per line per treatment for a total of 192 plants); note: the drought conditions were imposed before any flowering had initiated. To ensure that these maternal plants were experiencing significant drought stress, soil moisture levels were measured for every pot with a TDR probe (Delta-T Devices, Cambridge, UK) and stomatal conductance was measured on all 120 maternal plants with a steady-state leaf porometer (SC-1, Decagon Devices, Inc., Pullman, WA). Dry treatment plants had an average soil moisture level of 17.4% volumetric water content (VWC) and moist treatment plants had an average moisture level of 40.7% VWC. Maternal plants from all three sites had significantly lower stomatal conductance in dry conditions than in moist conditions (mean dry conductance = 188 mmol H_2O/m^2sec; mean moist conductance = 338 mmol H_2O/m^2sec).

Germination success and age-related plant analyses. After two weeks of the drought treatment, 30–40 cleistogamous seeds were collected from each maternal line across both dry and moist conditions. These seeds were stratified for three months at 4°C and planted into flats with Fertilome soil in a Percival growth chamber set to 22°C with a 14 h photoperiod (200 μmol photons/m^2sec of light with a neutral R : FR ratio). Percent germination success was recorded for each maternal line; germination was determined by the appearance of the radicle.

During the second week of growth, carbon assimilation rate of the plants was measured with an infrared gas analyzer [(IRGA ADC LCA4; Analytical Development Company, Hoddeson, UK) with an *Arabidopsis* chamber and low flow rate] and stomatal conductance (g_{ST}) was measured using a steady-state leaf porometer (Decagon Devices SC1, Pullman, WA). For both carbon assimilation and g_{ST}, the most-recent, fully expanded leaf was measured on its abaxial surface for 192 seedlings (8 lines per population per treatment). All data were recorded between 10 am and 3 pm and adjusted for differences in measurement times (see below). Both carbon assimilation and g_{ST} readings were taken with a red/blue diode light source set to about 800 µmol photons/m^2sec, which is at saturating levels for carbon assimilation in this species (Heschel and Hausmann 2001).

Plants analyzed at two weeks of age were grown for another two months in the Colorado College greenhouse in 4-inch plastic pots containing Fertilome. All plants were watered and fertilized as needed (200 ppm, Peters NPK) to maintain benign growth conditions and they were periodically rearranged in the greenhouse to minimize positional effects. During this time, the steady-state leaf porometer and the IRGA were used to measure g and carbon assimilation, respectively. A random subset of all the plants was selected for these gas exchange measurements (120 plants total). All data were recorded between the hours of 10 am and 3 pm and adjusted for differences in measurement times, as outlined below.

Seedling stomatal density. For each sample, one cotyledon from each of the 8 maternal lines per population was removed from a seedling in moist conditions and used to quantify stomatal density on the abaxial leaf surface (72 plants total). Nitro-cellulose in ethyl acetate was used to make impressions of the middle of each cotyledon. The nitro-cellulose peels were stained with toluidine blue and examined under a light microscope. All stomata within the field of view were counted, then the number of stomata was divided by 0.02 (area measured) to calculate the number of stomata/mm^2.

Seedling ABA content analysis and ELISA protocol. Seven maternal lines were utilized per population site, per maternal drought treatment, and eight seedlings were collected per line for a total of 336 seedlings. We chose to extract ABA from seedlings to ensure that we were sampling viable seeds. These seedlings were extra germinants that had not been planted but had been stored in distilled water in microfuge tubes at 4°C in dark conditions. For each line, subsets of seedlings were massed (mg) and compacted into 1.5 ml tubes, pulverized, and vortexed with 500 ml ABA extraction buffer (methanol, butylated hydroxytoluene, and citric acid monohydrate) and incubated overnight at 4°C (Boggs et al. 2010). The mixture was spun down, and the supernatant was mixed with TBS (with $MgCl_2$) and stored at –20°C for later ELISA work.

A serial dilution of ABA standards ranging from 1×10^{-6} to 1×10^{-13} M was prepared and the standards, samples, blanks, tracer, and substrate were then applied to ELISA microtiter wells (Agdia, Elkhart, IN). Samples were run in three groups with each group containing an equal number of maternal treatment and population replicates. Using an Optima Plate Reader (BMG LABTECH, Ortenberg, Germany), the absorbance of each sample was measured at 405 nm in relation to the known ABA standards and a blank sample containing buffer (Bibee et al. 2011). Based on log-odds calculations relative to a standard curve, mean ABA was calculated as moles of ABA per mg of sample fresh weight.

Statistical analyses. All data were analyzed with JMP (vs. 7.0.2, SAS Institute, Cary, NC) using standard least squares analyses; normality of error variances was examined for each analysis. Population and maternal treatment were considered fixed factors in our analyses. Stomatal density data were analyzed with a one-way ANOVA to determine whether densities were significantly different between populations. Germination success was analyzed with a three-way ANOVA, using population, line (nested within population), and maternal treatments as categorical variables. Data for carbon assimilation and g were ST analyzed with repeated-measures ANOVA using time (2 weeks or 2 months of growth), population, line (nested within population), and maternal treatments as categorical variables.

For each set of gas exchange data, carbon assimilation and conductance data were adjusted for effects of measurement day and time. Data for carbon assimilation and g_{ST} were regressed against measurement time; residuals from these regressions were added to carbon assimilation and g_{ST} grand means. Molar concentration values of ABA were calculated in JMP using the absorbance values and logistic standard curves; these values were divided by the mg fresh weight of seedlings. The ABA data were analyzed with two-way ANOVAs, using population and maternal treatment as categorical variables.

RESULTS

Seedlings from the woods site had significantly more stomata per unit area than seedlings at both of the other sites [significant population effect, one-way ANOVA, $F = 6.53$, $df = 2$, $p < 0.01$; mean stomata per mm^2 (± 1 SE): Clearing 514.6 ± 28.6, Pond 528.3 ± 29.3, Woods 647.9 ± 28.6]. Regardless of maternal treatment, the three populations had significantly different germination/development rates (Table 1; Figure 1). Also, germination success of the woods population decreased when maternal plants were drought stressed (marginally significant contrast, $F = 2.12$, $df = 1$, $p = 0.10$; Figure 1). The clearing population showed a

Table 1. Nested ANOVA for maternal drought treatment (Mat Trt), population (Pop), and line (Line; nested within population) on germination success and seedling ABA concentration. F and p values are reported: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; + $p < 0.10$.

Effect	Germination	Seedling ABA
Mat Trt	0.33	3.37*
Pop	12.10***	2.37+
Line [Pop]	1.40	–
Pop × Mat Trt	1.33	2.84+

slight increase in germination success when maternal plants were drought stressed, and the pond population was not affected by maternal treatment (Figure 1).

Relative to the clearing and woods populations, the pond population exhibited the lowest carbon assimilation at two weeks of age and the highest at two months (Figure 2); this trend was close to significant (time by population effect; Table 2). Regardless of population source, carbon assimilation was consistently greater at two weeks than at two months (significant time effect; Table 2; Figure 2). The effect of maternal treatment, however, was not significant at either age (non-significant time by maternal treatment interaction; Table 2; Figure 2).

Stomatal conductance (g_{ST}) in plants from all populations, at two weeks of age, was greater than at two months (significant time effect;

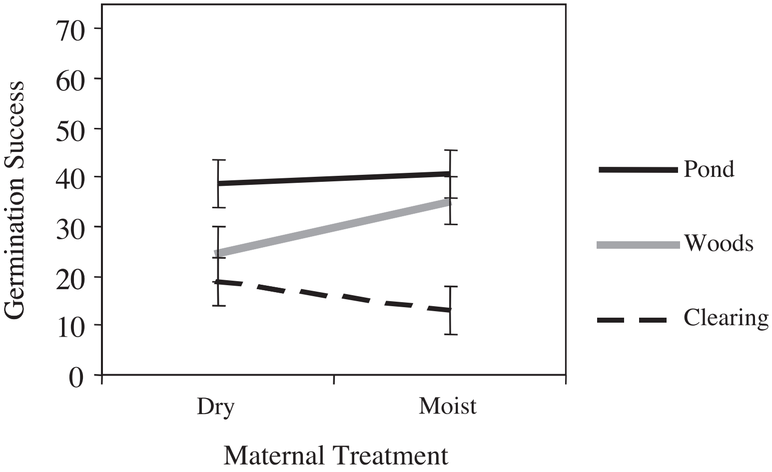

Figure 1. Mean (± 1 SE) % germination success for each population in response to maternal treatment.

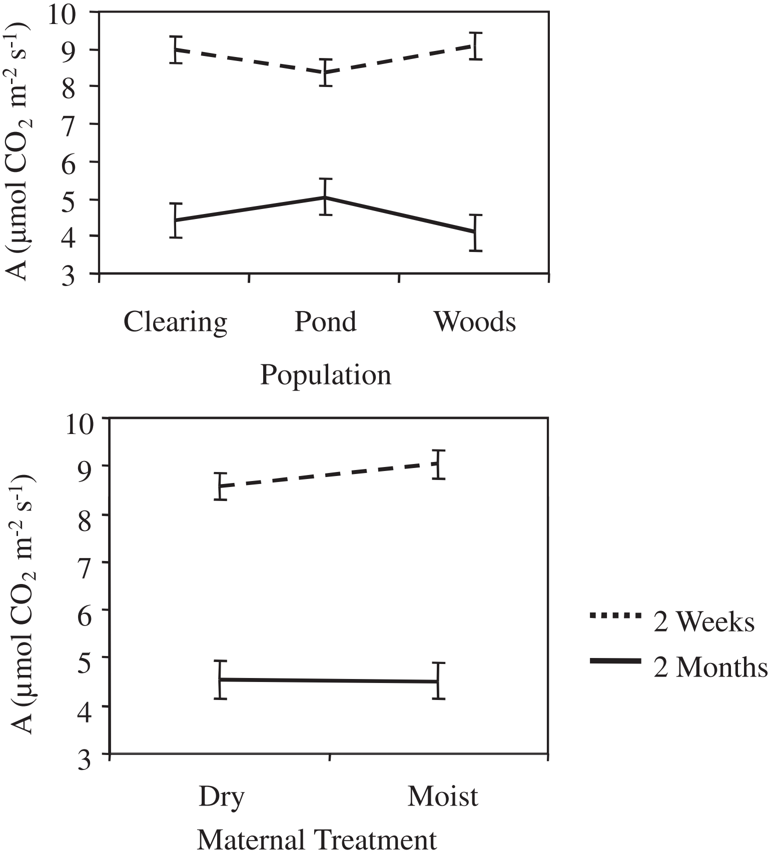

Figure 2. Mean (± 1 SE) carbon assimilation (A) by age, population, and maternal treatment. Data for the top frame are pooled across maternal treatments; data for the bottom frame are pooled across populations within maternal treatments.

Table 2; Figure 3). Measurements did not differ significantly between populations for either age (non-significant time by population interaction; Table 2; Figure 3). At two weeks of age, all plants demonstrated a significant decrease in g_{ST} when maternal plants were drought stressed (significant overall maternal treatment effect; Table 2; Figure 3). However, the strength of this decrease in conductance with maternal drought depended on population (significant time by maternal treatment by population interaction; Table 2) with the pond population exhibiting the greatest decrease in g_{ST}. Conversely, by two months there

Table 2. Repeated-measures nested ANOVA for maternal drought treatment (Mat Trt), population (Pop), and line (Line; nested within population) on stomatal conductance (g_{ST}) and carbon assimilation rate after 2 weeks and 2 months of seedling growth. F and p values are reported. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; + $p < 0.10$.

Effect	A	g_{ST}
Mat Trt	0.15	14.68**
Pop	0.22	0.37
Line [Pop]	1.25	1.29
Time	61.59***	24.28***
Pop × Mat Trt	0.39	6.72**
Time × Mat Trt	1.43	8.81*
Time × Pop	2.05+	0.013
Time × Line [Pop]	1.22	1.21
Time × Pop × Mat Trt	0.55	4.27*

was no statistical difference in the response to maternal drought (significant maternal treatment by time effect; Table 2; Figure 3).

Levels of ABA increased with maternal drought for seedlings from the clearing and woods populations (Figure 4). Seedlings from the pond site had equivalent ABA levels across both maternal treatments (Figure 4). As a result, we detected a marginally significant population by maternal treatment interaction (Table 1; Figure 4).

DISCUSSION

Drought is a common stressor for which plants must make adjustments in their physiology, morphology, and phenology in order to establish as seedlings. Past studies have examined ecotypic differences between regional populations (Bibee et al. 2011) and results have demonstrated that populations either seem to avoid or tolerate drought stress. Although the instantaneous adjustments made by plants have been studied before in this system, less research has been focused on the effects of maternal drought stress across generations (Riginos et al. 2007).

We found that maternal drought had a significant, but temporary, effect on establishment-related traits—maternal effects of drought were more pronounced at two weeks than at two months of age. We detected a significant maternal effect of drought on g_{ST}, such that lines from all three habitats had significantly lower stomatal conductance if the maternal plant was stressed. This decrease in g_{ST} was not just the consequence of increased ABA in seeds because ABA did not increase with maternal drought in seedlings from one site, indicating that ABA sensitivity might be a mechanism of maternal drought response.

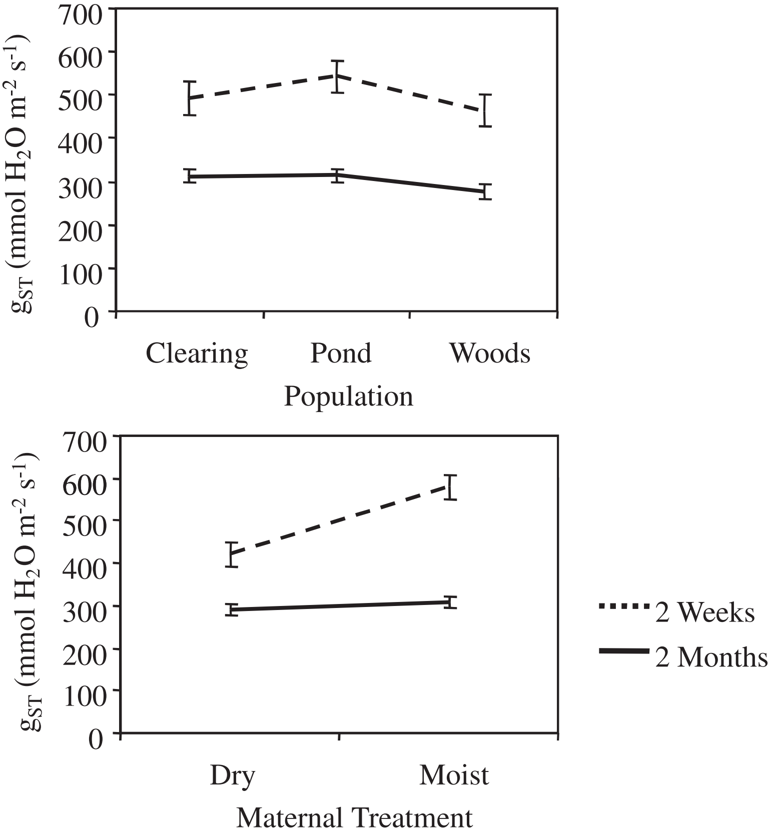

Figure 3. Mean (± 1 SE) stomatal conductance (g_{ST}) by age, population, and maternal treatment. Data for the top frame are pooled across maternal treatments; data for the bottom frame are pooled across populations within maternal treatments.

Germination success. Germination success varied between populations and may be attributed to a number of factors. The pond population demonstrated the highest rate of germination, which may have been related to the low concentration of ABA found in the seedlings of this population; this germination response might represent a drought escape response for this typically moist site (i.e., avoiding drought stress). Moreover, this response may be attributed to the highly competitive habitat at the pond site; this site had high intraspecific plant density, potentially making it beneficial to

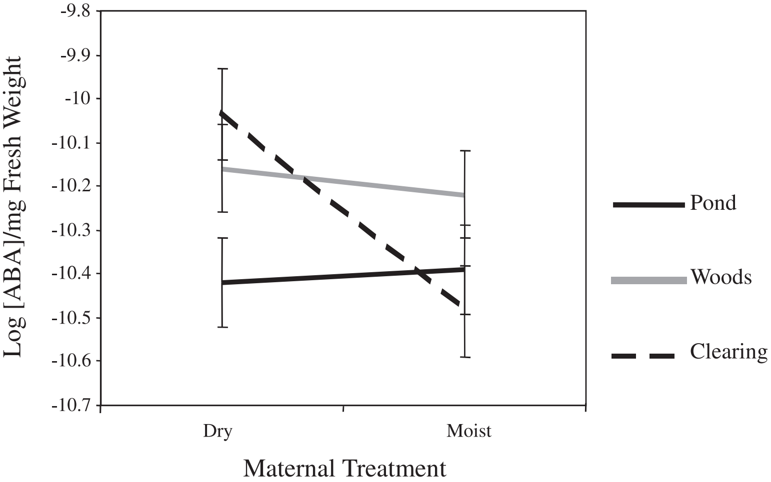

Figure 4. Mean (± 1 SE) log molar abscisic acid (ABA) concentration per mg fresh weight in seedlings by maternal treatment and population.

germinate early at higher frequencies in order to overtop neighboring plants (Schmitt et al. 2003).

The woods and clearing populations exhibited increased levels of ABA in seedlings from drought-stressed maternal plants (Figure 4), which supports the observed decreases in germination and decreased levels of stomatal conductance in these populations. This enforced dormancy due to maternal drought may represent a desiccation avoidance/drought tolerance strategy for these heterogeneously dry sites. If maternal plants are experiencing drought stress, it is possible they may supply embryos with more endogenous ABA to help them tolerate harsh conditions during establishment. The range of soil moisture conditions across the study sites may have caused selection for ABA content variation, indicating that ABA content plasticity might be evolutionarily important (cf. Heschel et al. 2014).

Water-use traits. For drought tolerant populations, stomatal conductance is expected to decrease with maternal drought stress, whereas the opposite is true for populations avoiding stress with drought escape mechanisms (Riginos et al. 2007). At two weeks of age, plants from all sites seemed to be drought tolerant in terms of conductance; however, we observed a greater decrease in stomatal conductance than in carbon assimilation. This represents an increase in water use efficiency by slowing water loss without sacrificing much carbon gain, which is likely more critical for young seedlings to become established. By two months of age, the maternal treatment was not evident in offspring gas exchange rates. Considering that drought is often an ephemeral condition, long-lasting maternal effects may not be advantageous if they subsequently slow growth and/or reproduction rates; this might be particularly true for the pond population, where drought escape responses might be important.

The slight variations observed in stomatal conductance and carbon assimilation rates between populations may be linked to ABA content and/or sensitivity to ABA (Heschel and Hausmann 2001). For both the woods and clearing sites, decreases in conductance with maternal drought may have been due to increases in ABA levels in embryos. The pond population maintained lower and more stable levels of ABA in the seedlings, whilst significantly decreasing stomatal conductance in response to drought, making elevated ABA sensitivity a likely mechanism. This indicates that the pond site may occasionally have dry episodes, perhaps on bright and hot days when overly high transpiration rates might be useful to ameliorate leaf temperature issues (Heschel and Hausmann 2001). On these sunny days, such high transpiration rates might lead to temporary water stress within a given plant, requiring stomatal closure; in this situation, greater sensitivity to ABA might allow for a more rapid response than would the endogenous production of ABA. Moreover, the edges of the pond site might occasionally experience decreased soil moisture levels. Such temporarily dry, edge habitats might also benefit from a rapid response to ABA.

Conclusions. *Impatiens capensis* inhabits a wide geographic range in the US, from the East Coast to the Rocky Mountains. The ecotypic differentiation observed stems from large disparities in regional conditions, such as relative humidity, soil moisture, and annual/diurnal temperature regimes (Bibee et al. 2011). The data presented here for maternal drought responses demonstrate both physiological differentiation and convergence between sites located within the same region. In response to maternal stress, seeds from one population seemed to accelerate development to escape drought, whereas seeds from another population delayed development to potentially tolerate stress. In contrast, seedlings from all three study sites responded to maternal stress by decreasing stomatal conductance, which is a desiccation avoidance strategy. However, this convergence of drought strategy with transpiration was achieved by differences in ABA content/sensitivity. The fact that we observed significant maternal drought effects for populations from different soil moisture conditions indicates that drought response has probably been a target of selection in early life history regardless of study site. Early life history is a fundamental determinant of fitness, so maintaining seedling drought responses might be important for populations across a range of soil moisture conditions.

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