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Exploring the Potential for Rare and Common *Borodinia* Species to Acclimate to Change

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Departmental Honors Thesis
The University of Tennessee at Chattanooga
Biology, Geology and Environmental Science

Examination Date: April 8, 2019

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Table of Contents

Abstract

An important ecological question that remains unanswered is why some species are rare while others are common. Because the natural world is dynamic, in order to persist, species must successfully respond to the environmental changes they experience. The ability to be plastic may be especially important to the survival of species in the face of rapid environmental change because such quick change does not offer species time to migrate or adapt. Consequently, differential plasticity between rare and common species, with rare species possessing less plasticity than common species, could help explain the differing successes of persisting in a large geographic distribution. Here, I used a comparative trait-based approach to assess the ability of a rare and common congeneric species pair to acclimate to environmental change with a focus on growth measures. Specifically, I evaluated the growth and plasticity of rare *Borodinia perstellata* and common *B. laevigata* to altered light, water, and temperature conditions in environmentally controlled growth chambers. I found that both species respond similarly to different environmental conditions and have similar plasticity, but some of my results suggest that the rare *Borodinia perstellata* could be generally less plastic than the common *Borodinia laevigata*. Specifically, *B. laevigata* possessed greater plasticity to grow taller and more leaves in both the altered water and temperature conditions while *B. perstellata* only contained greater plasticity for growing more shoot mass in the light condition. Since the common *B. laevigata* was found to be more plastic across a wider range of environmental differences than the rare *Borodinia perstellata*, the hypothesis that differential plasticity can help explain species rarity and commonness is limitedly supported, but further research should be conducted to confirm the hypothesis.

Introduction

The question of why some species are rare while others are common is important for advancing ecological theory and guiding rare species preservation efforts (Bevill & Louda 1999). This question has been addressed in the past (Bevil & Louda 1999, Murray et al. 2002, Comita et al. 2010, Preston 1962), but still does not have a definitive answer (May 1999). Rarity is defined as the differential relative abundance of species (Rabinowitz et al. 1986). Invasive species are an extreme example of high relative abundance (Van Clef & Stiles 2001) and have been extensively studied given their ecological and economic harm (Colautti & MacIsaac 2004, see reviews by: Katsanevakis et al. 2014, Vilá et al. 2011). One prevalent method utilized by researchers to understand invasiveness involves comparing traits of invasive versus non-invasive species (see reviews by Daehler 2003, Pyŝek & Richardson 2007, see meta-analysis by Van Kleunen et al. 2010), and this approach has been useful in revealing biological characteristics of species invasiveness including the increased growth rate and leaf area allocation found in invasive species (Pyŝek & Richardson 2007, Van Kleunen et al. 2010). Despite the utility of comparative research within the context of species invasiveness, less research has compared species traits toward elucidating the basis of species rarity (see review by: Murray et al. 2002). This could possibly be explained by the fact that rare species are more sparse, making research on them more difficult.

While comparing species' traits can be utilized to understand factors that influence species rarity (see Albert et al. 2011, Kunin & Gaston 1997), comparative studies of traits between congeneric pairs of rare and common species could be especially insightful by minimizing the effects of differing phylogenies or life histories (see review by: Murray et al. 2002). Since comparative studies of traits concerning species rarity, in general, have been limited

in the past, comparative studies of traits of congeneric pairs have been even more limited (see reviews by Bevil & Louda 1999, Murray et al. 2002). It would, therefore, be beneficial for more congeneric comparative trait studies of rare and common species to be conducted to help in the understanding of the underlying reason for species rarity and commonness.

Plasticity, which has become increasingly dynamic due to human influences (Williams et al. 2008), would be a particularly interesting trait to compare between rare and common congeneric plant species. Mainly, plasticity could help explain their differing geographical ranges as a wider geographic range generally equates to a broader ability to acclimate to environmental differences (Brown 1984, Futuyma & Moreno 1988). Additionally, plants are largely sedentary, which means their persistence could depend on their ability to acclimate to the changing environmental conditions around them (Bradshaw 2006, Sultan 2000) and that is why plants have relatively high levels of trait plasticity (Sultan 2000). Even when plants do migrate through their seeds, this is not an effective response for rare species as they tend to produce fewer seeds than more common species (Lavergne et al. 2004), indicating that plasticity is still an important trait to be studied. In addition, there seems to be a positive correlation between species invasiveness and plasticity (Ruprecht et al. 2014), which suggests that plasticity plays a role in species rarity and commonness. Despite all this, research concerning the influence of trait plasticity on species rarity has been limited in the past (see review by Murray et al. 2002) and continues to be limited, with mainly studies that have altogether produced mixed results (Pohlman et al. 2005, Marchin et al. 2009, Lovell & McKay 2015).

Studying species rarity is especially relevant in the southeastern United States, given its relatively large number of endemic plant species (Delcourt & Delcourt 1991). About 500 plant species that are new to science were named in the past 50 years and many of them were

southeastern endemics (A. Weakley, Director of University of North Carolina Herbarium, pers. comm. July 2016). In addition, Georgia, Florida, and Alabama are in the top ten states in the U.S. with the highest number of vascular plant species and the highest percentage of plants at risk of extinction (Stein et al. 2000). Furthermore, Florida ranks third for the most endangered species, Alabama ranks fourth, and Tennessee ranks sixth (USFWS 2019).

Borodinia (which includes species formerly classified as *Boechera* and/or *Arabis*) is a plant genus found throughout the United States including several species found within the southeastern United States. *Borodinia perstellata* is one such species that occurs sparsely in the southeastern United States within a few counties in Tennessee and Kentucky (Kartesz 2015) and is currently listed as federally endangered (USFWS 1997). *Borodinia laevigata* is another species found within the southeastern United States but is much more commonly distributed, being found in many counties in the southeastern, northeastern, and central United States (Kartesz 2015). These two congeneric species allow me to complete a congeneric comparative study of the traits associated with species rarity and commonness. The main threats to *B. perstellata* have been identified as grazing from wildlife and the habitat loss due to the development of roads and homes (USFWS 1995). By studying the ability of *B. perstellata* to acclimate to different environmental treatments, I hope to elucidate the potential role of plasticity in species rarity, while also aiding in the continued conservation efforts of this species.

To accomplish these aims, I conducted an experiment as part of a larger NSF funded project comparing multiple congeneric rare-common species pairs. My project utilized controlled-environment growth chambers to compare the performance and plasticity of rare *B. perstellata* and common *B. laevigata* in response to changes in environmental conditions that are associated with current habitat threats in the southeastern U.S. I focused on growth and biomass

allocation measures and phenotypic plasticity. I hypothesize that the rare *B. perstellata* is less plastic than the more common *B. laevigata*. Such reduced plasticity could help to explain why *B. perstellata* has a smaller geographic range than the common congener and why its populations are experiencing contemporary decline in the face of habitat disturbance.

Methods

Seed Collection and Plant Propagation

Seeds from four naturally occurring populations of *B. perstellata and* three naturally occurring populations of *B. leavigata* were collected during summer 2018. The four populations of *B. perstellata* were collected from private property in DeKalb County and Rutherford County, TN and Rutherford County and Jefferson County, KY. The three populations of *B. laevigata* were collected from Cheatham County, TN, Cook County, IL, and Clarion County, PA. The seeds were collected in early to late summer 2018 and then stored in paper envelopes in a refrigerator until planting in October 2018. To standardize methods across all species pairs treatments for the project funded by NSF, historical weather data for the first *Pityopsis* congeneric experiment was altered to reflect the ambient conditions found in the natural environment of both *B. perstellata* and *B. laevigata* (CustomWeather Inc. 2019). Prior to planting, the four controlled-environment growth chambers (PGR15, Conviron, Winnipeg, MB, Canada) were then programmed to these ambient conditions for both species to facilitate germination. These ambient conditions included a 20 ℃/30 ℃ night/day cycle and a cycle of light with 250 μmol photons m^{-2} s^{-1} as the midday. The seeds were planted in ~10-cm diameter x 9-cm deep plastic plots containing a commercially available potting medium (Pro-Mix BX Biofungicide + Mycorrhizae, Premier Tech Horticulture, Riviére-du-loup, QC, Canada). We planted multiple seeds from each of 12 parent plants from each population of each species in

each of four pots. The four pots of seeds from each parent plant were then divided among the four chambers such that one offspring of each parent plant was in each chamber. Pots were watered to saturation daily for the first few weeks, and then every other day as needed. We rotated the positions of the pots twice a week to account for any differences in their microclimate.

Environmental Treatments

Four weeks after the first plant germinated, we initiated environmental treatments in the growth chambers. One chamber continued to provide the conditions used during the germination period; this chamber served as the 'ambient' chamber in my experimental design. The three other chambers were programmed to each provide conditions similar to those in the ambient chamber but with a contrasting level of a single treatment (light, temperature, or water availability). The 'light' chamber was set to provide double the ambient daytime light level (i.e., 500 µmol photons $m^{-2} s^{-1}$ vs. 250 µmol photons $m^{-2} s^{-1}$) to imitate increased light that would occur due to deforestation. The 'temperature' chamber was set to provide maximum daytime and nighttime temperatures that were 2℃ warmer than those in the ambient chamber (22 ℃/32 ℃ vs. 20 ℃/30 ℃ night/day) to replicate predicted climate change in the southeastern US by the end of this century (Stocker et al. 2013). The water chamber was watered twice the amount as the ambient chamber (100% field capacity vs. 50% field capacity) every other day to provide more of that limited resource to the species pair as the species are typically found in dry, rocky soil (USFWS 1997, Bloom et al. 2001). The pots continued to be rotated around in the chambers every other day to control for possible spatial differences in the microclimate. Additionally, I randomly reassigned the treatment levels of each chamber each month and the plants were moved accordingly to reduce any effects of chamber and pseudoreplication (Gibson 2014).

Growth and Physiological Measurements

To assess the growth response and plasticity of each species to each environmental treatment, I focused on growth metrics. Before treatments were initiated, I determined the number of days after planting that each plant germinated and developed its first true leaf (i.e., non-cotyledon) to observe if there were any species or population differences in germination and establishment rate. After treatments were initiated, I measured the stem height and counted the number of leaves of each plant biweekly for 14 w to assess the influence of the environmental treatments on growth. To assess the final impacts the environmental treatments had on plant growth, I harvested plants after the 15th week of growth. Whole plants were sorted into shoots (leaves and stems) and roots and placed in a 40 ℃ oven for 1 w. The roots and shoots of each plant individual were then weighed to yield shoot mass, root mass, and total biomass of each individual.

Data Analyses

To examine biomass allocation, I calculated root:shoot biomass, the shoot mass fraction (shoot mass:total biomass), and the root mass fraction (root mass:total biomass) for each individual. I determined plasticity as the response coefficient (RC), which is the ratio of the mean values at greater and lesser resource availabilities for each individual (Valladares et al. 2006). Significant differences in trait values and biomass allocation between ambient and altered environmental conditions for each species were determined with one-way analysis of variance (ANOVA) with the environment treatment as the independent variable. Differences in plasticity between the two species were similarly determined with one-way ANOVA with species as the independent variable. Results of all statistical tests were considered significant if $p \leq 0.05$ and

marginally significant if p ≤ 0.1. All statistical analyses were performed using IBM SPSS

Statistics Version 25 software (IBM Corp., Armonk, NY).

Results

Growth and Allocation of Rare and Common *Borodinia* Species

There were significant differences in many of the mean growth metrics between the

ambient chamber and the various environmental treatment chambers (Figs. 1-3). Specifically,

individuals of both species were shorter ($p \leq 0.01$ for *B. perstellata; p = 0.020* for *B. laevigata*)

and produced fewer leaves ($p \leq 0.01$ for *B. perstellata; p = 0.027* for *B. laevigata*) on average

when grown in high vs. ambient light; however, their total biomass did not differ between light

treatment levels (Fig. 1). In contrast, both species grew taller ($p \leq 0.01$, $p = 0.022$ for *B.*

perstellata; p ≤ 0.01, p ≤ 0.01 for *B. laevigata*) and produced significantly more total biomass (p

$= 0.028$, $p = 0.016$ for *B. perstellata; p = 0.01, p = 0.049* for *B. laevigata*) when grown with

higher water and temperature availability than in ambient conditions (Fig. 2-3). However, only

B. laevigata leaf production was influenced by increased water and temperature availability.

Specifically, *B. laevigata* individuals produced more leaves when grown with more water

availability ($p \leq 0.01$) and greater temperature ($p \leq 0.01$) than in ambient conditions (Fig. 2-3).

There were also some significant differences in the biomass allocation of both species

between ambient and altered water and temperature availability, but biomass allocation was not

affected by light availability in either species (Table 1). When grown with more water, both

species significantly allocated more biomass to the shoots (i.e., had greater root:shoot mass) than

they did in ambient conditions ($p = 0.013$ for *B. perstellata; p = 0.013* for *B. laevigata*).

However, only *B. laevigata* biomass allocation was influenced by increased temperature.

Specifically, *B. laevigata* individuals had greater shoot fraction when grown in warmer conditions than in ambient temperature ($p \leq 0.01$; Table 1).

Differences in Plasticity between the Rare and Common Species

There were minimal significant differences in plasticity of the rare and common *Borodinia* species for trait values and biomass allocation measures. In response to light availability, *B. perstellata* had marginally greater plasticity of shoot weight than did *B. laevigata*. Specifically, the plasticity of this trait of *B. perstellata* was more than double that of *B. laevigata*. However, there were no other differences in plasticity of the two species in response to light availability (see Table 2). In contrast, *B. laevigata* exhibited greater plasticity of stem height and number of leaves than did *B. perstellata* in response to both temperature and water availability. Specifically, in response to temperature availability, the plasticity of stem height of *B. laevigata* was approximately double that of *B. perstellata*, while the plasticity of the number of leaves produced per individual was 50% greater in *B. laevigata* than *B. perstellata* (Table 2). In response to water availability, the plasticity of stem height of *B. laevigata* was approximately 50% greater than that of *B. perstellata*, while the plasticity of number of leaves produced per individual was about 65% greater in *B. laevigata* than *B. perstellata* (Table 2).

Discussion

Comparison of *Borodinia* Species

In response to increased light, both species significantly decreased in height and decreased their leaf number, while preserving equal levels of total biomass and biomass allocation. This decrease in height and leaf growth for *B. perstellata* and *B. laevigata* could be explained by the notion that it is common for stem elongation to occur in low-light conditions, like in the ambient environment, because the limitation of light leads to plants putting more

energy into aboveground biomass to help capture light (Kende & Lang 1964). When *B. perstellata* and *B. laevigata* were in the high light environment, they may not have allocated as much energy into stem growth and leaf production since light was not limited. *B. perstellata* also has a reported intolerance to high light availability (USFWS 1997) and this could possibly explain the reason this species grew more purple leaves in the high light treatment than in ambient conditions. The similar findings for *B. laevigata* suggest that this species may also share this intolerance to high light availability.

Increased water was associated with increased stem height and total biomass in both species, but only *B. laevigata* also produced more leaves with greater water availability. Additionally, both species had a significant decrease in root:shoot ratio and root fraction but a significant increase in shoot fraction, indicating that the species were allocating more biomass into shoots when receiving more water. Just as increased light caused the plants to shorten because the light was no longer limiting, increased water meant that the plants did not have to expend as much energy on root biomass production. With high water, the plants did not have to grow as much root material to search for water and could instead focus more on growing aboveground biomass, which is typical in plant species (see review by: Poorter & Nagel 2000). Since *B. laevigata* was better able to grow leaves in this high-water environment, this seems to suggest that this species would be better able to capture light than *B. perstellata* in environmental conditions with increased soil moisture.

With a greater temperature, both species grew taller and had significantly more biomass than the ambient chamber. Since growth in plants is controlled by enzymatic reactions, an increased temperature can help increase growth rate as long as the temperature is not high enough to denature the enzymes found within the individual plants (Went 1953). My results

suggest that the increase in temperature may have enhanced photosynthetic reactions of *B. perstellata* and *B. laevigata*, which helped the two species produce more energy for growth. Once again, only *B. laevigata* significantly had greater leaf number, possibly indicating that *B. laevigata* tends to have a strategy to absorb more light in high-temperature environments than *B. perstellata*. This idea may be further supported by the fact that the biomass allocation did not change from the ambient for *B. perstellata* but did for *B. laevigata*. Specifically, both the root:shoot ratio and root fraction were significantly decreased and the shoot fraction was significantly increased from the ambient. This difference might be explained by *B. perstellata* having a smaller optimal range of temperatures than *B. laevigata*, possibly because *B. laevigata* is found in a larger geographic range with a greater variation in climate (Kartesz 2015).

Plasticity in Rare vs. Common Species

Just as there were some differences in the way *Borodinia perstellata* and *Borodinia laevigata* grew and allocated biomass in response to the environmental treatments, there were also some limited differences in their plasticity in response to environmental changes. Overall, the hypothesis that the rare *B. perstellata* species would exhibit less plasticity in response to environmental change than the more common *B. laevigata* was not generally supported within the context of light availability but was supported within the context of both water availability and temperature. Specifically, when grown in high light, *B. perstellata* exhibited greater plasticity of shoot biomass production, while in the high water and temperature environments, *B. laevigata* exhibited greater plasticity of stem height and numbers of leaves produced. This differential ability to change phenotypes in response to environmental change could reflect and explain the more restricted range of *B. perstellata* relative to the range of *B. laevigata*, as temperature and water availability would vary more across a wider geographic area. More

generally, these data provide some support to the overarching ecological idea that an important difference between rare and common plant species is their ability to acclimate to new environments.

Conservation Implications

In the recovery plan for *B. perstellata* (published during its previous classification as *Arabis perstellata*), it is stated that an important aspect of helping this species be reclassified from endangered to threatened is the determination of prime habitat conditions (USFWS 1997). By knowing where *B. perstellata* grows best, conservationists can better manage its habitat and evaluate sites that may require active management to maintain suitable conditions. My research suggests that *B. perstellata* has greater plasticity for shoot biomass production in high-light conditions than does common *B. laevigata*. This could indicate that *B. perstellata* may be equipped to deal with problems from deforestation that could increase the light intensity to these plants. Specifically, *B. perstellata* will be better able to increase shoot biomass, potentially aiding in producing seeds.

My research also suggests that *B. perstellata* was able to grow taller and larger and produce more leaves with increased water availability and temperature relative to its ambient conditions. As such, the warming of the earth's climate due to anthropogenic influences could benefit *B. perstellata*. However, the decrease in soil moisture likely to confound rising temperatures (Dai et al. 2004) may offset any positive responses to warming. These results indicate that it may be useful to condition ways to modify the moisture availability to natural populations of *B. perstellata* as temperatures warm.

Future Directions

My experiment examined the effects of environmental treatments on rare *B. perstellata* and common *B. laevigata* as distinct factors. However, as the climate continues to warm and land-use change continues to occur, multiple environmental conditions will likely change in interacting ways. Future research analyzing the effects of multiple, interacting environmental conditions on the growth and plasticity of *B. perstellata* and *B. laevigata* would help to continue to elucidate the differential plasticity of rare and common species while also continuing to aid in conservation efforts for *B. perstellata*. Additional studies could be conducted in field settings that could include a focus on potential biotic factors that could influence species rarity, such as competition, predation, and pollination. Future research also might investigate growth and plasticity measures not included in this study. For example, the plasticity of specific leaf area (leaf area per unit leaf mass) might be particularly interesting to examine in response to environmental change. Since both species produced significantly fewer leaves in the high light environment, perhaps one species grew thicker leaves in response to a decreased need to capture more light (Gratani 2014). Other measures to condition for future study could include leaf-level physiology and reproductive effort.

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Tables

Measure	Species	Ambient Water	High Water	Ambient Temperature	High Temperature	Ambient Light	High Light
Root:Shoot	*B. perstellata*	0.98 ± 0.17	0.50 ± 0.048 **	0.98 ± 0.17	0.88 ± 0.17	0.98 ± 0.17	0.94 ± 0.11
	B. laevigata	1.53 ± 0.39	0.49 ± 0.050 **	1.53 ± 0.39	0.69 ± 0.20 *	1.53 ± 0.39	2.89 ± 0.95
Shoot Fraction	*B. perstellata*	0.56 ± 0.035	0.68 ± 0.021 **	0.56 ± 0.035	0.58 ± 0.033	0.56 ± 0.035	0.54 ± 0.034
	B. laevigata	0.51 ± 0.035	0.72 ± 0.029 **	0.51 ± 0.035	0.66 ± 0.034 **	0.51 ± 0.035	0.46 ± 0.052
Root Fraction	*B. perstellata*	0.44 ± 0.035	0.32 ± 0.021 **	0.44 ± 0.035	0.42 ± 0.033	0.44 ± 0.035	0.46 ± 0.034
	B. laevigata	0.49 ± 0.035	0.28 ± 0.029 **	0.49 ± 0.035	0.34 ± 0.034 **	0.49 ± 0.035	0.54 ± 0.052

Table 1. Mean root to shoot ratio, shoot mass fraction, and root mass fraction of rare *Borodinia perstellata* and common *B. laevigata* in response to different treatments following 15 weeks in controlled-environment chambers. Two asterisks denote significant differences in the means of the ambient and high resource availability ($P \leq 0.05$) and one asterisk denotes marginally significant differences ($P \leq 0.10$).

Treatment	Measure	Species		p-value
		B. perstellata	B. laevigata	
Light	Stem height	0.81 ± 0.18	1.04 ± 0.21	0.5
	Number of leaves	0.77 ± 0.054	0.85 ± 0.076	0.45
	Root length	0.86 ± 0.14	1.6 ± 0.46	0.17
	Shoot mass	3.76 ± 1.54	1.59 ± 0.35	0.1 *
	Root mass	4.93 ± 3.27	2.19 ± 0.79	0.4
	Total mass	4.33 ± 2.45	1.59 ± 0.38	0.22
	Root:shoot	1.1 ± 0.20	4.05 ± 1.61	0.12
	Shoot fraction	1.13 ± 0.13	1.07 ± 0.22	0.82
	Root fraction	1 ± 0.093	1.2 ± 0.17	0.33
Water	Stem height	2.72 ± 0.44	4.02 ± 0.54	0.09 *
	Number of leaves	1.03 ± 0.044	1.71 ± 0.11	≤ 0.01 **
	Root length	1.23 ± 0.15	1.82 ± 0.27	0.11
	Shoot mass	13.76 ± 4.46	23.74 ± 4.18	0.12
	Root mass	5.74 ± 1.39	13.06 ± 4.92	0.24
	Total mass	9.54 ± 2.42	16.79 ± 3.97	0.18
	Root:shoot	0.48 ± 0.073	0.45 ± 0.078	0.85
	Shoot fraction	1.5 ± 0.12	1.92 ± 0.33	0.31
	Root fraction	0.62 ± 0.051	0.59 ± 0.060	0.73
Temperature	Stem height	2.2 ± 0.30	4.43 ± 0.91	0.048 **
	Number of leaves	1.15 ± 0.091	1.75 ± 0.15	≤ 0.01 **
	Root length	1.22 ± 0.17	2.7 ± 0.78	0.11
	Shoot mass	16.87 ± 5.60	26.6 ± 9.04	0.41
	Root mass	14.87 ± 5.42	9.47 ± 3.42	0.4
	Total mass	14.19 ± 4.63	11.19 ± 2.75	0.58
	Root:shoot	1.23 ± 0.42	0.77 ± 0.23	0.34
	Shoot fraction	1.22 ± 0.14	2.02 ± 0.52	0.16
	Root fraction	1.03 ± 0.22	0.71 ± 0.11	0.19

Table 2: Mean response coefficient measures of plasticity of all growth and allocation measures between rare *Borodinia perstellata* and common *B. laevigata* in response to different treatments following 15 weeks in controlled-environment chambers. Two asterisks denote significant differences in the mean plasticity between the two species (P ≤ 0.05) and one asterisk denotes marginally significant differences (P ≤ 0.10).
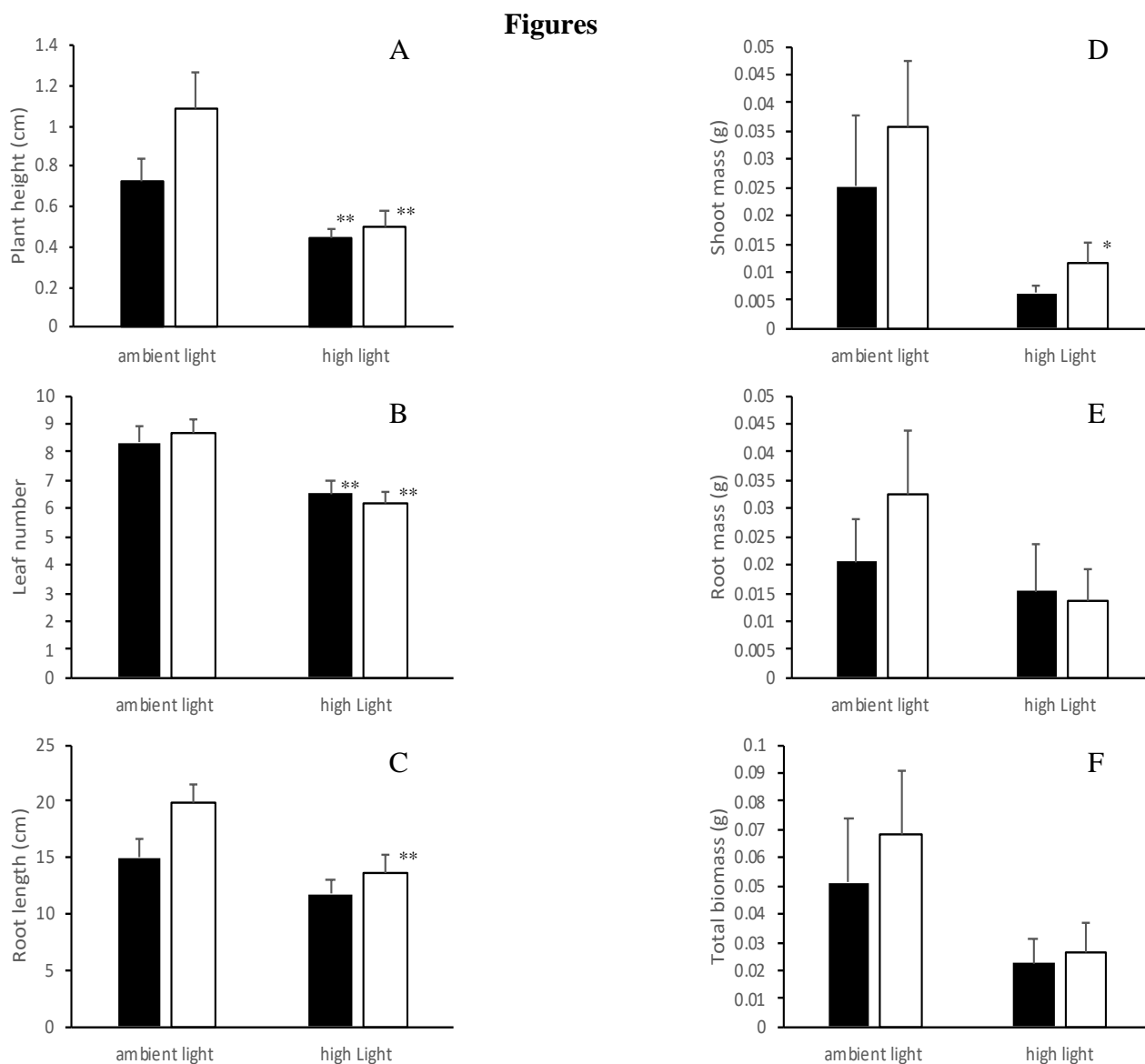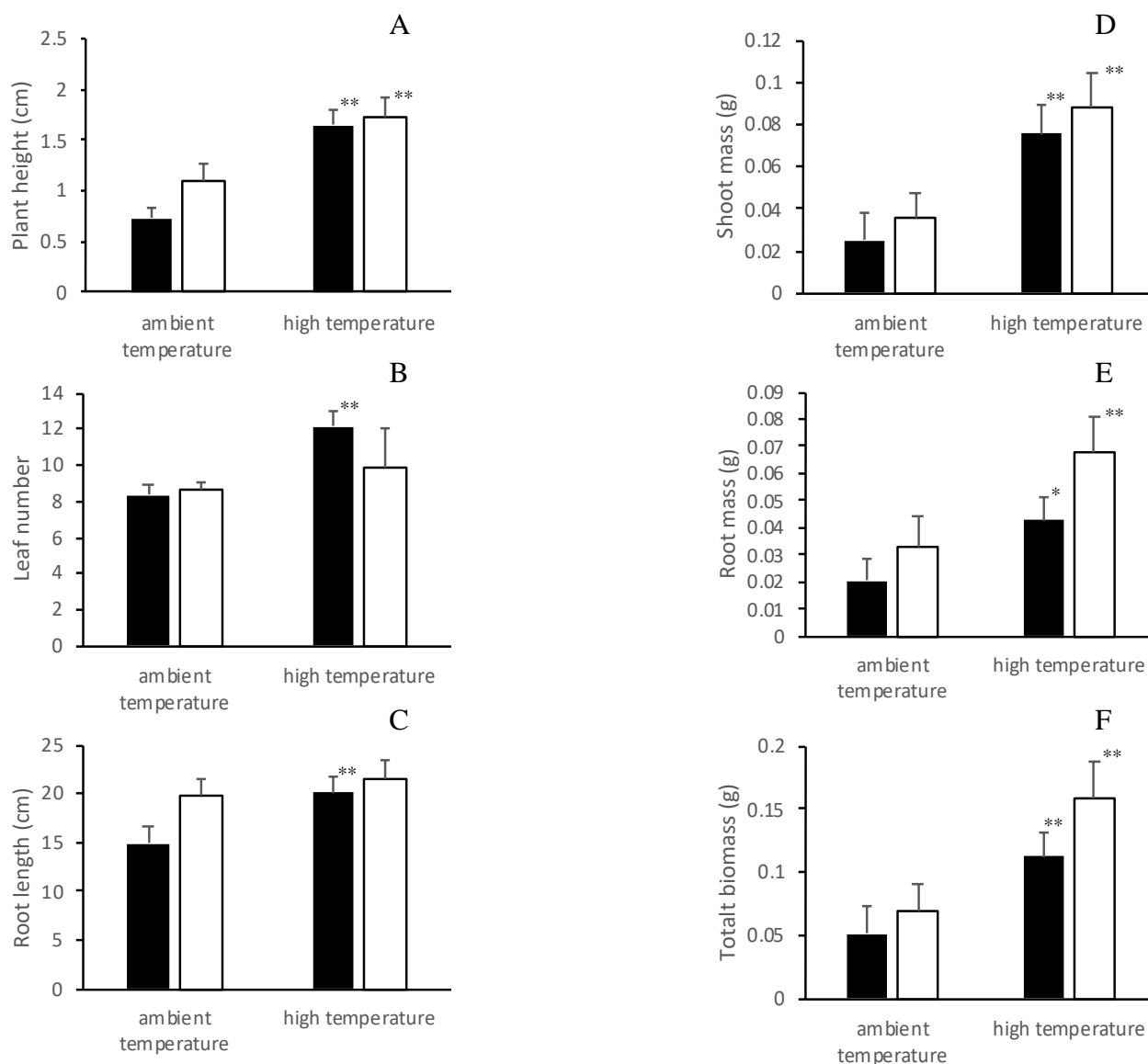
Figures

Figure 1. Height (**A**), number of leaves (**B**), root length (**C**), shoot mass (**D**), root mass (**E**), and total biomass (**F**) of rare *Borodinia perstellata* (open bars) and common *B. laevigata* (shaded bars) in response to light availability following 15 weeks in controlled-environment chambers. Bars represent means +/- 1 SE of the mean. Significances are reported if the mean trait in the high light is significantly different from ambient light conditions within each species. Two asterisks denote p ≤ 0.05 and one asterisk denotes p ≤ 0.10.
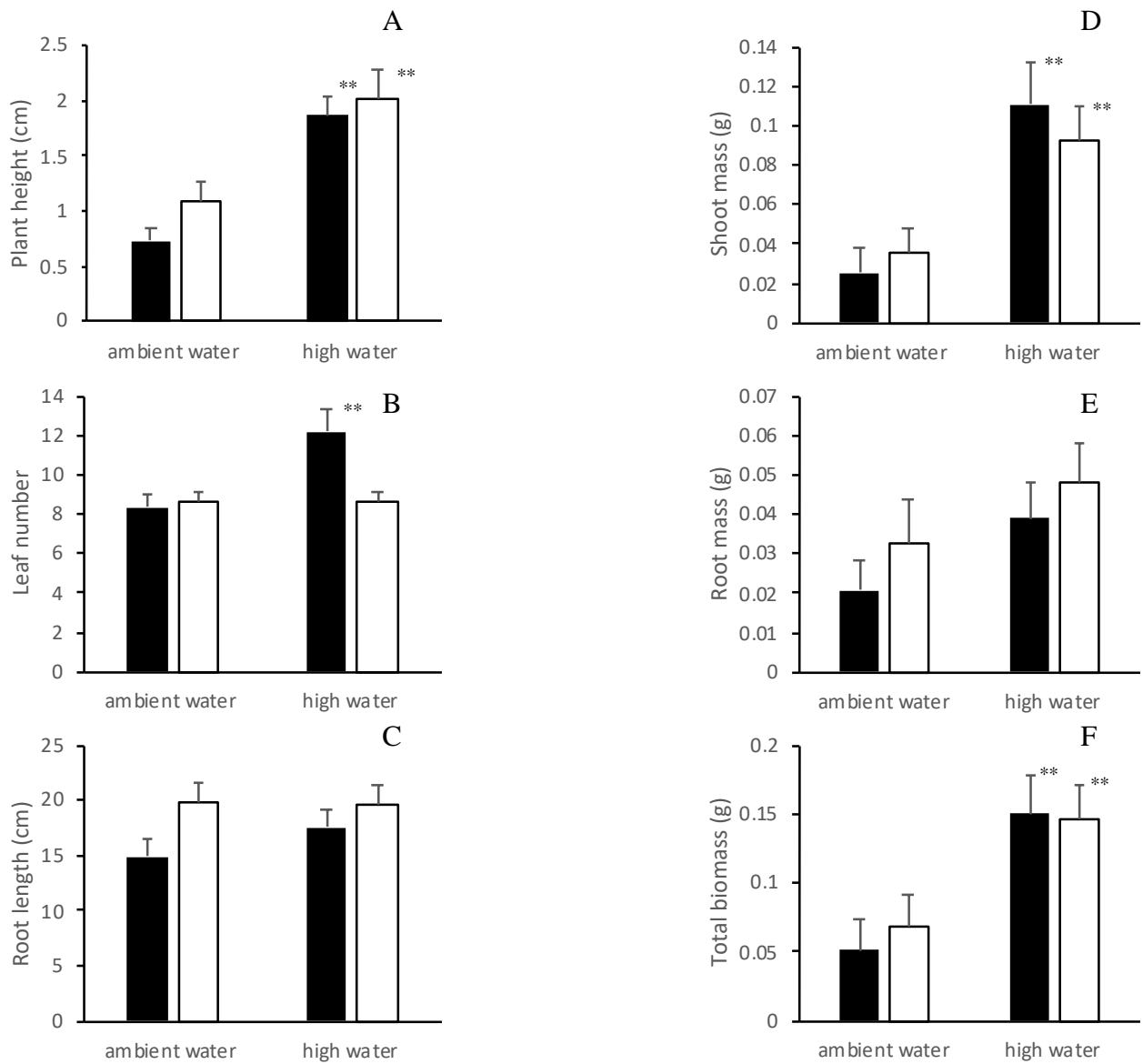
Figure 2. Height (**A**), number of leaves (**B**), root length (**C**), shoot mass (**D**), root mass (**E**), and total biomass (**F**) of rare *Borodinia perstellata* (open bars) and common *B. laevigata* (shaded bars) in response to water availability following 15 weeks in controlled-environment chambers. Bars represent means +/- 1 SE of the mean. Significances are reported if the mean trait in the high water is significantly different from ambient water conditions within each species. Two asterisks denote $p \leq 0.05$ and one asterisk denotes $0.05 \leq p \leq 0.10$.

Figure 3. Height (**A**), number of leaves (**B**), root length (**C**), shoot mass (**D**), root mass (**E**), and total biomass (**F**) of rare *Borodinia perstellata* (open bars) and common *B. laevigata* (shaded bars) in response to temperature level following 15 weeks in controlled-environment chambers. Bars represent means +/- 1 SE of the mean. Significances are reported if the mean trait in the high temperature is significantly different from ambient temperature conditions within each species. Two asterisks denote $p \leq 0.05$ and one asterisk denotes $0.05 \leq p \leq 0.10$.