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Exploring the role of local adaptation in the response
of *Maianthemum canadense* to climate warming

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Abstract

By the year 2100, it is projected that average global temperatures will increase by ~4°C. Shifts in species distributions have been evidenced as a common response to climate warming across taxonomic groups with migration to higher latitudes and elevations in response to warming being common. Species responses to climate warming can be influenced by the local adaptations of their populations. I hypothesized that populations of *M. canadense* from warmer locations would respond negatively to warming, while populations from cooler sites would exhibit neutral or positive responses to warming. *Maianthemum canadense* is a species that is associated with cool, moist microsites across its distribution. To examine the role of local adaptation within the context of projected climate warming across a wide-ranging species in the Appalachian region, I grew *Maianthemum canadense* individuals in controlled-environment growth chambers that simulated current and future projected average growing season temperatures throughout the sampled range. The individuals were propagated from rhizomes collected from distinct naturally occurring populations of this species in Tennessee, Virginia, Pennsylvania, and New York. As such, populations from warmer locations may already be experiencing the high temperature range limit for this species. I used a two-way factorial design with temperature assigned to growth chambers as main plots and population as a split-plot factor within chambers. Findings suggest that *M. canadense* does not respond well to warming overall at the species level and that populations in warmer parts of the current range could be most negatively impacted by future climate warming. Since *M. canadense* is a common understory monocot herb with wide

distribution throughout the Appalachian region, and as such, could represent the responses of similar species as a response to future warming.

Introduction

Global average temperatures are projected to warm by ~4°C by the year 2100 (IPCC 2014) due primarily to rising CO_2 emissions associated with anthropogenic activities (IPCC 2014). Studies suggest that plant species can be highly sensitive to climatic warming (Lindner 2010), and shifts in plant species distributions toward higher latitudes and elevations have been evidenced as a common response to climate warming (Chen 2011; Hickling et al. 2006; Hughes 2000; IPCC 2014; McCarty 2001; Parmesan et al. 1999; Parmesan & Yohe 2003; Thomas 2012; Walther et al. 2002). But the direction and magnitude of such responses can be species-specific due to distinct adaptations at the species level (Davis 2001; Dawes et al. 2010; Körner et al. 2005). Climate conditions have been associated with considerable local adaptations within species, and such local adaptations also could play a key role in how plant species as a whole will respond to climate warming. Such intraspecific differences can complicate our ability to predict species responses to climate warming (Linhart 1996; Joshi 2001; De Frenne 2011; Ågren 2012; De Frenne 2013; O'Neill 2008). But, recent ecological modeling efforts revealed that neglecting to consider the possible role of local adaptation in species responses to climate warming could lead to inaccurate predictions of future range shifts (Valladares 2014). Research investigating this potential role could improve our ability to make such predictions and could allow for generalizations of patterns of local adaptation across species.

Preliminary research recently conducted by Dr. Jennifer Boyd, who is serving as my research advisor at the University of Tennessee at Chattanooga, utilized a common garden approach to detect significant local adaptations in the responses of both herbaceous dicot (*Solidago caesia*; blue-stemmed goldenrod) and graminoid (*Carex aestivalis*; summer sedge) species distributed throughout the Appalachian region to projected climate warming. Specifically, her findings indicated that more southern populations of these species could respond negatively to future climate warming, while northern populations are more likely to exhibit neutral or positive responses to such warming. These results could reflect the fact that southern populations occur at or closer to the high temperature range limits of their species (Loehle 1998). Species of plants have increased in abundance at the higher elevation limits of their distribution while decreasing in abundance in their lower elevation limits, which demonstrates that they may be nearing the limit to which they can withstand warmer temperatures and will have a better chance of survival in cooler temperatures (Kopp 2013). Incorporating different plant life forms/functional types into this ongoing research could allow for broader generalizations of findings toward providing a better overall understanding of the potential role of local adaptation in species responses to climate warming.

To expand exploration of the potentially important role of local adaptation in the response plant species to climate warming, I conducted a common garden approach to compare growth and physiological responses to warming of distinct populations of the common herbaceous monocot *Maianthemum canadense* (Canada mayflower) sampled throughout the Appalachian region. Ultimately, my research aimed to elucidate how intraspecific variability in the response of *M. canadense* to climate warming could

influence its future distribution. My findings also could contribute to broader ongoing research to improve conceptual understanding of the influence of local adaptation in the responses of Appalachian plant species to climate warming. General trends in population-level responses to warming could be used to inform future species distribution modeling efforts for this region. Given the results of previous related research, I hypothesized that populations of *M. canadense* from currently warmer locations would respond negatively to simulated future climate warming, while populations from cooler sites would exhibit neutral or positive responses to warming.

Methods

To investigate the potential role of local adaptation in the response of *M. canadense* to climate warming throughout its Appalachian range, I conducted a common garden experiment in controlled-environment growth chambers at the University of Tennessee at Chattanooga. This experiment involved growing *M. canadense* individuals propagated from parent individuals collected from four distinct populations representing a wide distribution in the Appalachian region in conditions that simulated current and future growing season temperatures across the sampled range. A two-way factorial design was used with temperature assigned to growth chambers as main plots and population as a split-plot factor within chambers. Observable performance traits (i.e., growth rate, productivity, reproductive effort) were assessed along with physiological traits to help understand potentially underlying mechanisms of observed responses.

Field Collection of Propagules

Naturally occurring populations of *M. canadense* were sampled by Dr. Boyd and several UTC students during summer 2015 across the Appalachian region. Specifically, multiple rhizomes to allow for vegetative propagation of offspring were collected from ~18-20 parent plants of this species from each of four populations in the Cherokee National Forest, Monroe County, TN (elevation: ~1500 meters; 35.346579, -84.057580); Shenandoah National Park, Page County, VA (elevation: ~1200 meters; 38.285100, -78.673394); Prospect, Butler County, PA (elevation: ~400 meters ; 40.902943, -80.044883; and the Black Rock Forest, Orange County, NY(elevation: ~430 meters; 41.419906, -74.009343). Because this species is clonal, rhizomes were collected from ramets within each population that were at least ~5 m from each other. Rhizomes were stored in plastic bags with a small amount of moist field-collected soil at 4 ℃, and small samples were tested periodically to ensure that they remained viable until the onset of my experiment in May 2016.

Temperature Treatment

Environmental conditions, which included multiple levels of a temperature treatment, were controlled in three growth chambers (PGR15, Conviron, Winnipeg, MB). Light intensity, photoperiod, and relative humidity that simulated conditions of these factors typical in *M. candense* habitat were kept constant across the three chambers. Specifically, light, assessed as photosynthetically active radiation (PAR), was set to 200 μmol photons m^{-2} s^{-1} during 14 daylight hours followed by darkness during 10 hours each day to replicate forest understory conditions; relatively humidity of 80% was constant to simulate the moist habitat characteristic of this species and CO_2 was set to 400 ppm. One

chamber was programmed to provide current late spring/early summer average temperature in the coldest parts of the sampled range (14-22 ºC, day-night). A second chamber was programmed to provide late spring/early-summer average temperature in the warmest parts of the sampled range (18-26 ºC, day-night); this chamber also represented projected future late spring/early summer average temperature in the coldest parts of the sampled range as was estimated by adding 4 ºC to current average summer temperature. The third chamber was programmed to replicate late spring/early summer average temperature by adding 4 ºC to the current future temperature treatment level (22-30 ºC, day-night). We added 4 ºC to current average temperatures in accordance with projections of warming across the Appalachian region for the year 2100 that are based on a balanced emissions scenario that includes a combination of continued fossil fuel use and alternative energy sources scenario (IPCC 2014).

Plant Propagation & Care

Three rhizomes sampled from each of 7-8 parent plants from each of the four sampled populations (i.e., NY, PA, TN, VA) were planted in each of three 1-quart pots filled with a commercially available potting medium (Evergreen Top Soil, Rainbow Technology, Pelham, AL). The three pots from each parent plant were then evenly divided amongst the three chambers so that each individual was represented by three clones in each chamber (see Figure 1). All pots were watered every 2-3 d to saturation, and pots were rotated within chambers regularly to help minimize any effect of spatial homogeneity of conditions inside each chamber.

Data Collection

My experiment required that the emergence of *M. canadense* be recorded to detect which populations showed first signs of growth in each temperature treatment level. Emergence was recorded by daily observation when the plant was visible above the soil level. Because vegetative *M. canadense* individuals are characterized by simple single-leaf architecture, plant height from soil to the leaf base of each plant was assessed periodically as an observable performance trait. Leaf-level photosynthesis (A; μmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s; mol H_2O m^{-2} s^{-1}), and transpiration($E;$ mmol m^{-2} s^{-1}), were measured as potentially mechanistic traits underlying observable performance with a portable gas-exchange analyzer (LI-6400XT, LI-COR, Lincoln, Nebraska, USA). Chlorophyll content was measured as a related physiological metric using a chlorophyll content meter (CCM- 200, Optisciences, Serial No: 002326). All measurements were made at 6 w after emergence and again at 12 w after emergence following the date that emergence was first observed during the experiment. To assess the overall productivity of *M. canadense* as an additional performance measure, whole plants were harvested after 24 w. Specifically, I harvested the largest individual per pot, separated it into roots and shoots, and dried these parts separately in a laboratory oven at 58°C for 1 week. Once dry, roots and shoots were weighed and added together to calculate total biomass measurements. Intraspecific competition within pots would not have been a likely complication in my experiment because resources were not limited and the plants did not seem to be root bound when they were pulled up. Therefore, intraspecific competition would not have had a large impact on fitness in the experiment. Leaf mass per unit area was calculated by cutting out and weighing a $4cm^2$ block out of a piece of paper. Once

this was completed, I then traced the leaf of each remaining plant, cut them out and took the weight of the tracing. I then used a formula (4cm^2 /known weight (g) = unknown weight/y grams) to solve for the unknown area of the leaf.

Data analyses

The main effects and interactions of temperature and population as independent variables were determined on all measured dependent variables with two-way analysis of variance (ANOVA) performed with SPSS statistics software (Rel. 7.5.1., SPSS Inc., Chicago, IL). To assess the overall effect of climate warming at the species-level, I analyzed the main effect of temperature on *M. canadense* individuals across populations. To assess the potential role of local adaptation in the responses of this species to climate warming, I analyzed the main effect of population and its interaction with temperature. Mean differences were considered significant if $p \leq 0.05$. In the case of a significant interaction, I compared means of treatment combinations with least-significant difference (LSD) post-hoc analysis at the 0.05 probability level.

<div align="center">

Results

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Species-level responses to temperature

When considering the main effect of temperature (across populations) of *M. canadense,* my results indicate that this species has a generally negative response to increasing temperatures. Overall, *M. canadense* exhibited mostly negative responses of productivity and gas-exchange activity with more limited positive responses with increased temperature treatment levels. Specifically, plants were less productive in the

warmest two treatment levels than in the coolest treatment level ($F_{2,61}$ = 85.942, $p \leq$ 0.001). Specifically, plants grown in current northern temperature conditions produced more than triple the root mass and total dry mass than plants grown in warmer temperatures (see Figure 2). Plants grown in the coolest two temperature treatment levels also had up to three-times greater overall leaf mass than plants grown in projected future southern temperature conditions ($F_{2,61}$ = 89.591, $p \leq 0.001$ (see Figure 2). In contrast, temperature did not significantly affect the average height of *M. canadense* individuals ($F_{2,62}$ = 0.945, $p = 0.395$). The success of rhizome emergence also was not influenced significantly by temperature ($F_{2,74}$ = 0.476, $p = 0.623$).

Like many productivity measures, mean *A* ($F_{2,63}$ = 12.404, $p \leq 0.001$), *G* ($F_{2,63}$ = 53.769, $p \leq 0.001$), and *E* ($F_{2,63}$ = 1.022, $p \leq 0.001$) measured at 6w all declined significantly with warming, with the coolest temperature treatment exhibiting the highest rates, followed by the warmer, and warmest temperature treatments, respectively (see Figure 3). At 12 w, plants from the two warmest temperature treatment levels had lower rates of measured gas-exchange variables (*A*, $F_{2,60}$ = 17.016, $p \leq 0.001$; conductance, $F_{2,60}$ = 59.697, $p \leq 0.001$; *E*, $F_{2,60}$ = 61.004, $p \leq 0.001$) than plants grown in coolest conditions (see Figure 3). Specifically, in the warmest treatment conditions *A* was less than half of that exhibited in the coolest temperature treatment ($F_{2,60}$ = 17.016, $p \leq 0.001$). *G* ($F_{2,60}$ = 59.697, $p \leq 0.001$) in the warmest condition was approximately half of the mean conductance of the cooler conditions (see Figure 3). Leaf mass per unit area ($F_{2,61}$ = 12.734, $p \leq 0.001$) was greatest in the coolest temperature treatment and exhibited decreases in response to the warmest two temperature treatments.

Differences between populations

There were significant differences among sampled populations for the success of emergence and all measured physiological variables, but differences in measured growth variables between populations were more limited. Specifically, rhizomes collected from the most southern population (TN) exhibited the most successful emergence compared with rhizomes collected from the other three populations ($F_{3,74} = 8.274$, $p \leq 0.001$; Figure 4). Mean height of *M. canadense* individuals also varied significantly among the sampled populations ($F_{3,62} = 11.391$, $p \leq 0.001$) with plants propagated from the TN population having nearly double the average height of individuals propagated from other populations (Figure 6). In contrast, there were no significant differences in leaf mass ($F_{3,61} = 1.461$, $p = 0.236$), root mass ($F_{3,61} = 1.053$, $p = 0.377$), or total biomass ($F_{3,61} = 1.016$, $p = 0.394$) among the four populations.

When assessed at 6 w after emergence, A ($F_{3,63} = 5.503$, $p = 0.002$), G ($F_{3,63} = 4.561$, $p = 0.007$), and E ($F_{3,63} = 2.071$, $p = 0.115$) differed significantly among the distinct populations. Rates of all three variables were more than double for plants propagated from the TN population followed by plants propagated from the VA, NY, and PA populations, respectively (see Figure 5). At 12 w after emergence, plants propagated from the most southern population (TN) exhibited greater A ($F_{3,60} = 8.344$, $p \leq 0.001$), conductance ($F_{3,60} = 14.384$, $p \leq 0.001$), and E ($F_{3,60} = 16.406$, $p \leq 0.001$) than those propagated from the other sampled populations (see Figure 5). Leaf mass per unit area was did not differ significantly among populations ($F_{3,61} = 1.158$, $p = 0.335$).

Interactions between temperature and population

Although *M. canadense* was influenced by temperature and populations of this species differed significantly in numerous ways, these differences did not reflect local adaptations in growth responses to climate warming and local adaptations in physiological responses were limited. Specifically, emergence ($F_{6,74} = 1.696$, $p = 0.137$), , plant height ($F_{6,62} = 0.496$ $p = 0.828$), leaf mass ($F_{6,61} = 0.722$, $p = 0.634$), root mass ($F_{6,61} = 1.293$, $p = 0.278$), and total productivity ($F_{6,61} = 1.087$, $p = 0.383$) were not influenced significantly by the interaction of temperature and population.

When assessed at 6 w after emergence, A ($F_{6,63} = 1.450$, $p = 0.214$), conductance ($F_{6,63} = 2.044$, $p = 0.076$), and E ($F_{6,63} = 1.177$, $p = 0.333$) also were not influenced significantly by the interaction of temperature and population. However, when assessed at 12 w after emergence, both E ($F_{6,60} = 6.641$, $p \leq 0.001$) and conductance ($F_{6,60} = 6.684$, $p \leq 0.001$) were influenced significantly by this interaction. Specifically, E and conductance rates in the TN population that were subjected to the warmest temperature conditions exhibited negative responses compared with those in coolest temperature conditions. The direction of this response exhibited by the TN population was also exhibited by the NY, PA, and VA populations. Both E and G of plants from the most southern latitude (i.e., TN) experienced positive responses to warming. In contrast, PA populations were significantly different than all other populations in A ($F_{6,60} = 1.743$, $p = 0.131$), G ($F_{6,60} = 6.684$, $p \leq 0.001$) and E ($F_{6,60} = 6.641$, $p \leq 0.001$)(see Figure 5). Leaf mass per unit area ($F_{6,61} = 0.610$, $p = 0.721$) was the least in the TN population and greatest in the PA population, but also did not show significant differences.

Discussion

Potential impacts of climate warming on *M. canadense*

Overall, my results do not support the hypothesis that local adaptations would influence the response of *M. canadense* to warming in a way that could be predicted by the current locations of distinct populations of this species. Although the distinct sampled populations of *M. canadense* utilized for this experiment exhibited some significant differences in measured variables across temperature treatment levels, which suggests there are genetic differences between populations (i.e., local adaptations), local adaptations specific to warming responses were very limited. In general though, my results suggest that *M. canadense* may not respond well to projected warming throughout its distribution. Specifically, I found that many measured growth and physiological variables were affected negatively by warming as a main effect across populations of this species (see Figure 2 and Figure 3).

Due to its generally negative response to warming, the overall range of *M. canadense* may exhibit shifts to higher latitude and elevation in response to the ~4°C temperature increase that is expected to occur by year 2100 (IPCC 2014) because these areas are more likely to provide suitable habitat. Such shifts have been evidenced for other wide-ranging species of various taxonomic groups, including many plant species (Chen 2011; Hickling et al. 2006; Hughes 2000; IPCC 2014; McCarty 2001; Parmesan et al. 1999; Parmesan & Yohe 2003; Thomas 2012; Walther et al. 2002). For example, a global meta-analysis of nearly 100 species of birds, butterflies, and alpine herbs reported that the range limits of these species shifted ~6 km poleward and/or ~6 m upward in

elevation per decade on average in response to recent climate warming (Parmesan and

Yohe 2003).

       Previous studies of plant species have reported a link between growth and/or

physiological variables and fitness (which is ultimately measured by successful

reproduction; Mooney 1972; Reich et al. 2015). Although I did not measure reproductive

indicators of fitness directly in my study, the response of measured growth and

physiology variables to temperature across populations suggests that *M. canadense* may

experience its greatest fitness in relatively cool conditions. These ramifications could lead

to potential latitudinal and elevational shifts to more suitable habitats. In the southeastern

United States, *M. canadense* already is generally restricted to relatively cool microsites

found in very high elevations, which could suggest that it may disappear from the

southern end of its range in the future as climate warms.

The role of local adaptation in species responses to climate warming

       Local adaptations of plant species to climate have been evidenced across latitudes

(see Etterson & Shaw 2001, Joshi et al. 2001, Maron et al. 2004, Macel et al. 2007, De

Frenne et al. 2011); however, meta-analysis suggests that such adaptations may be less

common than generally assumed (Leimu & Fischer 2008). Within the context of

projected climate change, the study of intraspecific variability of species in response to

climate change could elucidate the potential role of local adaptations in future species

range shifts. But few studies have focused on patterns of local adaptations of plant

species within this context (Pauls et al. 2013). While the TN population exhibited the

most successful emergence and plants propagated from this population grew the tallest on

average when compared to all other populations, it was also the population for which field-collected rhizomes were most quickly placed into storage at 4°C prior to propagation for this experiment, which could have played a role in the positive responses that were observed. At 12w, the PA population exhibited a more negative response to temperature warming and was different than the NY, VA, and TN populations (see Figure 5). Because the PA population occurs at the lowest elevation of my sampled populations, this could suggest that low elevation populations of *M. canadense* may be most negatively impacted by future climate warming.

During historical periods of past climate warming, high elevation sites at low latitudes have acted as refugia for some plant species because they provided cooler conditions in regions that otherwise became too warm for the viability of those species (Ulrey 2016). For example, *Abies fraseri* (Frasier fir), *Geum radiatum* (Appalachian avens), and *Picea rubens* (red spruce) in the southern Appalachians are currently found growing in high elevation sites that are thought to have acted as refugia for these species as climate warmed following the Last Glacial Maximum (Moore 2012; Ulrey 2016). Modeling efforts have suggested that negative responses to future warming will be exhibited by these and other plant species that are generally restricted at present to high elevations in the southern Appalachians, including *Liatris helleri* (Heller's blazing star), *Calamagrostis cainii* (Cain's reedgrass)*, Carex misera* (wretched sedge), *Hustonia purpurea* (Venus' purpleflower)*, Solidago spithamaea* (Blueridge goldenrod)*, Trichophorum cespitosum* (deergrass; Godt 1996; Wiser 1994; Wiser 1998).

Confounding abiotic and biotic considerations

Although not studied in my experiment, soil moisture availability due to the combination of warming and altered precipitation regimes is another factor that could influence the response of *M. canadense* to future climate change. While climate models generally agree that climate will warm, there is disagreement among models about how precipitation amounts will change in the future across the eastern United States (IPCC 2014); however, models do suggest that warming will be accompanied by more variable rainfall regimes that could lead to more instances of drought conditions in between rainfall events (IPCC 2014). If such conditions become more common in the future, *M. canadense* could be negatively affected given its typical association with relatively moist microsites across its range (Cronan 1985).

Although the frequent determination of species range boundaries by temperature and precipitation limits (Woodward 1987) suggests that climate is fundamentally influential to differences in species distributions, variations in non-climatic abiotic factors, dispersal strategies, and biotic interactions also could influence species ranges (Chen et al. 2011). Even if a species is able to shift to an area with more suitable climate (e.g., populations of *M. canadense* could shift to higher latitudes or elevations in the future), new locations may not provide suitable edaphic conditions. As an example, *M. canadense* is reported to be intolerant of acidic soil conditions (TWC Staff 2014), and soil pH could become more acidic in response to climate warming (Rengel 2011). In addition, *M. canadense* is often found in a soil that is rich in humus (TWC Staff 2014), and soil humus may decrease in response to future climate change (Prietzel 2016).

Biotic conditions also play a role in the distributions of plant species (Brown 1984) and future changes in these conditions could influence the ability of plant species

to migrate in response to climate change. Although vegetative reproduction is the dominant mode of reproduction for *M. canadense* (Wilson 2005), sexual reproduction does occur in this species and is important for maintaining genetic diversity among individuals (Bengtsson 2003). As such, the presence of suitable pollinators, such as solitary bees, bee flies, and syrphids (Barrett 1987), also could impact the future distribution of *M. canadense*. Many of these and other pollinators have exhibited a decline in abundance and diversity in response to recent climate warming (Archer 2014), and such losses in response to future warming could have negative consequences for *M. canadense*. In addition, climate warming has the potential to impact the phenology of plant and pollinator species, which could lead to pollinator 'mismatches' that negatively impact *M. canadense* (Hegland 2008). In addition to its potential dependence on insect pollinators, *M. canadense* relies on animals like (*Bonasa umbellus*) ruffed grouse, *Peromyscus leucopus* (white-footed mouse), and *Tamias striatus* (eastern chipmunk) for seed dispersal (Hilty 2016), and the presence of these species also could impact the ability of *M. canadense* to migrate.

Although also not studied in my research, mycorrhizal associations of *M. canadense* also could play a role in the future distribution of this species given their often vital role in nutrient acquisition. However, because *M. canadense* can be colonized by many species of mycorrhizal fungi (Burke 2008), these relationships are not as concerning as other biotic conditions.

Conclusion

Overall, my findings suggest that *M. canadense* may be negatively impacted by predicted future climate warming and may experience changes in its distribution toward cooler locations, but that such changes will occur similarly across the species and not be influenced heavily by local adaptations. Because many other climatic and non-climatic factors also could influence the distribution of *M. canadense*, including edaphic conditions and the presence of effective pollinators and seed dispersers, I suggest that future research investigate these factors as main effects and within the context of future warming. Understanding the potential response of *M. canadense* and other plant species to projected climate change could provide land managers with knowledge that could guide species conservation efforts.

Literature Cited

Ågren J, Schemske DW (2012) Reciprocal transplants demonstrate strong adaptive
differentiation of the model organism *Arabidopsis thaliana* in its native range. *New Phytologist* 194: 1112-1122.

Archer CR, Pirk CWW, Carvalheiro LG, Nicolson SW (2014) Economic and ecological
implications of geographic bias in pollinator ecology in the light of pollinator declines. *Oikos 123*: 401-407.

Atkins KE, Travis JMJ (2010) "Local adaptation and the evolution of species' ranges
under climate change." *Journal of Theoretical Biology* 266: 449-457.

Barrett, S. C., & Helenurm, K. (1987). The reproductive biology of boreal forest herbs. I.
Breeding systems and pollination. *Canadian Journal of Botany* 65: 2036-2046.

Bengtsson BO (2003) Genetic variation in organisms with sexual and asexual
reproduction. *Journal of evolutionary biology* 16: 189-199.

Berliner R, Torrey JG (1989) Studies on mycorrhizal associations in Harvard Forest,
Massachusetts. *Canadian Journal of Botany 67*: 2245-2251.

Bischoff A, Cremieux L, Smilauerova M, Lawson CS, Mortimer SR, Dolezal J, Lanta V,
Edwards AR, Brook AJ, Macel M, Leps J, Steinger T, Muller-Sharer H (2006) Detecting local adaptation in widespread grassland species–the importance of scale and local plant community. *Journal of Ecology* 94: 1130-1142.

Brown JH (1984) On the relationship between abundance and distribution of species. *The american naturalist* 124: 255-279.

Burke DJ (2008) Effects of Alliaria petiolata (garlic mustard; Brassicaceae) on mycorrhizal colonization and community structure in three herbaceous plants in a mixed deciduous forest. *American Journal of Botany*, 95: 1416-1425

Chan KY (2011) Climate Change on Soil Structure and Soil Health: Impacts and Adaptation. *Soil Health and Climate Change* 49-67. Springer Berlin Heidelberg.

Chen IC, Hill JK, Ohlemuelleer R, Roy DB, Thomas CD (2011) Rapid range shift of species associated with high levels of climate. *Science* 333: 1024-1026.

Cronan CS, DesMeules MR (1985) A comparison of vegetative cover and tree community structure in three forested Adirondack watersheds. *Canadian Journal of Forest Research.* 15:881-889.

Davis MB, Shaw RG (2001) Range shifts and adaptive responses to quaternary climate change. *Science* 292: 673-679.

Dawes MA, Hättenschwiler S, Bebi P, Hagedorn F, Handa IT, Körner C, Rixen C (2010) Species-specific tree growth responses to 9 years of CO_2 enrichment at the alpine treeline. *Journal of Ecology* 99: 383-394.

De Frenne P, Brunet J, Shevtsova A, Kolb A, Graae BJ, Chabrerie O, Cousins SAO, Dococq G, De Schrijver A, Diekmann M, Gruwez R, Heinken T, Hermy M, Nilsson

C, Stanton S, Tack W, Willaert J, Verheyen K (2011) Temperature effects on forest
herbs assessed by warming and transplant experiments along a latitudinal gradient.
Global Change Biology 17: 3240-3253.

De Frenne P, Coomes DA, De Schrijver A, Staelens J, Alexander JM, Bernhardt-
Römermann M, Brunet J, Chabrerie O, Chiarucci A, den Ouden J, Lutz Eckstein R,
Graae BJ, Gruwez R, Hédl R, Hermy M, Kolb A, Mårell A, Mullender S, Olsen SL,
Orczewska A, Peterken G, Petrík P, Plue J, Simonson WD, Tomescu CV,
Vangansbeke P, Verstraeten G, Verterdal L, Wulf M, Verheyen K (2013) Plant
movements and climate warming: intraspecific variation in growth responses to
nonlocal soils. *New Phytologist* 202: 431-441.

Etterson JR, Shaw RG (2001) Evolution in response to global warming. *Science* 294:
151-154.

Godt MJW, Johnson BR, Hamrick JL (1996) Genetic diversity and population size in
four rare southern Appalachian plant species. *Conservation Biology* 10: 796-805.

Hegland SJ, Nielsen A, Lázaro A, Bjerknes AL, Totland Ø (2009) How does climate
warming affect plant-pollinator interactions? *Ecology letters*, 12: 184-195.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide
range of taxonomic groups are expanding polewards. *Global change biology* 12:
450-455.

Hilty J (2016) Woodland wildflowers of Illinois. Canada Mayflower.

Illinoiswildflowers.info

Hughes L (2000) Biological consequences of global warming: is the signal already

apparent? *Trends in Ecology & Evolution* 15: 56-61.

Hungate BA, Dukes JS, Shaw MR, Luo Y, Field CB (2003) Nitrogen and climate change.

Science 302: 1512-1513.

Ikeda H, Senni K, Fujii N, Setoguchi H (2009) High mountains of the Japanese

archipelago as refugia for arctic–alpine plants: phylogeography of Loiseleuria

procumbens (L.) Desvaux (Ericaceae). *Biological Journal of the Linnean Society*

97: 403-412.

IPCC, 2014: Summary for policymakers. In: *Climate Change 2014: Impacts, Adaptation,*

and Vulnerability.   Part A: Global and Sectoral Aspects. Contribution of Working

Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate

Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E.

Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel,

A.N. Levy, S. MacCracken,   P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge

University Press, Cambridge,   United Kingdom and New York, NY, USA, pp. 1-

32.

Joshi J, Schmid B, Caldeira MC, Dimitrakopoulos PG, Good J, Harris R, Hector A, Huss-

Danell K, Jumpponen A, Minns A, Mulder CPH, Pereira JS, Prinz A, Scherer-

Lorenzen M, Siamantziouras A-SD, Terry AC, Troumbis AY, Lawton JH (2001)

Local adaptation enhances performance of common plant species. *Ecology Letters* 4: 536-544.

Kopp CW, Elsa EC (2014) Shifts in plant species elevational range limits and abundances observed over nearly five decades in a western North America mountain range. *Journal of Vegetation Science* 25:135-146.

Körner C, Asshoff R, Bignucolo O, Hättenschwiler S, Keel SG, Paláez-Riedl S, Pepin S, Siegwolf RW, Zotz G (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. *Science* 309:1360-1362.

Kimball S, Gremer JR, Angert AL, Huxman TE, Venable DL (2012) Fitness and physiology in a variable environment. *Oecologia* 169, 319-329.

Leadley P, Pereira HM, Alkemade R, Fernandez-Manjarres JF, Proenca V, Scharlemann JPW (2010) Biodiversity scenarios: projections of 21st century change in biodiversity and associated ecosystem services. *Secretariat of the Convention on Biological Diversity* 1–132

Leimu R, Fischer M (2008) A meta-analysis of local adaptation in plants. *PloS one* 3: e4010.

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolstrom M, Lexer MJ, Marchetti M (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management* 259: 698-709.

Linhart YB, Grant MC (1996) Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* 27: 237-277.

Loehle C (1998) Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography* 25: 735-742.

Luo Y, Su B, Currie WS, Dukes JS, Finzi A, Hartwig U, Hungate B, McMurtrie RE, Oren R, Parton WJ, Pataki DE, Shaw RM, Zak DR, Field CB (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience* 54: 731-739.

Macel M, Lawson CS, Mortimer SR, Smilauerova M, Bischoff A, Crémieux L, Dolezal J, Edwards AR, Lanta V, Bezemer TM, van der Putten WH, Igual JM, Rodriguez-Barrueco C, Müller-Schärer H, Steinger T (2007) Climate vs. soil factors in local adaptation of two common plant species. *Ecology* 88: 424-433.

Maron JL, Vila M, Bommarco R, Elmendorf S, Beardsley P (2004) Rapid evolution of an invasive plant. *Ecological Monographs* 74: 261-280.

McCarty J (2001) Ecological consequences of recent climate change. *Conservation biology* 15: 320-331.

Moore M (2012) Ancient mountaintop species are most vulnerable as Appalachia warms. *The Appalachian Voice* 3: 12-13.

Mooney HA (1972) The carbon balance of plants. *Annual Reviews of Ecology and Systematics* 3:315–346.

O'Neill GA, Hamann A, Wang T (2008) Accounting for population variation improves

   estimates of the impact of climate change on species' growth and distribution.

   Journal of Applied Ecology 45.4: 1040-1049.

Parmesan C, Ryrholm N, Stefanescu C, Hill J (1999) Poleward shifts in geographical

   ranges of butterfly species associated with regional warming. *Nature* 399: 579-583.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts

   across natural systems. *Nature* 421: 37-42.

Parolo G, Rossi G (2008) Upward migration of vascular plants following a climate

   warming trend in the Alps. *Basic and Applied Ecology* 9: 100-107.

Prietzel J, Zimmermann L, Schubert A, Christophel D (2016) Organic matter losses in

   German Alps forest soils since the 1970s most likely caused by warming. *Nature

   Geoscience* 9: 543-548.

Reich PB, Sendall KM, Rice K, Rich RL, Stefanski A, Hobbie SE, Montgomery RA

   (2015) Geographic range predicts photosynthetic and growth responses to

   warming in co-occurring tree species. *Nature Climate Change* 5:148–152

Rengel Z (2011) Soil pH, soil health and climate change. *Soil health and climate

   change* 69-85.

Richter GM, Seminov MA (2005) Modelling impacts of climate change on wheat yields

   in England and Wales: assessing drought risks. *Agricultural Systems* 84.1: 77-97.

Thomas CD, Gillingham PK, Bradbury RB, Roy DB, Anderson BJ, Baxter JM, Bourn
NAD, Crick HQP, Findon RA, Fox R, Hodgson JA, Holt AR, Morecroft MD,
O'Hanlon NJ, Oliver TH, Pearce-Higgins JW, Procter DA, Thomas JA, Walker KJ,
Walmsley CA, Wilson RJ, Hill JK (2012) Protected areas facilitate species' range
expansions. *Proceedings of the National Academy of Sciences* 109.35: 14063-14068.

TWC Staff (2014) The University of Texas at Austin. Ladybird Johnson Wildflower
Center. Plant Database. *Maianthemum canadense*. wildflower.org

Ulrey C, Quintana-Ascencio PF, Kauffman, G, Smith AB, Menges ES (2016) Life at the
top: Long-term demography, microclimatic refugia, and responses to climate
change for a high-elevation southern Appalachian endemic plant. *Biological
Conservation* 200: 80-92.

Valladares F, Matesanz, Guilhaumon F, Araújo, Balaguer L, Benito-Garzón M, Cornwell
W, Gianoli E, van Kleunen M, Naya DE, Nicotra AB, Poorter H, Zavala MA (2014)
The effects of phenotypic plasticity and local adaptation on forecasts of species
range shifts under climate change. *Ecology Letters* 17: 1351-1364.

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM,
Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change.
Nature 416: 389-395.

Wilson AS, Van der Kamp BJ, Ritland C (2005) Opportunities for geitonogamy in the
clonal herb Maianthemum dilatatum. *Botany 83*: 1082-1087.

Wiser SK (1994) High-elevation cliffs and outcrops of the southern Appalachians:

    vascular plants and biogeography. *Castanea* 85-116.

Wiser SK, Peet RK, White PS (1998) Prediction of rare-plant occurrence: a Southern

    Appalachian example. *Ecological Applications* 8: 909-920.

Woodward FI (1987) Climate and Plant Distribution. Cambridge University Press, Cambridge,

    UK.

Figure Legends

Figure 1. My experimental design consisting of three growth chambers used as main temperature treatment plots, each containing clones of 7-8 parent plants from each of four populations of *Maianthemum canadense* throughout the Appalachian region (i.e., population as a split-plot treatment). Current chambers represented average late spring/early summer night/daily maximum temperatures in the coolest part of the sampled range; future chambers simulated 4°C warming relative to current conditions.

Figure 2. Total dry mass, leaf lass and root mass of *Maianthemum canadense* individuals propagated from rhizomes collected from distinct naturally occurring populations throughout the Appalachian region grown in current and projected future average daily maximum temperatures. Bars depict mean values +/- 1 SD of the mean. Different lowercase letters above bars depict significant differences between mean values.

Figure 3. Photosynthetic, transpiration, and conductance rates of *Maianthemum canadense* individuals propagated from rhizomes collected from populations sampled throughout its Appalachian range grown in current and projected future mean growing season temperatures across the sampled range. Bars depict mean values +/- 1 SD of the mean. Different lowercase letters above bars depict significant differences between mean values.

Figure 4. Total Emergence (the number of plants that emerged throughout the first 12 weeks of my experiment) of *Maianthemum canadense* individuals propagated from rhizomes collected from distinct naturally occurring populations throughout the Appalachian region grown in future mean growing season temperatures.

Figure 5. Photosynthetic, transpiration, and conductance rates of *Maianthemum canadense* individuals propagated from rhizomes collected from populations sampled throughout its Appalachian range grown in current and projected future mean growing season temperatures across the sampled range. Bars depict mean values +/- 1 SD of the mean. Different lowercase letters above bars depict significant differences between mean values.

Figure 6. Height of *Maianthemum canadense* individuals propagated from rhizomes collected from distinct naturally occurring populations throughout the Appalachian region grown in current and projected future mean growing season temperatures Bars depict mean values +/- 1 SD of the mean.
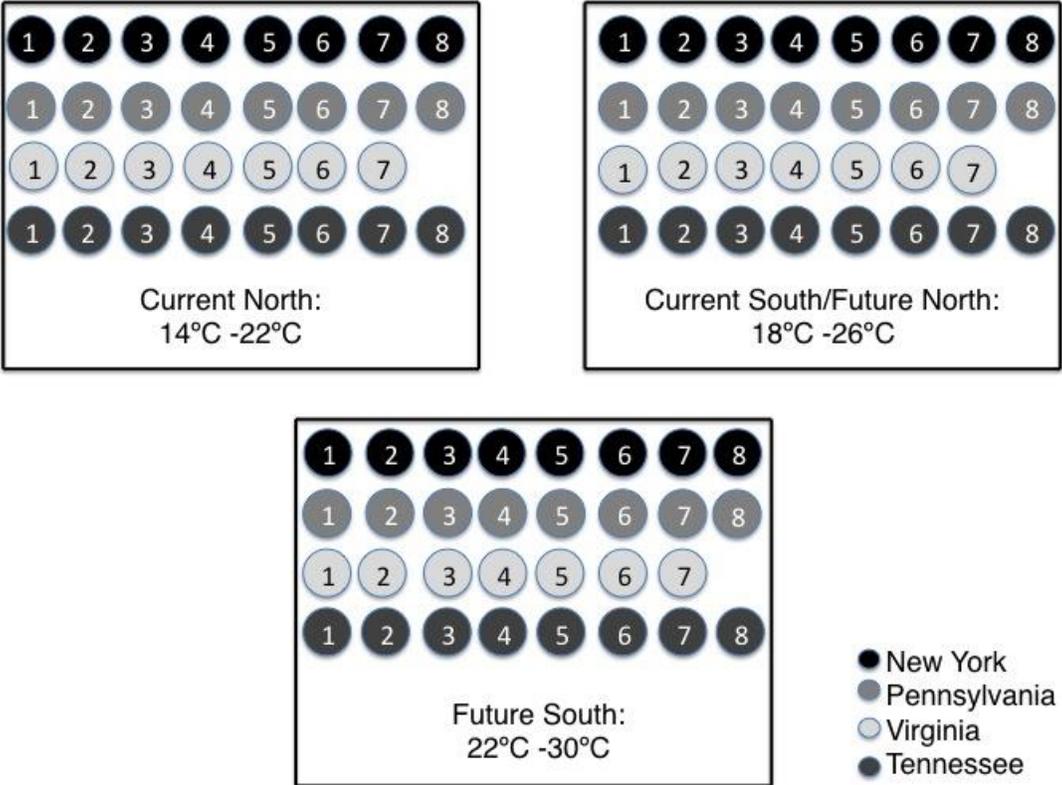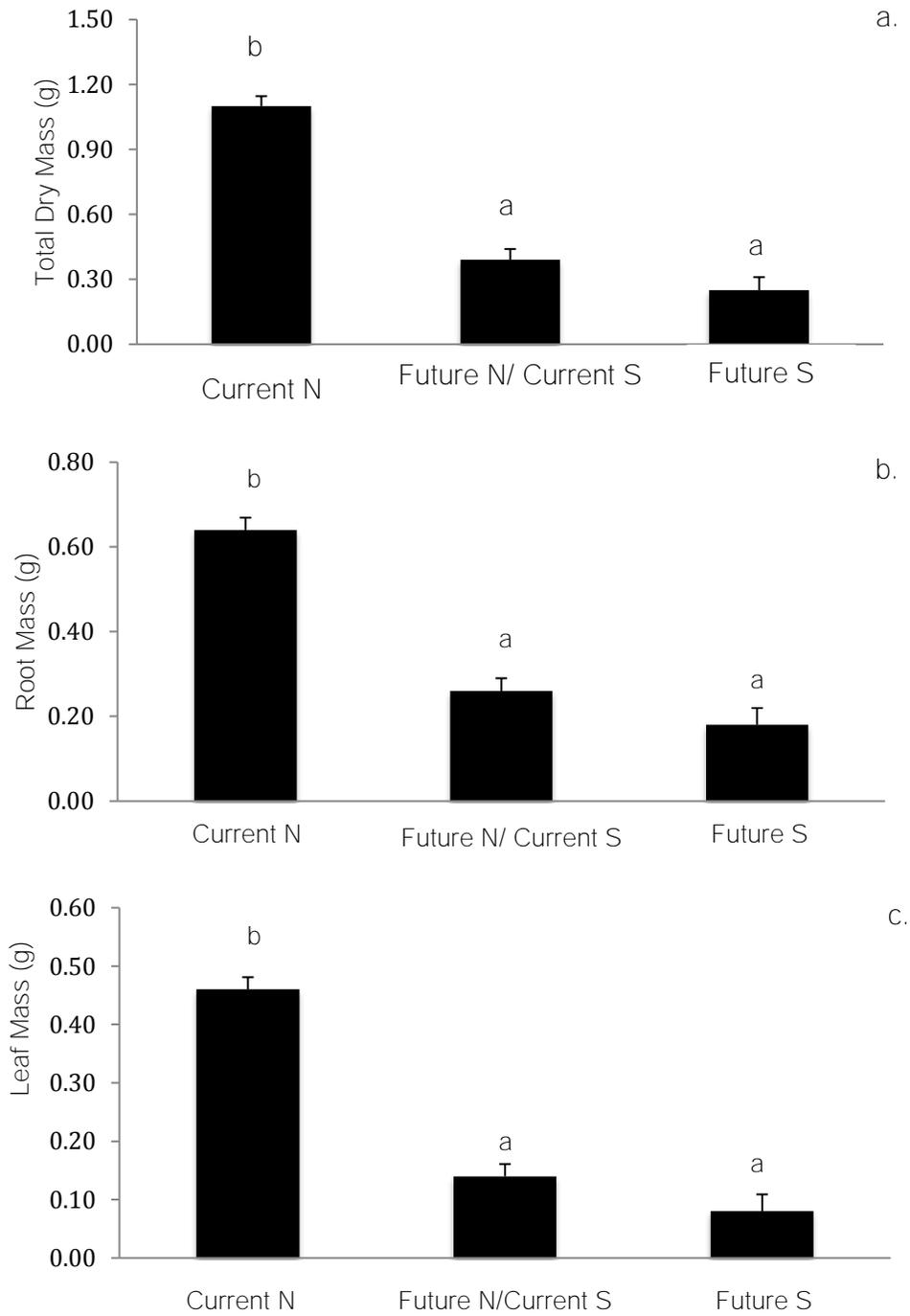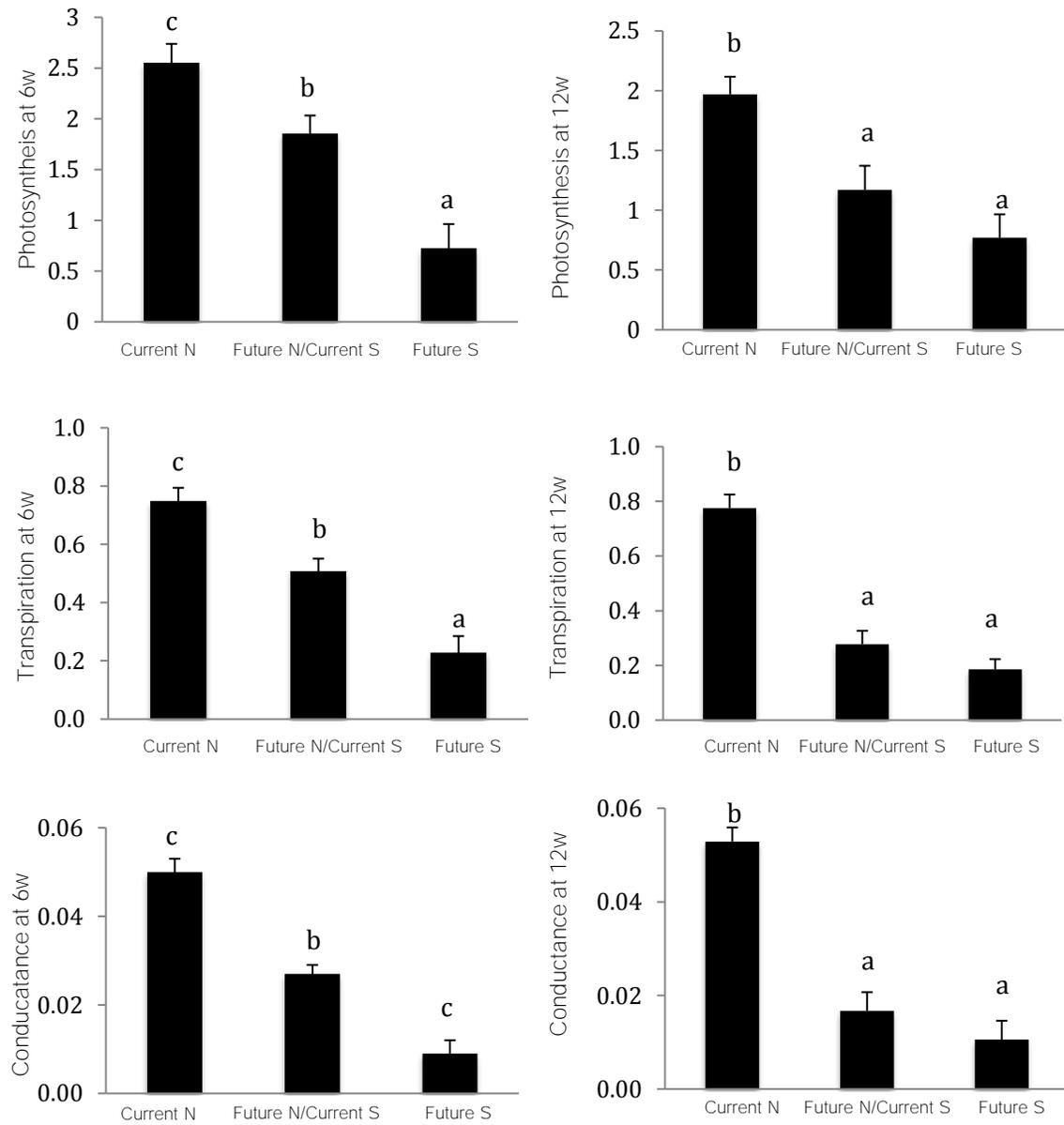
Figure 1.

Current North:
14°C -22°C

Current South/Future North:
18°C -26°C

Future South:
22°C -30°C

● New York
● Pennsylvania
○ Virginia
● Tennessee

Figure 2.

a.

b.

c.

Figure 3.

Figure 4.

Figure 5.

Figure 6.