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Intraspecific variation in response to warming across levels of organization: a test with *Solidago altissima*

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Abstract. Plant species, and the traits associated with them, can help buffer ecosystems to environmental perturbations. Few studies have examined whether within species variation, both among and within populations, can similarly buffer ecosystems to environmental perturbations, such as climatic warming, across levels of organization. Using a dominant plant species in the eastern US, *Solidago altissima*, we examined whether genotypes of the same species from both southern and northern latitude populations exhibited differential short-term responses to temperature at the cell, leaf, and plant level. At the cell level we quantified the production of reactive oxygen species (by-product of temperature stress) and total oxygen radical antioxidant capacity (which ameliorates temperature stress by-products). At the leaf and plant levels, we measured CO_2 assimilation. Increasing temperatures had strong negative impacts on plant-level carbon gain, but weak impacts on cell-level antioxidant capacity. Southern latitude genotypes had greater total antioxidant capacity, but lower leaf-level carbon gain, than did northern genotypes under elevated temperature. At the plant level, northern and southern genotypes exhibited similar declines in carbon gain under elevated temperature, likely because total plant leaf area was higher for southern genotypes than northern genotypes, which compensated for their lower per unit area leaf-level carbon gain. Overall, short-term temperature-induced declines in carbon gain at the plant level may scale to reduce within species variation, both across and within populations, potentially altering ecosystem carbon cycling.

Key words: carbon gain; cell level; leaf level; northern genotypes; plant level; population; *Solidago altissima;* southern genotypes; temperature; warming.

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INTRODUCTION

Predicting the responses of species to climate change is a fundamental challenge, especially near range boundaries where the effects of warming are likely to be most dramatic (Angert 2011, De Frenne 2011*a*). Plant species can vary considerably in morphological and physiological traits both within and across latitudinal gradients and such variation may influence that species' responses to climate change along with associated ecosystem processes such as net primary productivity (NPP) and carbon (C) cycling (Hooper et al. 2005). Studies on plants along

temperature gradients show there is extensive trait variation among and within species, especially between northern and southern populations (Diaz et al. 2004, De Frenne et al. 2011*b*). Linking plant traits to ecosystem processes within and across species along latitudinal gradients may lead to a better understanding of the underlying processes shaping C cycling locally and globally in the context of climatic change.

Variation in morphological and physiological traits within species, like variation across species, has been shown to influence individual performance, community dynamics and ecosystem processes (Booth and Grime 2003, Schweitzer et al. 2005, Crutsinger et al. 2006, Johnson et al. 2006, Classen et al. 2007, Hughes et al. 2008, Cianciaruso et al. 2009, Crutsinger et al. 2009, Albert et al. 2010, Jung et al. 2010). Crutsinger et al. (2006) documented that plots with greater intra-specific diversity in a dominant old-field species (*Solidago altissima*) led to greater aboveground net primary productivity (ANPP) and higher arthropod diversity than plots with lower intra-specific diversity. One interpretation of this result is that variance in physiological and morphological traits among *Solidago altissima* genotypes promoted greater resource complementarity in diversity treatments generating greater ANPP and greater diversity across trophic levels (Hooper et al. 2005). Few studies, however, have examined the influence of within-species variation, especially comparing individuals from range boundaries (De Frenne et al. 2011*a*), in terms of how such trait variation influences C cycling under warming.

To date, research addressing the impact of climatic warming on individual species largely focused on a single level of organization without examining whether the observed responses to warming scale across levels of organization (Petchey et al. 2004, Bailey et al. 2009, Purdy et al. 2010, Woodward et al. 2010). Scaling biochemical and physiological constraints to elevated temperature, from cells to leaves to individuals may enable scientists to better predict the underlying processes associated with atmospheric and climatic change impacts at local and global scales. At the lowest level of organization, the cell level, studies have documented an increase in the production of reactive oxygen species (ROS) H_2O_2 (Chen and Hartman 1995, Kim and Portis 2004) under elevated temperature linked to reduced photosynthetic capacity both within and across species (Snider et al. 2010, Weston et al. 2011). The ability of species and/or genotypes to scavenge ROS therefore will determine leaf and potentially plant-level photosynthetic capacity under warming (e.g., reviewed in Berry and Bjorkman 1980). Recently a number of studies have implicated increased cell-level antioxidant activity with enhanced thermal tolerance among plant genotypes (Larkindale and Huang 2004, Snider et al. 2010). Furthermore, linking biochemical and physiological constraints to morphological trait variation will elucidate potential trade-offs in temperature responses both within and across species (Bailey et al. 2009).

Our study addressed differences in temperature responses at the cell (ROS production and total antioxidant capacity), leaf, and plant level (CO_2 assimilation) among genotypes from populations near the range boundaries of a dominant old-field plant species distributed along a latitudinal gradient. We assessed whether constraints to heat stress scaled across levels of organization among genotypes in the same species and whether temperature responses vary in northern vs. southern *Solidago* genotypes. To examine whether temperature may differentially alter the responses of *Solidago* genotypes from southern and northern populations, we conducted a growth chamber experiment. We measured temperature response curves, across 8 temperature levels, on southern and northern latitude genotypes of *Solidago altissima* and quantified cell, leaf, and plant level responses. We predicted that: (1) *Solidago* temperature responses would be greatest at the lowest level organization, the cell level, because of fewer levels below to counteract the overall effect of temperature. *Solidago* temperature responses would be the lowest at the highest level of organization, the plant level, because of several levels below that would likely counteract the overall effect of temperature. Thus, structure and functional complexity at higher levels of organization may buffer warming effects, (2) greater cell-level antioxidant capacity of southern than northern populations under heat stress would promote greater leaf and plant-level C gain due to the reduction of heat stress by-products that may be detrimental to

photosynthetic capacity, and (3) variation in morphological traits across southern and northern populations will likely shape temperature responses as bigger individuals from southern populations may outperform smaller individuals from northern populations simply by having greater C reserves for allocation toward heat stress defense and C gain than northern populations.

Methods

Solidago altissima (hereafter *Solidago*) is a dominant plant species in old-field ecosystems (Schmitz 2003, Abrahamson et al. 2005, Schmitz 2008, Wise and Abrahamson 2008, Souza et al. 2011; Souza et al., *in press*), across a range of thermal zones in eastern North America, from Florida (average January and July temperatures = 26.6°C and 32.3°C, respectively) to Maine (average January and July temperatures = 4.2°C and 26.6°C, respectively), and has significant morphological trait variation shaping ecosystem processes (Crutsinger et al. 2006, Crutsinger et al. 2008, Crutsinger et al. 2009). Additionally, predicted increases in global temperatures range from 1.5–1.9°C to 3.4–6.1°C, which would raise the average growing season temperature of *Solidago* up to ~37°C in Florida and ~31°C in Maine.

We chose genotypes from near the northern and southern ends of *Solidago*'s geographic distribution because we were interested in documenting temperature responses of 'warm-adapted' (southern individuals) and 'cool-adapted' (northern individuals) populations. We collected 35 *Solidago* genotypes across northern (15 genotypes from three old-field sites near Stafford, Connecticut) and southern (20 genotypes from three old-field sites near Oak Ridge, Tennessee) latitude populations in 2009. *Solidago* genotypes from northern populations experience a mean annual temperature of 15.5°C (winter = −0.4°C, summer = 23.2°C), while *Solidago* genotypes from southern populations experienced a mean annual temperature of 22.5°C (winter = 2.4°C, summer = 24.8°C). Each old-field site we surveyed, in northern and southern locations, represented a continuous *Solidago* population. We excavated rhizomes from each *Solidago* genotype from natural patches growing 50–150 m apart. Given the majority of *Solidago*'s reproduction takes place vegetatively rather than sexually, such spatial separation (50–150 m) between patches ensured that we were obtaining different individuals (i.e., genotypes) (Crutsinger et al. 2006). Rhizomes were cut into 3-cm sections, placed in flats containing sterilized potting soil (Pro-Mix BX, Premier Brands, New Rochelle, NY) and root stimulator (Roots 2, Roots OSIA, Independence, MO). They were grown in a greenhouse (at 25°C) for 12 weeks and fertilized as needed. Northern and southern populations did not differ in rhizome volume ($F = 0.0004$, $P = 0.98$). Similarly, within southern populations rhizome volume did not differ among genotypes ($F = 1.26$, $P = 0.37$), but at northern populations there was a significant difference in rhizome volumes amongst genotypes ($F = 6.72$, $P = 0.01$). Previous studies addressing temperature responses within and across species have also grown species and/or genotypes at 25°C prior to conducting temperature response curves (Snider et al. 2010, Weston et al. 2011).

In June and July of 2009, we selected ten *Solidago* genotypes that significantly diverged in morphological traits (i.e., represented a full range of morphological traits within northern and within southern genotypes) from across northern and southern populations (southern $n = 5$, northern $n = 5$). The morphological traits we used to select genotypes included: leaf width, leaf length, leaf area, and internode space. The selected genotypes originated from all three sampled populations in southern and northern locations, and for each genotype we had three replicate individuals. We then placed individuals across genotypes in a growth chamber, acclimated the plants to 22°C over 24 hours so genotypes could better adjust to the temperature curves (in particular the low temperature ends). We then exposed all of the genotypes to the following temperatures: 14°C, 18°C, 22°C, 26°C, 30°C, 34°C, 38°C, 42°C to generate photosynthetic temperature response curves (Berry and Bjorkman 1980). At each of the eight temperature levels, plants were allowed to acclimate for approximately 30 minutes. Cell (ROS and total antioxidant capacity) and plant-level C gain were measured at suboptimum (14°C), optimum (26°C), and inhibition (38°C) temperatures (Weston et al. 2011); leaf-level C gain was measured at each of the 8

temperature levels. Growth chamber and cuvette (leaf and plant) were maintained at 55% relative humidity (average leaf-level VPD = 1.6). Temperature responses at the cell, leaf, and plant levels were measured between 9:30 and 11:30 am and between 11:30 am and 2:00 pm which is the most photosynthetically active time period. We also measured two morphological traits that can shape short-term temperature responses at the cell, leaf and plant levels but are independent of the manipulations (Crutsinger et al. 2006, Crutsinger et al. 2008): total plant leaf area (cm^2) and total aboveground biomass. For total leaf area, we clipped all leaves of each individual and ran them through a leaf area scanner (WinFolia, Ottawa, Canada). We then clipped the stems and placed both leaves and stems into paper bags and oven dried them at 65°C for approximately 48 hours to obtain total aboveground biomass.

To determine the short-term cell-level response to temperature, we measured the production of reactive oxygen species (ROS) and oxygen radical antioxidant capacity (ORAC). We estimated ROS production using the total H_2O_2 assay where we extracted 500 l cold leaf extraction buffer (10 mM Tris-HCL pH 7.3, 1 mM EDTA, 20% glycerol, 2 mM DTT and 1 mM PMSF, all from EMD, Gibbstown, NJ) and centrifuged the extract at 13,000 rpm for 10 min at 4°C. The oxidation of H2DCF-DA to fluorescent 2', 7'-dichlorofluoriscein (DCF) was measured using a Fluoroscan Ascent microplate fluorometer (Volkov et al. 2006). Total antioxidant capacity was estimated using the ORAC assay using fluorescein (Sigma-Aldrich). Decay area curves were generated from a microplate fluorometer and total protein concentration was estimated with Coomassie Blue assay using Quick start Bradford reagent (Bio-Rad, Hercules, CA) (Gillespie et al. 2007). We determined total protein concentration with Coomassie Blue assay using Quick start Bradford reagent (Bio-Rad, Hercules, CA), but we found no differences between northern and southern genotypes in total protein concentration ($P = 0.49$, $F = 0.52$).

To examine leaf-level CO_2 assimilation (i.e., C gain), we took instantaneous measurements of leaf net photosynthetic rate using a LI-6400 gas exchange system (Li-Cor, NE, USA). We placed one attached *Solidago* leaf per genotype in a cuvette and allowed it to acclimate (between 5–15 minutes) to saturating PPFD (1500 μmol m^{-2} s^{-1}), temperature, relative humidity, and ambient [CO_2]. We recorded leaf-level CO_2 assimilation at each temperature level; data are expressed as the rate of C gain per unit leaf area (m^2) per second.

We measured plant-level CO_2 assimilation (hereafter C gain), using an LI-7500 infrared gas analyzer (IRGA; Li-Cor). It was housed in a plant cuvette (0.75 m wide × 0.75 m long × 0.75 m tall) attached to a laptop with two fans mixing the air within the plant cuvette. The cuvette was covered with tightly sewn polyethylene sheet (Shelter Systems, CA) (Arnone and Obrist 2003, Huxman et al. 2004, Potts et al. 2006). Specifically, in each plant-level measurement, we placed a single individual *Solidago* genotype at the center of the large cuvette, and adjacent to the plant we placed the IRGA with fans mounted on the plant cuvette metal frame. At the base of the cuvette, we installed foam that was impermeable to [CO_2] to ensure the cuvette system was well-sealed minimizing CO_2 leaks. CO_2 concentrations were allowed to draw down overtime, and from such draw down CO_2 flux was determined. We did not record CO_2 flux data for the first 20 seconds that the plant cuvette was put in place to allow a complete mix of air within the chamber. We then recorded the concentration of CO_2 overtime for approximately 90 seconds in order to calculate the slope of change in CO_2 concentration across time. We corrected the slope of CO_2 depletion overtime with the chamber volume and corrected these values with total plant leaf area in order to obtain a plant-level C gain value.

In order to compare the responses of cells, leaves, and whole plants, we estimated the effect sizes of warming at the cell, leaf, and plant level as the log-response ratio (ln R)

$$\ln R = \left[\frac{\bar{X}_e}{\bar{X}_a}\right]$$

where $\bar{X}_e$ is the mean of the response variable for each northern and each southern *Solidago* genotype ($n = 5$) under elevated temperature (38°C) and $\bar{X}_a$ is the mean of the response variables or each northern and each southern *Solidago* genotype ($n = 5$) under ambient conditions (26°C) (Hedges et al. 1999). Positive or negative values indicate a positive or negative effect of warming on cell-, leaf-, and plant-level responses. A two-way analysis of variance (ANOVA) followed by a

Tukey HSD mean separation test was used to determine if the log-response ratio differed among the cell, leaf, or plant level, between northern and southern populations, and if there was an interaction between population source and level of organization.

The impacts of warming on northern and southern genotypes were investigated using one-way ANOVA models with population source (northern, southern) as the main effect at each temperature (14°C, 26°C, 38°C) and total antioxidant capacity (cell level) and C gain (leaf and plant level) as the response variables. To better understand how trait variation within a species shapes short-term temperature responses, we used linear regression to examine whether variation in total aboveground biomass, across southern and northern genotypes, predicted temperature responses at the cell (total antioxidant capacity) and leaf level (C gain).

Results

We found the standardized effect of warming to be the greatest at the highest level of organization (plant level) and to be smallest at the lowest levels of organization (leaf and cell levels) ($F = 8.95$, $P = 0.0012$). In other words, warming did not have a negative impact on cell-level antioxidant capacity, but it had a strong negative impact on plant-level C gain. We found an interaction between level of organization (cell, leaf, plant) and population source (northern vs. southern population) on the standardized effect of warming (Fig. 1, $F = 5.05$, $P = 0.0026$). The standardized effect of warming, for the northern population, was significantly more negative at plant-level C gain than at both leaf-level C gain and cell-level antioxidant capacity. The standardized effect of warming for the southern population, however, was significantly more negative at the plant level (C gain) than cell level (antioxidant capacity), but did not differ from leaf-level C gain.

Solidago genotypes from northern and southern populations varied in their response to increasing temperature at the cell and leaf, but not at the plant level. At the cell level, southern genotypes had 32% greater production of reactive oxygen species and antioxidants under elevated temperature than did northern genotypes (Fig. 2, Table 1; Appendix A: Fig. A1, Appendix B: Fig. B1). At the leaf level, southern genotypes had 25% lower leaf-level C gain than northern genotypes indicating a potential tradeoff between defense at the cell level (higher ORAC production) and investment towards leaf growth (lower C uptake) under warming (Fig. 2, Table 1). Nonetheless, plant-level C gain significantly declined with increasing temperature across northern and southern genotypes (Fig. 2, Table 1). Finally, we found that both leaf and plant-level C gain did not differ within northern ($F = 0.195$, $P = 0.93$; $F = 0.110$, $P = 0.972$) and southern ($F = 0.792$, $P = 0.566$; $F = 0.858$, $P = 0.557$) populations. This result indicates that warming will negatively impact individual genotypes in northern and southern ranges equally (Appendix C: Fig. C1, Appendix D: Fig. D1).

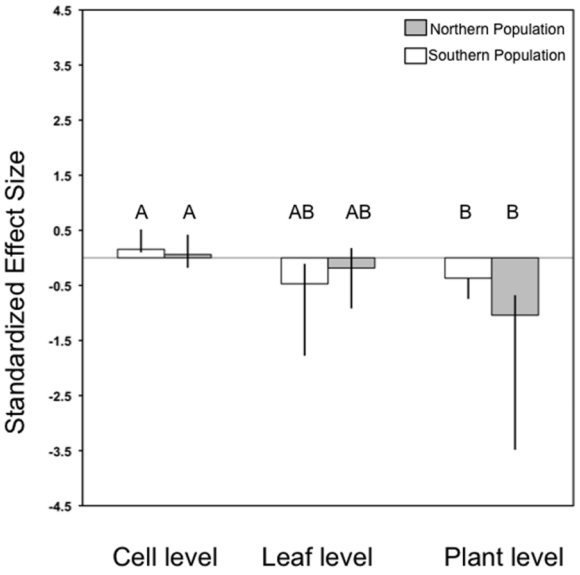

Fig. 1. Mean (± 95% CI) standardized effect size of temperature on carbon processes between populations (northern and southern) at the cell, leaf, and plant level. Temperature effects were greatest at the highest level of organization (plant level) and lowest at the smallest level of organization (cell level).

Trait variation across northern and southern genotypes, at the plant level, predicted temperature responses at the cell and leaf level. Southern genotypes had 30% more leaf area ($P = 0.02$, $F = 8.13$, df = 1, 8) and 40% greater aboveground biomass ($P = 0.01$, $F = 11.62$, df = 1, 8) than northern genotypes. Variation in leaf area

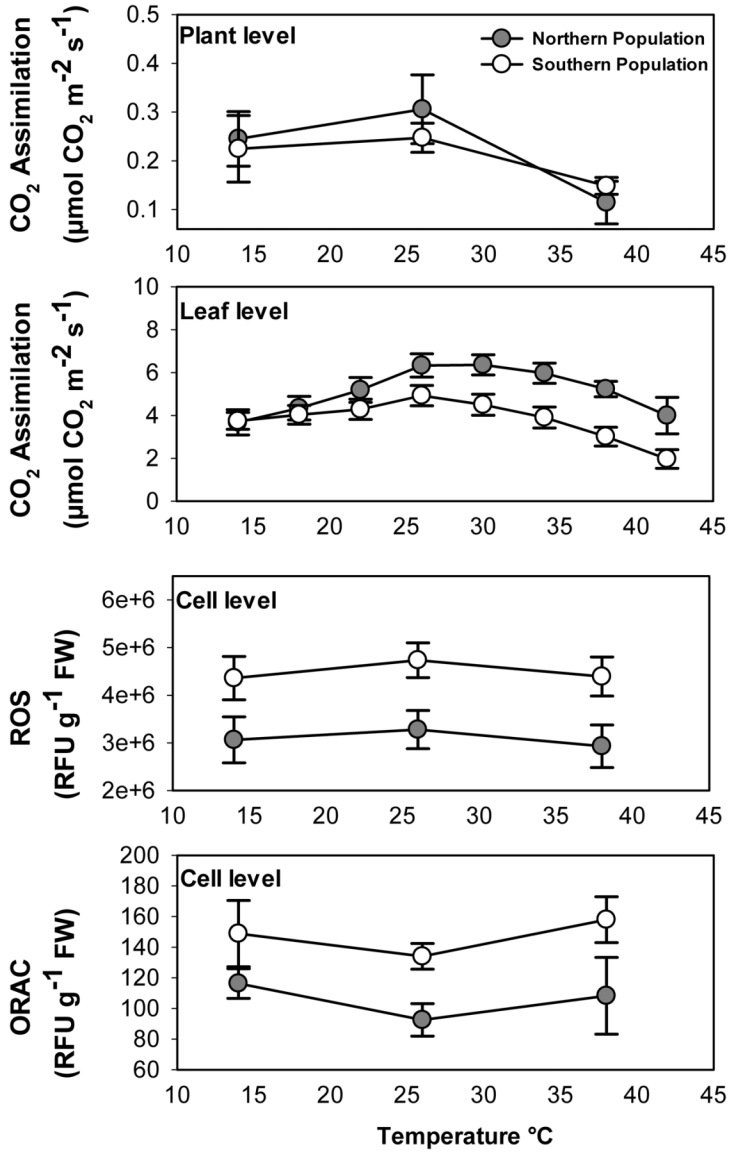

Fig. 2. Mean (± SE) temperature response at the cell, reactive oxygen species (ROS) and total antioxidant capacity (ORAC); and at the leaf and plant level (CO_2 assimilation) between northern and southern populations. Cell- and leaf-level responses to temperature differed between northern and southern populations, yet plant-level responses to temperature were similar between northern and southern populations.

and biomass ranged from 505–726 cm^2 and 5–10 g in southern populations and 295–533 cm^2 and 3–5 g in northern populations. *Solidago* genotypes with more biomass, generally from southern populations, tended to have both higher cell-level antioxidant capacity (Fig. 3, $R^2 = 0.36$, $P = 0.065$) and lower leaf-level C gain than northern genotypes with less biomass ($R^2 = 0.52$, $P = 0.028$) (Fig. 3).

Discussion

Temperature effects on *Solidago* individuals were greatest at the plant level and weakest at the cell level. Even though we predicted temperature responses to be the weakest at the highest level of organization, the plant level, levels below it likely responded similarly without counteract-

Table 1. Impacts of warming (ANOVA) on southern and northern genotypes at the cell (ROS, ORAC), leaf, and plant level (C gain). Significant P-values are bold ($\alpha = 0.10$).

Metric	df	MS	*F*	*P*
14°C				
Plant-level C gain	1, 7	2.2×10^{-4}	0.01	0.93
Leaf-level C gain	1, 7	0.44	0.31	0.59
Cell-level ROS	1, 8	4.19×10^{12}	3.81	**0.09**
Cell-level ORAC	1, 8	2649.6	1.89	0.21
26°C				
Plant-level C gain	1, 7	0.02	1.45	0.27
Leaf-level C gain	1, 7	4.4	3.57	**0.1**
Cell-level ROS	1, 8	5.29×10^{12}	7.25	**0.03**
Cell-level ORAC	1, 8	4305.58	9.42	**0.02**
38°C				
Plant-level C gain	1, 7	0.001	0.86	0.38
Leaf-level C gain	1, 7	10.97	15.4	**0.01**
Cell-level ROS	1, 8	5.35×10^{12}	5.84	**0.04**
Cell-level ORAC	1, 8	6179	2.9	0.12

ing overall temperature effects. Elevated temperature appears to have greater negative effects at higher levels of organization despite increasing structural and functional complexity. Previous studies have addressed temperature effects at the cell and leaf levels, not at the plant level where we found temperature effects to play the strongest role. Thus adding a level of complexity (plant level) might explain the divergence of results found in previous studies (Petchey et al. 2004, Bailey et al. 2009, Purdy et al. 2010, Woodward et al. 2010). Although our study demonstrated that short-term temperature effects were stronger at higher levels of organization (i.e., plant level), it is clear that future studies should address both short- and long-term effects of temperature at even higher (community and ecosystem) levels of organization as in De Frenne (2011*a*).

Southern *Solidago* genotypes had higher antioxidant capacity and lower leaf-level C gain than northern genotypes indicating a potential tradeoff between defense at the cell level (higher ORAC production) and investment towards growth at the leaf level (lower C gain). This suggests that southern genotypes, which experience longer and warmer growing seasons than northern genotypes, have greater antioxidant capacity to combat the by-products of warming. These results support previous findings documenting both inter- and intra-specific variation in antioxidant capacity under heat stress generated

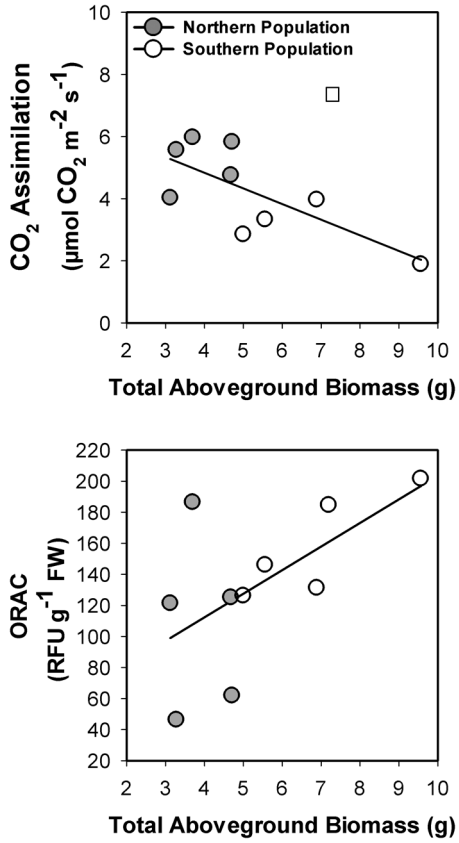

Fig. 3. Intra-specific variation in aboveground biomass across northern and southern *Solidago* individuals vs. cell-level ORAC (bottom panel) and vs. leaf-level CO_2 assimilation (top panel). The square point has not been considered in the analysis, but is shown in the figure, because it was identified as an outlier. Overall, variation in aboveground biomass between northern and southern populations influenced cell- and leaf-level responses to temperature.

from local adaptation (Snider et al. 2010). Likewise, recent studies show species from southern ranges outperform northern range species under climatic warming (Parmesan 1996, Parmesan et al. 1999, Parmesan and Yohe 2003, Walther 2010). Our results suggest that if cell-level antioxidant capacity promotes thermal tolerance within *Solidago*, then southern populations may persist while northern populations may not, potentially leading towards a reduction of geographic range, assuming dispersal is minimal.

Our findings contradict previous work indi-

cating that thermal tolerance at the cell level maintains C gain at the leaf level. This contradiction may be due to the lack of temperature acclimation of fully expanded leaves in our study relative to measurements made on newly developed leaves in other studies (Atkin and Tjoelker 2003). Unlike leaf-level responses, plant C gain did not differ between northern and southern populations because southern genotypes had greater leaf area than northern genotypes thereby compensating for lower C gain at the leaf level. In fact, total plant leaf area predicted total plant C gain ($R^2 = 0.4$, $P < 0.005$) whereby increases in total plant leaf area equaled increased rates of CO_2 assimilation. Overall, our findings suggest that short-term temperature effects can negatively impact C gain at the individual level in the same ways among northern and southern *Solidago* genotypes. Further our results indicate that a reduction in population size and loss of genotypic variation in this dominant plant species could occur with increasing atmospheric temperatures - an idea that needs to be tested in large-scale, long-term field manipulations. While short-term temperature exposure provides us with valuable information on responses within and across populations to climatic warming, long-term studies and experiments could provide a more realistic picture of plant population responses to changing temperature.

Intraspecific variation in morphological traits, such as plant leaf area or aboveground biomass, can shape both short-and long-term plant responses to global change. We found that intraspecific variation in *Solidago* aboveground biomass across northern and southern genotypes shaped both cell- and leaf-level responses to elevated temperature. Understanding the role of trait variation and its relationship to variation in function is key to understanding key physiological processes in the context of global change and predict the consequences of such changes (Reusch et al. 2005, Hughes et al. 2009).

Conclusions

The most salient results of our experiments are that (1) temperature effects are more detrimental to C processes at the plant level leading to the decline in C gain across *Solidago* populations; (2) greater cell-level antioxidant capacity in southern genotypes than northern genotypes does not infer greater leaf and plant-level C gain; and (3) intra-specific variation in temperature responses between northern and southern genotypes likely results from tradeoffs between higher cell defense at a cost of lower leaf-level C uptake under warming. Overall, the negative impact of short-term warming on plant-level C gain across northern and southern genotypes could lead to a reduction in individual (i.e., genotypic) variation both within and between populations at range boundaries. The consequences for these reductions for other key ecosystem processes remain an open, but important, question to be addressed. To test the generality of our findings future studies should address long-term effects of warming within and across species and across levels of biological organization including a larger sample of genotypes and several species, thereby increasing ecological inference of generated results. Long-term growth chamber studies would allow plants to be grown under different temperature regimes providing a more realistic scenario of warming effects.

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SUPPLEMENTAL MATERIAL

APPENDIX A

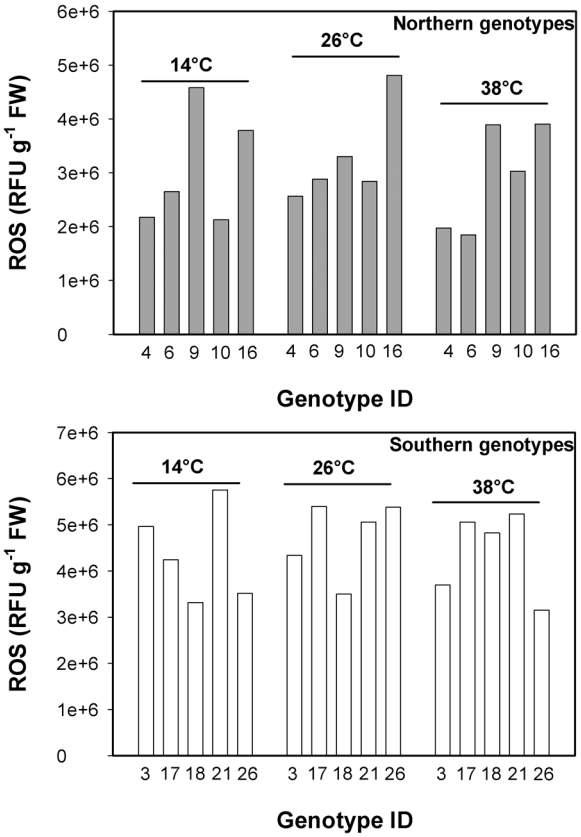

Fig. A1. Reactive oxygen species production at the cell level in northern (top panel) and southern (bottom panel) genotypes at three temperatures (14°C, 26°C, and 38°C).

APPENDIX B

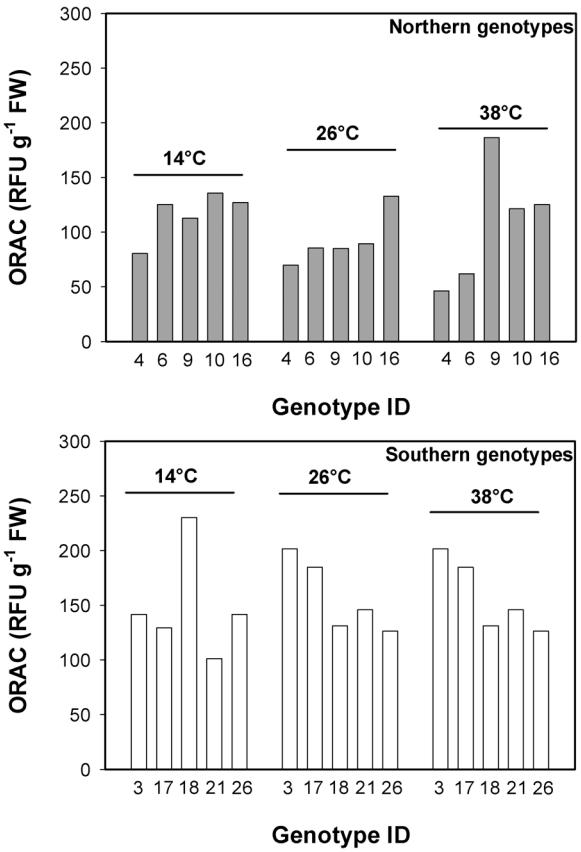

Fig. B1. Antioxidant capacity production at the cell level in northern (top panel) and southern (bottom panel) genotypes at three temperatures (14°C, 26°C, and 38°C).

APPENDIX C

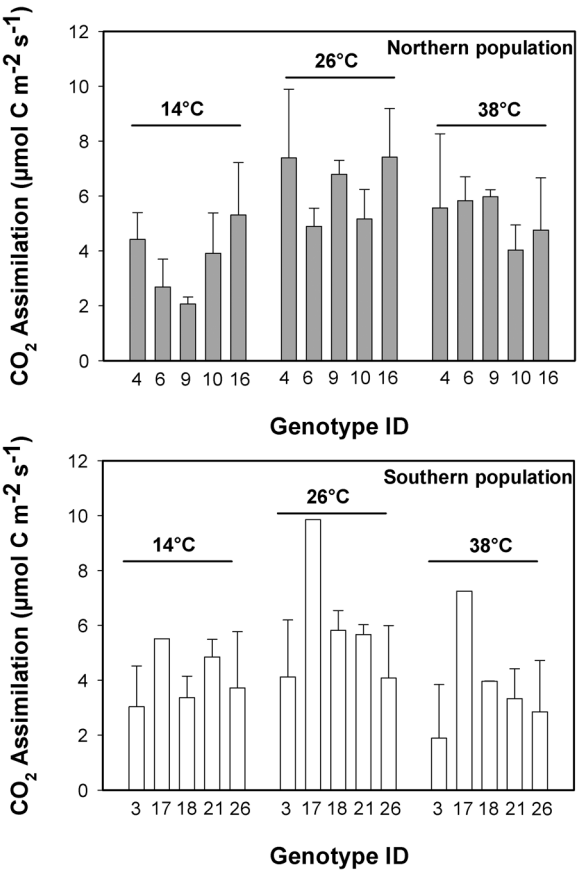

Fig. C1. Mean CO_2 assimilation and SE at the leaf level in northern (top panel) and southern (bottom panel) genotypes at three temperatures (14°C, 26°C, and 38°C).

APPENDIX D

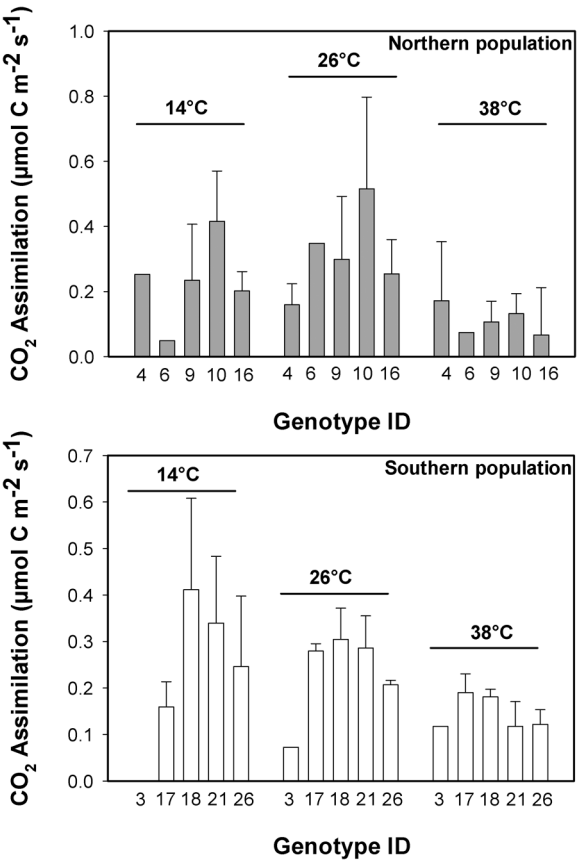

Fig. D1. Mean CO_2 assimilation and SE at the plant level in northern (top panel) and southern (bottom panel) genotypes at three temperatures (14°C, 26°C, and 38°C).