

Within and between population variation in plant traits predicts ecosystem functions associated with a dominant plant species

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Keywords

Aboveground biomass, inflorescence mass, intraspecific variation, net ecosystem carbon exchange, *Solidago altissima*.

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Funded by UT Undergraduate Research Office (Summer Research Internship to L. B.) UT Science Alliance Program (Junior Directed Research and Development to A. T. C.) American Fellowship from AAUW (to L. S.).

Received: 22 November 2011; Revised: 24 January 2012; Accepted: 6 February 2012

Ecology and Evolution 2012, 2(6): 1151–1161

doi: 10.1002/ece3.223

Abstract

Linking intraspecific variation in plant traits to ecosystem carbon uptake may allow us to better predict how shift in populations shape ecosystem function. We investigated whether plant populations of a dominant old-field plant species (*Solidago altissima*) differed in carbon dynamics and if variation in plant traits among genotypes and between populations predicted carbon dynamics. We established a common garden experiment with 35 genotypes from three populations of *S. altissima* from either Tennessee (southern populations) or Connecticut (northern populations) to ask whether: (1) southern and northern *Solidago* populations will differ in aboveground productivity, leaf area, flowering time and duration, and whole ecosystem carbon uptake, (2) intraspecific trait variation (growth and reproduction) will be related to intraspecific variation in gross ecosystem CO₂ exchange (GEE) and net ecosystem CO₂ exchange (NEE) within and between northern and southern populations. GEE and NEE were 4.8× and 2× greater in southern relative to northern populations. Moreover, southern populations produced 13× more aboveground biomass and 1.4× more inflorescence mass than did northern populations. Flowering dynamics (first- and last-day flowering and flowering duration) varied significantly among genotypes in both the southern and northern populations, but plant performance and ecosystem function did not. Both productivity and inflorescence mass predicted NEE and GEE between *S. altissima* southern and northern populations. Taken together, our data demonstrate that variation between *S. altissima* populations in performance and flowering traits are strong predictors of ecosystem function in a dominant old-field species and suggest that populations of the same species might differ substantially in their response to environmental perturbations.

Introduction

Understanding variation in ecosystem function across space and time has become an increasingly important task in ecology especially in the context of global change. Studies have documented threefold variation in ecosystem function, such as net ecosystem CO₂ exchange (NEE), among plant communities, which demonstrates variation in the capacity of ecosystems to take up CO₂ (Bousquet et al. 2000; Gurney et al. 2002; Janssens et al. 2003; Baldocchi 2008). General patterns of NEE include substantially greater net ecosystem CO₂ uptake in temperate (i.e., greater CO₂ sinks) than in arid

ecosystems (i.e., lower CO₂ sinks) (Verburg et al. 2004; Wilsey and Polley, 2004; Patrick et al. 2007; Risch and Frank, 2010), and lower NEE uptake in northern than southern latitude communities (Valentini et al. 2000; Van Dijk and Dolman 2004; Li et al. 2005; Kato and Tang 2008; Yuan et al. 2009). Documenting regional variation in NEE is necessary to understand whether particular ecosystems, or the components of those ecosystems, will be sources or sinks of atmospheric CO₂.

Variation in net primary productivity (NPP) is often associated with variation in NEE among plant communities. In general, NPP is higher in temperate than in arid

ecosystems (Ni 2000; Huxman et al. 2004a) and in southern latitude ecosystems than in northern latitude ecosystems (Kicklighter et al. 1999; Saugier et al. 2001; Huston and Wolverton 2009); this systematic variation in NPP likely promotes concomitant variation in whole ecosystem CO₂ uptake. Although it is clear that climatic variation drives variation in NPP (and therefore whole ecosystem CO₂ uptake), variation in biodiversity also influences NPP and whole ecosystem CO₂ uptake (Hooper et al. 2005). Generally speaking, previous studies that have manipulated plant biodiversity found that the number of species is positively associated with an increase in NPP (Tilman et al. 2001) and NEE (Wilsey and Polley 2004). One common explanation for the positive effect of interspecific diversity is that trait differences among species increase NPP and NEE (Hooper et al. 2005).

Recently, a growing number of studies have demonstrated that intraspecific diversity, or within species diversity, can also shape NPP (Booth and Grime 2003; Classen et al. 2006; Crutsinger et al. 2006, 2008; Johnson et al. 2006; Whitham et al. 2006; Hughes et al. 2008). The effects of within species diversity might be due to either sampling effects (Huston 1997; Wardle 1999) or niche complementarity (Tilman et al. 2001; Hooper et al. 2005), as is the case with studies on interspecific diversity. Intraspecific trait variance can be as great as interspecific trait variance, thereby generating greater NPP (Crutsinger et al. 2006). While it is increasingly clear that NPP is correlated with ecosystem CO₂ uptake at the plot level from several interspecific diversity studies (Wilsey and Polley 2004; Klumpp and Soussana 2009; Hirota et al. 2010), we do not know if this pattern holds for intraspecific diversity and what the mechanisms may be—variation in NPP or variation in soil respiration, driving NEE.

Similarly, understanding variation in patterns of NPP allocation within species should allow us to understand better the underlying processes shaping ecosystem function. Previous studies have documented variation in growth and/or reproduction strategies among plant species including among species within the genus *Solidago* (Abrahamson and Gadgil 1973; Abrahamson and McCrea 1986; Abrahamson and Weis 1997; Abrahamson et al. 2005) and across environmental gradients (Oleksyn et al. 1998; Ladinig and Wagner 2005; Milla et al. 2009). However, to our knowledge, only a few empirical (Fox and Stevens 1991; Houssard and Escarre 1991; Tilman and Wedin 1991; Abrahamson et al. 2005; Knops et al. 2007; Koenig et al. 2009), and theoretical (Roff 1992; Enquist et al. 1999) studies have examined the links between biomass allocation, growth and reproduction within species, and these studies have produced idiosyncratic results. Further, we are not aware of any studies that show how such variation in life-history traits may shape an ecosystem function, such as NEE, and how life-history traits of populations in high latitude versus low latitude influence ecosystem function.

While linking life-history trait variation, both within and among species, to ecosystem function will be key to understanding how traits of species shape ecosystems locally, it is also important to elucidate whether such relationships between traits and ecosystem function vary between populations. A suite of studies has documented spatial variation in NEE, NPP, and plant flowering, with the typical result being that populations from higher latitudes exhibit lower NEE (Valentini et al. 2000; Jarvis et al. 2001; Van Dijk and Dolman 2004; Li et al. 2005; Jacobs et al. 2007; Kato and Tang 2008; Yuan et al. 2009), lower NPP (Oleksyn et al. 1998, 1999), and lower reproductive output (Sills and Nienhuis 1995; Tungate et al. 2002; Bohlenius et al. 2006; Hall et al. 2007; Breen and Richards 2008; Chuine 2010; Dainese 2011) when compared to populations from lower latitudes. Although temperature influences ecosystem function across latitudinal gradients, variation in photoperiod along the same gradient may be just as critical in determining variation in aboveground net primary productivity (ANPP), flowering, and ecosystem function (Enquist 2011).

Here, we ask whether intraspecific variation between *Solidago* populations from Tennessee and Connecticut in plant performance and flowering shapes ecosystem function within a dominant old-field plant species in the eastern United States. We quantified variation among *Solidago altissima* (hereafter *Solidago*) genotypes and between *Solidago* populations (northern and southern range) in performance traits (total leaf area and productivity), plant reproduction dynamics (first- and last-day flowering, flowering duration, and inflorescence mass), as well as NEE, GEE, and ecosystem respiration. Additionally, we quantified whether intraspecific variation in performance traits and/or plant reproduction predicted NEE and GEE. Specifically, we predicted that (1) southern and northern *Solidago* populations will differ in aboveground productivity, leaf area, flowering time and duration, and ecosystem functions; (2) intraspecific trait variation (growth and reproduction) will be related to intraspecific variation in GEE and NEE within and between northern and southern populations.

Materials and Methods

To test if intraspecific variation in plant performance traits (biomass, and leaf area) and/or reproductive traits (first- and last-day flowering, flowering duration, and inflorescence mass) predicted NEE, we measured traits between and within populations of *Solidago* (Fig. 1), a dominant old-field plant species in the eastern United States (Schmitz 2003, 2008; Abrahamson et al. 2005; Wise and Abrahamson 2008; Souza et al. 2011a,b); *Solidago* can make up 20–30% of the total aboveground productivity in old-field communities near our study site (L. Souza and W. A. Bunn, unpubl. data) and influences the structure of subdominant old-field



Figure 1. *Solidago altissima* inflorescence.

communities and associated ecosystem processes such as productivity (Crutsinger et al. 2006; Souza et al. 2011a,b).

Solidago collection and site description

In 2009, we collected individual genotypes of *Solidago* from naturally occurring populations. We collected 15 genotypes among three old-field sites near Stafford, Connecticut (northern populations), and 20 genotypes from three old-field sites near Oak Ridge, Tennessee (southern populations). At each location, we identified *Solidago* patches growing 50–150 m apart and excavated individual rhizomes within each patch using a small hand trowel. Based on AFLP analyses by Crutsinger et al. (2006), a spatial distance of 50–150 m between *Solidago* patches ensures a mean genetic dissimilarity of 25.1% between genotypes. We propagated each *Solidago* genotype by cutting the collected rhizomes into 3-cm sections and planting them in flats containing sterilized potting soil (Pro-Mix BX, Premier Brands, New Rochelle, NY). Although rhizome volume did not vary between southern and northern populations ($F = 1.54$, $P = 0.25$), it did vary among genotypes within southern populations ($F = 4.5$, $P = 0.01$) and among genotypes within northern populations ($F = 3.38$, $P = 0.02$). Given differences in rhizome volume among genotypes in southern and among genotypes in northern populations, we used rhizome volume as a covariate in an analysis of variance model where genotype was the categorical factor predicting NEE. We found that for both southern and northern populations, rhizome volume was not a significant covariate explaining NEE (for northern genotypes P -value = 0.67; for southern genotypes P -value = 0.99). All of the *Solidago* ramets emerged after seven days and were established in a greenhouse (25°C) for approximately 12 weeks. Plants were watered as needed and fertilized monthly with a water-soluble fertilizer (15:20:25, N:P:K, Scotts Sierra Horticultural Co. Marysville, OH). Root-stimulating solution was

applied to all ramets at the onset of the experiment (Roots 2, Roots Inc., OSIA Independence, MO, 1 g per 3.79 L) and similar to other experiments (Crutsinger et al. 2006).

Common garden experiment

In 2009, we transplanted *Solidago* individuals from the 35 genotypes into 20-gallon pots located within a mown field at the University of Tennessee's Agricultural Experimental Station, Knoxville, TN (35°53'47.84"N, 83°57'22.86"W). Mean annual rainfall at the site is 102 mm, mean air temperature ranges from 7.7°C (January) to 30.6°C (July). We established *Solidago* monocultures by planting three *Solidago* individuals from the same genotype within a single pot ($n = 2$); each pot contained sterilized potting soil (Pro-Mix BX).

In August 2009, we measured NEE ($\mu\text{mols CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) on a subset of 10 genotypes by recording the flux of carbon dioxide (CO_2) from each *Solidago* monoculture using a Li-COR 7500 infrared gas analyzer (Lincoln, NE). Measurements were recorded between the hours of 11 am and 2 pm on a clear, sunny day to ensure maximum photosynthetic activity. We placed a portable chamber (0.49 m² in area and 0.37 m³ in volume) covered with semitransparent woven rip-stop polyethelene material over each experimental pot and recorded CO_2 for approximately 120 sec (Arnone and Obrist 2003; Huxman et al. 2004b; Potts et al. 2006). NEE is an integrative measure of CO_2 assimilation by photosynthesis and CO_2 loss by plant and microbial respiration. We measured whole ecosystem respiration, loss of CO_2 via plant, and microbial respiration (R_e , $\mu\text{mols CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) by placing a dark cloth over the portable chamber and then recording CO_2 for an additional 120 sec. NEE and R_e were calculated by measuring and recording the slope of CO_2 over time and then correcting for chamber volume and sampled area. Finally, gross ecosystem CO_2 exchange (GEE) was calculated by summing NEE and R_e . Greater negative values indicate increasing NEE (i.e., greater whole ecosystem CO_2 uptake), while greater positive values indicate greater net ecosystem carbon efflux (i.e., greater whole ecosystem CO_2 release). Likewise, greater positive values indicate greater total ecosystem CO_2 loss, while smaller positive values indicate lower total ecosystem CO_2 loss.

We estimated aboveground biomass and total leaf area using allometric equations that were developed by linear regressions of morphological traits (height [cm], stem diameter [cm], leaf width [cm], leaf length [cm], and internode length [cm]) with aboveground biomass on a subset of genotypes collected in CT and in TN. The area of the largest leaf was the best predictor for total plant leaf area ($y = 9.986x + 196$, $R^2 = 0.22$, $P = 0.0036$), while both diameter and height were the best predictors for aboveground biomass ($y = 0.010x + 1.055$, $R^2 = 0.83$, $P < 0.0001$) among all genotypes.

We measured plant reproduction by recording (1) the Julian day the first flower within an inflorescence flowered (i.e., first-day flowering) and (2) the Julian day that all the flowers within an inflorescence finished flowering (i.e., last-day flowering). We then calculated flowering duration by subtracting the last-day flowering from the first-day flowering. Finally, we collected inflorescence masses from each *Solidago* genotype, oven-dried at 60°C for approximately 48 h, and recorded their oven-dry mass.

Statistical analyses

We used a one-way analysis of variance (ANOVA) to test for the effects of genotype identity on plant reproduction (first- and last-day flowering, flowering duration, and inflorescence mass), total leaf area, aboveground biomass, NEE, GEE, and R_e both within and between *Solidago* populations (CT or TN). We also performed linear regressions to determine whether plant traits (performance and reproduction) were related to ecosystem function (NEE, GEE, and R_e). We also tested for homoscedasticity in all our response variables by calculating the coefficient of variation and found that we met the distribution of our dataset to meet homogeneity of variance. Variables that were not normal were log-transformed and all analyses were performed using JMP 9 software.

Results

GEE was 4.8× higher ($P = 0.0005$) and NEE was 2× higher ($P = 0.0005$) in southern populations than in northern populations (Table 1, Fig. 2). However, southern and northern *Solidago* populations did not differ in R_e ($P = 0.36$) (Table 1, Fig. 2). In addition, we found no differences among genotypes within southern or within northern populations in GEE ($P = 0.57$ and $P = 0.92$, respectively) or NEE ($P = 0.27$ and $P = 0.90$, respectively). On the other hand, R_e dif-

fered among northern ($P = 0.056$) genotypes, but not among southern genotypes ($P = 0.49$) (Table 2, Fig. 2).

Aboveground biomass in southern *Solidago* populations was 13× greater ($P < 0.0001$) than in northern populations (Table 1, Fig. 3), but the populations did not differ in total leaf area ($P = 0.62$) (Table 1, Fig. 3). There were also no differences within southern or within northern populations in aboveground biomass ($P = 0.18$ and $P = 0.39$, respectively) or total leaf area ($P = 0.26$ and $P = 0.10$, respectively; Table 2, Fig. 3).

Relative to genotypes from northern populations, *Solidago* genotypes from southern populations flowered later and produced greater inflorescence mass, but did not differ in flowering duration. *Solidago* genotypes from southern populations began flowering approximately 45 days later ($P = 0.006$), finished flowering 44 days later ($P = 0.011$), and produced 1.6× more inflorescence mass ($P = 0.0082$) than did genotypes from northern populations (Table 1, Fig. 4). *Solidago* genotypes from southern and northern populations did not differ ($P = 0.4877$) in length of flowering (CT = 25.6 ± 2.8 days, TN = 23.6 ± 1.35 days) (Table 1). However, there were differences within southern and within northern populations in length of flowering ($P = 0.0004$ and $P < 0.0001$, respectively), first day of flowering ($P < 0.0001$ and $P < 0.0001$, respectively), and last day of flowering ($P = 0.0004$ and $P < 0.0001$, respectively) (Table 2, Fig. 4). For example, genotypes in northern populations showed larger variation in the range of first- and last-day flowering (77–224, 92–249 Julian day, respectively). Similarly, genotypes from southern populations also varied significantly in first- and last-day flowering (226–265, 262–281 Julian day, respectively).

Intraspecific variation in plant performance (i.e., productivity) and reproduction (inflorescence mass) between southern and northern *Solidago* populations was related to GEE and NEE. Productivity explained 57% ($P = 0.011$) and 76% ($P = 0.0009$) of the total variation in both GEE and NEE, respectively (Fig. 5). Likewise, inflorescence mass accounted for 43% ($P = 0.038$) and 42% ($P = 0.039$) of the total variation in both GEE and NEE, respectively (Fig. 5). Neither productivity ($R^2 = 0.05$, $P = 0.523$) nor inflorescence mass ($R^2 = 0.00$, $P = 0.901$) predicted R_e between southern and northern populations. On the other hand, intraspecific variation in plant performance and reproduction was not related to GEE and NEE within southern and northern populations. We found no relationship between total aboveground biomass and GEE (southern: $P = 0.475$; northern population: $P = 0.691$) or NEE (southern: $P = 0.980$; northern population: $P = 0.572$) within populations. Likewise, we found no relationship between total inflorescence mass and GEE (southern: $P = 0.394$; northern population: $P = 0.964$) or NEE (southern: $P = 0.530$; northern population: $P = 0.818$) within populations. Finally, we also found no

Table 1. ANOVA results testing for the effects of intraspecific variation (CT vs. TN) on gross ecosystem exchange (GEE), net ecosystem exchange (NEE), respiration (R_e), aboveground net primary productivity (ANPP), total plant leaf area, first day of flowering, last day of flowering, flowering duration, and inflorescence mass. P -values in bold are statistically significant ($P < 0.05$).

	df	Mean square	F -value	P -value
GEE	1,16	120.49	23.86	<0.001
NEE	1,16	99.23	31.33	<0.001
R_e	1,16	1.22	0.88	0.360
ANPP	1,27	63,930.90	136.39	<0.001
Total plant leaf area	1,27	3512.9	0.25	0.619
First day of flowering	1,27	13,981.40	9.38	<0.001
Last day of flowering	1,27	12,796.50	7.40	0.011
Flowering duration	1,27	26.23	0.49	0.488
Inflorescence mass	1,27	867.41	8.13	0.008

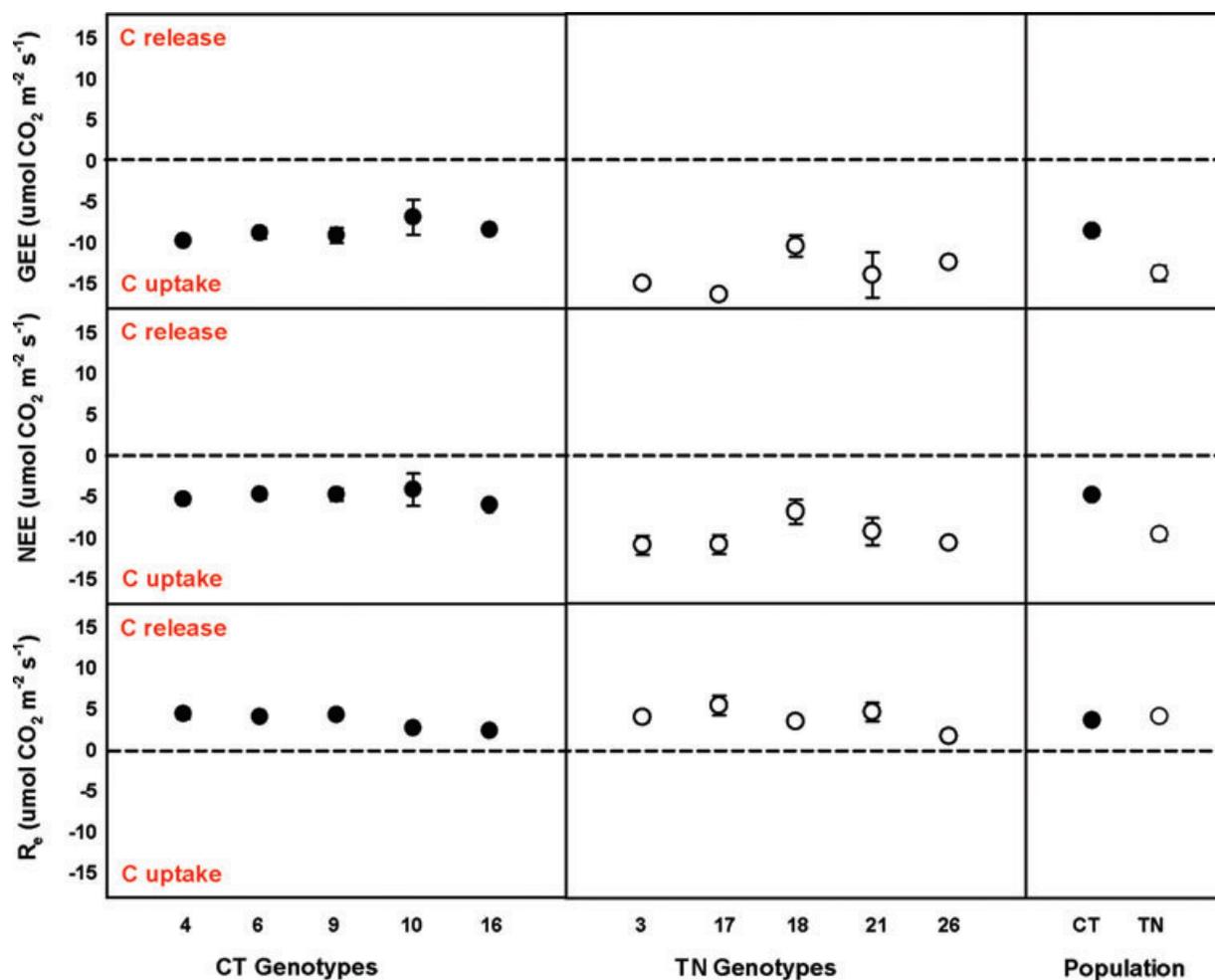


Figure 2. Intraspecific variation in GEE (top panel), NEE (middle panel), and Re (bottom panel) within CT genotypes (left panel), within TN genotypes (center panel), and between CT and TN populations (right panel). Values are mean \pm SE.

relationship between total aboveground biomass or total inflorescence mass and ecosystem respiration within northern (total aboveground biomass and ecosystem respiration: $P = 0.753$; total inflorescence mass and ecosystem respiration: $P = 0.841$) and within southern populations (total aboveground biomass and ecosystem respiration: $P = 0.371$; total inflorescence mass and ecosystem respiration: $P = 0.739$).

Discussion

The most salient result of our study is that ecosystem function varied among genotypes within the same population and between populations within a dominant old-field species. In particular, southern *Solidago* populations assimilated more atmospheric CO₂ (i.e., GEE and NEE) than northern *Solidago* populations. The results of our experiments generally agree with studies investigating interspecific variation in eco-

system CO₂ assimilation in grasslands. For example, (Wilsey and Polley 2004) documented significant interspecific variation in NPP and NEE, and they found that NEE and net C uptake were greater in species-rich plots than species-poor plots. They suggest that these patterns were the result of high interspecific variation among species in NPP and NEE. Our study emphasizes the role of intraspecific variation in CO₂ exchange found between northern and southern old-field ecosystems.

Other studies investigating variation in NEE across latitudinal gradients have documented that NEE declines with increasing latitude; thus, southern ecosystems have greater net ecosystem C uptake when compared to northern ecosystems (Valentini et al. 2000; Jarvis et al. 2001; Van Dijk and Dolman 2004; Li et al. 2005; Jacobs et al. 2007; Kato and Tang 2008; Yuan et al. 2009). Yuan et al. (2009) suggested that latitudinal patterns of NEE are likely determined by a decline

Table 2. ANOVA results testing for the effects of intraspecific variation (within CT vs. within TN) on gross ecosystem exchange (GEE), net ecosystem exchange (NEE), respiration (R_e), aboveground net primary productivity (ANPP), total plant leaf area, first day of flowering, last day of flowering, flowering duration, and inflorescence mass. *P*-values in bold are statistically significant ($P < 0.05$).

	df	Mean square	<i>F</i> -value	<i>P</i> -value
Connecticut				
GEE	3,4	9.25	1.072	0.456
NEE	3,4	0.46	0.183	0.902
R_e	3,4	1.27	6.131	0.056
ANPP	10,27	247.93	1.113	0.388
Total plant leaf area	10,27	36,9924	1.834	0.102
First day of flowering	10,27	34,843.9	9.427	<0.001
Last day of flowering	10,27	45,457.7	10.112	<0.001
Flowering duration	10,27	1010.22	5.551	<0.001
Inflorescence mass	10,27	0.46	1.077	0.41
Tennessee				
GEE	3,4	21.43	1.875	0.275
NEE	3,4	7.14	1.875	0.275
R_e	3,4	1.43	0.941	0.499
ANPP	10,27	15,723.5	1.449	0.181
Total plant leaf area	10,27	400,559	1.298	0.257
First day of flowering	10,27	7836.72	3.853	<0.001
Last day of flowering	10,27	7618.2	2.891	<0.001
Flowering duration	10,27	289.71	2.867	<0.001
Inflorescence mass	10,27	0.45	1.56	0.149

in gross primary production (GPP) and/or an increase in ecosystem respiration in higher latitudes compared to lower latitudes. Across European forest ecosystems, Valentini et al. (2000) demonstrated that increases in ecosystem respiration in higher latitudes, rather than changes in GPP, influenced NEE and overall CO₂ balance at the regional scale. However, Van Dijk and Dolman (2004) suggested that variation in GPP, not ecosystem respiration, determined NEE across a latitudinal gradient. Finally, Yuan et al. (2009) found that latitudinal variation in GPP shapes NEE in evergreen boreal forests, whereas latitudinal variation in ecosystem respiration influences NEE in deciduous broadleaf forests. In our study, variation in GPP rather than ecosystem respiration drives NEE within a dominant old-field species. While it has been documented that respiration has an effect on NEE at higher latitudes, the bulk of studies suggests that variation in GPP influences NEE more strongly. Our study contributes to the majority finding and shows that variation in GPP rather than ecosystem respiration drives NEE within a dominant old-field species.

Southern *Solidago* populations had significantly greater aboveground productivity likely contributing to greater ecosystem carbon uptake than northern *Solidago* populations, indicating that there is a lot of variation in carbon uptake within *Solidago* across its range. This interpretation is supported by previous work that documented that an

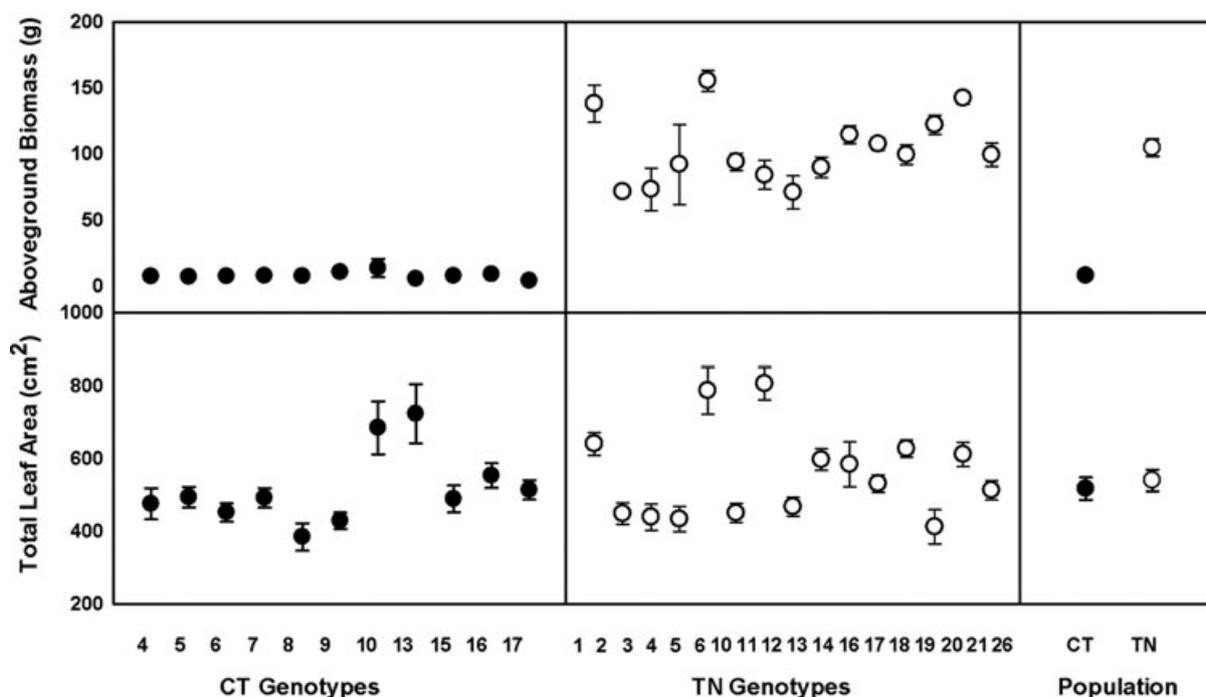


Figure 3. Intraspecific variation in aboveground biomass (top panel) and total leaf area (bottom panel) within CT genotypes (left panel), within TN genotypes (center panel), and between CT and TN populations (right panel). Values are mean ± SE.

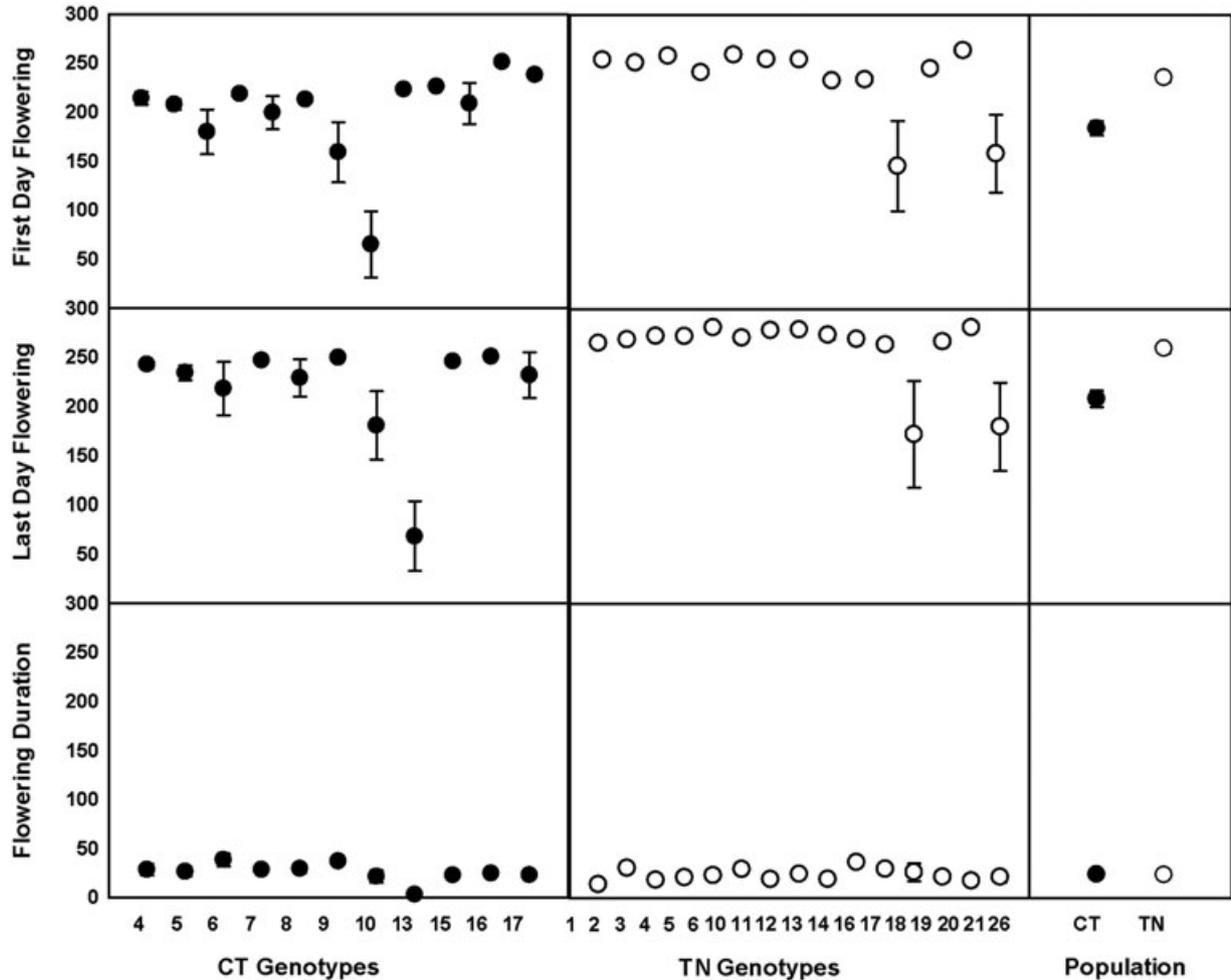


Figure 4. Intraspecific variation in first day flowering (top panel), last day flowering (middle panel), and inflorescence mass (bottom panel) within CT genotypes (left panel), within TN genotypes (center panel), and between CT and TN genotypes (right panel). Values are mean \pm SE.

increase in intraspecific variation leads to an increase in productivity within *Solidago* (Crutsinger et al. 2006, 2008), as well as within other plant species (Hughes et al. 2008; Fridley and Grime 2010). Latitudinal gradient studies have also documented an increase in among population productivity with decreasing latitudes (Oleksyn et al. 1999, 2000). For example, Oleksyn et al. (2000) found that European *Pinus sylvestris* populations vary in ANPP across their geographic ranges and northern populations had significantly lower productivity when compared to central populations. They suggest that variation in productivity between northern and central *P. sylvestris* populations resulted from variation in biomass allocation whereby northern populations had lower shoot:root allocation than that of central populations. Strong variation in productivity between northern and southern populations may also represent local adaptations to different climatic conditions in northern versus southern geographic ranges (Angert 2011; De Frenne 2011).

Our results show that *Solidago* ANPP varies dramatically near the edges of its geographic range; specifically, southern populations produce more biomass than northern populations, which is likely due to local adaptations to the regional climate.

Northern *Solidago* populations began reproducing (i.e., first day of flowering) significantly earlier and producing lower inflorescence mass than southern *Solidago* populations; such differences are likely associated with local adaptations across *Solidago*'s geographic range. A recent study by Genung et al. (2010) supports these results; their study documented intraspecific variation in flowering traits within local populations of *Solidago*. Intraspecific variation among *Solidago* genotypes in inflorescence abundance promoted greater inflorescence abundance with increasing genotypic diversity likely through complementarity effects (Hooper et al. 2005).

Differences in intraspecific flowering time and overall reproduction output (i.e., seed mass production) across

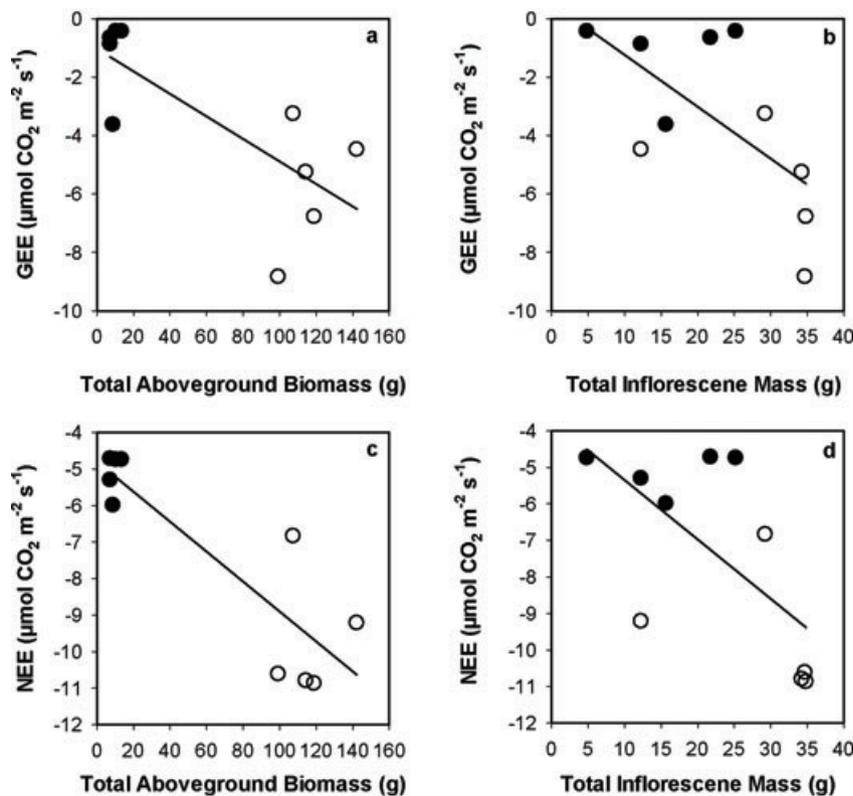


Figure 5. Linear regressions of gross ecosystem CO₂ exchange and aboveground biomass (a); gross ecosystem CO₂ exchange and inflorescence mass (b); net ecosystem CO₂ exchange and aboveground biomass and inflorescence mass (c and d). Black circles illustrate CT genotypes and clear circles illustrate TN genotypes.

tree/shrub/herbaceous populations along latitudinal and altitudinal gradients has also been documented, suggesting longer flowering intervals and greater reproduction output in southern than northern populations (Sills and Nienhuis 1995; Tungate et al. 2002; Bohlenius et al. 2006; Hall et al. 2007; Breen and Richards 2008; Chuine 2010; Dainese 2011). For instance, Dainese (2011) found variation in the reproductive performance of *Dactylis glomerata* across hay meadows in an elevational gradient with low-elevation individuals having larger inflorescences and larger seed masses than higher elevation individuals, meaning higher reproductive output in warmer/longer growing seasons than in colder/shorter growing seasons. Dainese (2011) suggested that longer growing seasons and/or warmer climates in lower elevation sites promote higher photosynthetic rates (i.e., greater C acquisition toward growth) and/or higher nutrient availability generating greater plant allocation toward reproductive performance than colder climates in higher elevations. Likewise, De Frenne (2011) documented increases in reproductive output of understory herbs in southern than northern populations. Our results documenting lower inflorescence mass in northern than southern *Solidago* populations support the finding by Dainese (2011) and De Frenne (2011) that northern climate-adapted populations (e.g., higher latitude/elevation) are functioning on lower levels of photo-

synthesis, where warm climate-adapted populations (e.g., lower latitude/elevation) are functioning on higher levels of photosynthesis that promote greater reproductive output (i.e., inflorescence mass).

Intraspecific variation in plant traits, in particular productivity and inflorescence mass, predicted an ecosystem function within a dominant old-field species. More productive individuals from southern populations delayed reproduction and were able to uptake more C than individuals from northern populations. Because of the shorter growing season in the northeastern United States (Conover and Present 1990), we suspect that individuals in northern populations were less productive and thus switched their allocation from growth to reproduction earlier in the year. A study by Abrahamson et al. (2005) supports this finding; they found great interspecific variation in allocation among five cooccurring *Solidago* species. Specifically, *S. altissima* had lower biomass allocation to roots relative to shoots and inflorescence mass, whereas *S. juncea* had high allocation toward roots and inflorescence mass, but low-biomass allocation to shoots. Abrahamson et al. (2005) suggested that interspecific variation in biomass allocation among cooccurring *Solidago* species was associated with local adaptations to environmental gradients. Likewise, we have shown that intraspecific variation in biomass allocation within *S. Altissima* varied among *Solidago* populations

preadapted to varying environmental conditions. Our data extend the work by Abrahamson *et al.* (2005) to include intraspecific variation in allocation toward reproduction and growth, which then leads to changes in ecosystem functions.

Our work contributes to the growing body of literature demonstrating that intraspecific variation in plant performance traits can influence ecosystem function. Old fields, like grassland ecosystems, are C sinks (Gilmanov *et al.* 2010; Peichl *et al.* 2011; Zhang *et al.* 2011). However, grasslands can switch from carbon sinks to sources during drought years (Zhang *et al.* 2011), suggesting that abiotic stresses can alter the function of grassland ecosystems. As the climate continues to warm, the southern most *Solidago* populations may become larger C sinks, and northern populations must be able to change allocation regimes in order to accommodate the possible warmer and longer growing season. Future work should consider belowground production of rhizomes to assess biomass allocation more completely, which could be another important predictor of whole ecosystem carbon exchange.

Acknowledgments

We thank J. Areson, E. Austin, M. Cregger, L. Marsh, A. Proffit, O. Schmitz, T. Simberloff, H. Smith, K. Stuble, H. Tran, J. Welch, and P. Wright for help with field and laboratory work. K. McFarland provided space, advice, and resources at the UT greenhouse. This work was funded by grants from the UT Undergraduate Research Office (Summer Research Internship to L. B.) and from the UT Science Alliance Program (Junior Directed Research and Development to A. T. C.). L. S. was supported by an American Fellowship from AAUW.

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