Plant genotypic variation and intraspecific diversity trump soil nutrient availability to shape old-field structure and function

Lara Souza*[1,2], Katharine L. Stuble[1,3], Mark A. Genung[4] and Aimee T. Classen[2,5]

[1]*Oklahoma Biological Survey and Microbiology and Plant Biology Department, University of Oklahoma, 111 E. Chesapeake Street, Norman, OK 73019, USA;* [2]*Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996, USA;* [3]*The Holden Arboretum, Kirtland, OH 44094, USA;* [4]*Department of Ecology, Evolution and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, NJ 08901, USA; and* [5]*Center for Macroecology, Evolution and Climate & the Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, Copenhagen Ø 2100, Denmark*

Summary

1. Individual plant genotypes as well as genotypic diversity can shape the structure and function of ecosystems; however, the abiotic environment may modify these genotypic influences on ecosystem-level responses.

2. To explore how the interactions between plant genotype, genotypic diversity and soil nutrient availability affect the structure and function of a temperate grassland ecosystem, we manipulated the genotypic diversity of a common perennial herbaceous plant, *Solidago altissima* (single genotype monoculture and diversity plots) and soil nutrient availability (+nitrogen, +phosphorus, +nitrogen and +phosphorus, unmanipulated control) in a common garden setting. We tracked temporal changes in ecosystem structure (e.g. leaf area index and net primary productivity) as well as a variety of ecosystem functions (e.g. net ecosystem carbon and water exchange and soil carbon efflux) over a growing season.

3. We found that variation in plant genotype identity consistently shaped ecosystem structure (above-ground net primary productivity) while it inconsistently altered several ecosystem functions across time. For instance, variation in plant genotype identity influenced net ecosystem carbon dynamics early in the growing season while it influenced water dynamics later in the growing season. The strength of the relationship between genotypic diversity and ecosystem function declined over the season and the relationship between ecosystem structure (above-ground net primary productivity) and function (net ecosystem carbon and water exchange) varied across treatments. Overall, there was a strong correlation between ecosystem structure and function across monoculture genotype plots but a weak relationship between ecosystem structure and function across mixed genotype plots. Surprisingly, soil nutrients did not influence ecosystem structure and had minimal impacts on carbon and water flux.

4. Our data suggest that plant genetic variation, and to some extent plant genotypic diversity, strongly influence ecosystem structure and function in an old-field ecosystem, but nutrient availability did not directly or interactively influence ecosystem structure or function.

Key-words: carbon, ecosystem function, ecosystem structure, genotypic diversity, genotypic variation, grassland, intraspecific diversity, soil nutrients, water

Introduction

Genotypic variation within a species can alter community interactions as well as ecosystem functions (Whitham *et al.* 2003; Crutsinger *et al.* 2008; Breza *et al.* 2012), but these

*Correspondence author. E-mail: lara.souza@ou.edu

effects may be contingent on the nutrient status of an ecosystem (Johnson & Agrawal 2005; Fisher *et al.* 2014). While plant genetic variation and intraspecific diversity can shape both community dynamics (Johnson, Lajeunesse & Agrawal 2006; Hughes *et al.* 2008; Genung *et al.* 2010; Genung, Bailey & Schweitzer 2012; Burkle *et al.* 2013) and

ecosystem structure (Crutsinger *et al.* 2006), the degree to which genotypic variation and genotypic diversity scale up to influence larger ecosystem fluxes of carbon (CO_2) and water (H_2O) is less clear (but, see Breza *et al.* 2012). In part, these linkages are driven by the potential for plant traits to alter ecosystem function (Breza *et al.* 2012). For example, Breza *et al.* (2012) documented *Solidago altissima* genotypes with higher specific leaf area, stem height and diameter, as well as higher inflorescence mass to exhibit greater above-ground net primary productivity and ecosystem functions such as GEE and NEE.

Similarly, species richness in a community is positively correlated with net primary productivity, leaf area index (Tilman, Wedin & Knops 1996; Hughes *et al.* 2008) and net ecosystem exchange (Wilsey & Polley 2004). The positive correlation between ecosystem function and interspecific diversity is likely driven by trait divergence among species that allow for niche differentiation (Hooper *et al.* 2005; Cardinale *et al.* 2012). Trait divergence among species and genotypes can lead to greater niche partitioning, enhanced resource utilization, reduced interspecific competition and, ultimately, may alter ecosystem carbon and water dynamics. Ecosystem nutrient status can also significantly influence plant trait expression and ecosystem function (Treseder & Vitousek 2001; Madritch, Donaldson & Lindroth 2006) and may negate or reduce the influence of genotype on these processes. Further, carbon and water dynamics are influenced by plant traits as well as by ecosystem properties such as nutrient availability. For instance, nutrient availability will likely promote an increase in mean trait values of shoot and root traits (e.g. foliar vs. root production), generating greater productivity and thus altering carbon and water dynamics (De Deyn, Cornelissen & Bardgett 2008, Diaz *et al.* 2016).

Clearly, plant genotype, plant genotypic diversity and nutrient availability are important drivers of plant trait expression and ecosystem net primarily productivity, but less is known about how these drivers may interact to alter larger scale ecosystem carbon and water dynamics. In addition, environmental context, including seasonality and nutrient availability, will influence genotypic variation and diversity effects on ecosystem structure and function. Factors including nutrient availability as well as seasonality are likely to dictate which genotypes are most successful, the relative divergence in traits among genotypes and ultimately the importance of intraspecific diversity.

We explored how ecosystem nutrient status, variation in genotypic identity and genotypic diversity altered the carbon and water dynamics of a dominant old-field plant, *Solidago altissima*. We manipulated soil nutrient availability (control, nitrogen addition, phosphorus addition, nitrogen + phosphorus addition), *Solidago* genotypic identity (75 total *Solidago* genotype monoculture plots representing 10 *Solidago* genotypes, with each monoculture plot containing six individuals belonging to the same genotype) and *Solidago* genotypic diversity (12 total *Solidago* mixture plots each containing six

individuals belonging to different genotypes). Specifically, we asked whether plant genotype, intraspecific diversity and soil nutrient availability act independently or interdependently to affect ecosystem structure, ultimately scaling to influence function by altering ecosystem carbon and water fluxes.

Materials and methods

STUDY SYSTEM

Solidago altissima, tall goldenrod, is a well-studied (Maddox & Root 1987; Wise & Abrahamson 2008) and common old-field species in the eastern USA (Semple & Cook 2006; Souza, Weltzin & Sanders 2011). The species' range extends from Florida northward to Quebec and westward to California (USDA Plants Database). In old fields in eastern Tennessee, *S. altissima* can constitute over 47% of the above-ground biomass (L. Souza, unpublished data). *Solidago altissima* populations spread locally by rhizomes, creating patches, which can consist of clones of a single genotype (monocultures) or multiple genotypes (Gross & Werner 1983; Halverson *et al.* 2008). Previous work in this ecosystem found that intraspecific variation in *S. altissima* at the individual level can influence ecosystem functions (Souza *et al.* 2011b) with litter decomposition rates among *S. altissima* genotypes varying by 50% (Crutsinger, Sanders & Classen 2009) and southern and northern populations varying by twofold in net ecosystem CO_2 exchange (Breza *et al.* 2012; and see Lojewski *et al.* 2012 for genetic based influences on ANPP and soil CO_2 efflux). Finally, intraspecific variation and diversity influence ecosystem structure (ANPP) and community dynamics (Crutsinger *et al.* 2006), yet scaling the effects of intraspecific diversity to the level of ecosystem function has not yet been explored.

PLANT GENOTYPE COLLECTION AND EXPERIMENTAL ESTABLISHMENT

We sampled genotypes from 17 old-field communities located in Eastern Tennessee, USA (35°54′12″ N, 84°20′22″ W) and identified twenty distinct patches of *S. altissima*, spaced 50–150 m apart in March 2009. Sampled old-field communities had similar soil types and land-use histories (Souza *et al.* 2011a). From each of these patches, we excavated the rhizomes from a single ramet of *S. altissima* to ensure the collection of 20 individual genotypes (Crutsinger *et al.* 2006). Each rhizome was divided into 3 cm pieces and transplanted into flats containing sterilized potting soil and root stimulator (Roots 2; Roots Inc., OSIA Independence, MO, USA). Plants were grown in a greenhouse (at 25 °C) and were watered and fertilized as needed for 12 weeks.

In June of 2009, three randomly selected ramets of a single genotype were transplanted into 76-L pots in the field. Each of the 20 genotypes was planted in two to four of these monoculture pots for a total of 48 monocultures. Pots were located within a fenced (to exclude deer) common garden at the University of Tennessee Institute of Agriculture (35°53′47·84″ N, 83°57′22·86″ W). From May to August of 2009, we quantified morphological traits (leaf width, leaf length, inter node length, stem height, stem diameter), physiological traits (specific leaf area), reproductive traits (first day flowering, flowering duration, inflorescence mass) and herbivory traits (aphid density, per cent leaf damage) for all genotypes. We targeted the selected plant functional traits because they are associated with plant performance, are commonly measured and thus relatable to other studies and ultimately influence ecosystem carbon and water dynamics (Cornelissen *et al.* 2003; Kattge *et al.* 2011).

EXPERIMENTAL DESIGN

To select the genotypes used in the field experiment, we performed a principal component analysis that included all of the plant traits (e.g. morphological, physiological, reproductive, herbivory) measured among the 20 *S. altissima* genotypes in the summer of 2009. We selected the 10 genotypes that maximized trait variance across the first two principal component axes (see Burkle *et al.* 2013 for further trait information for each of the genotypes) for use in the field experiment.

In June of 2010, we established a common garden experiment where we manipulated genotypic diversity and soil nutrients in a completely randomized plot design. Clones for each plant of the chosen genotypes were collected from monoculture pots described in the previous section. Each experimental plot was 1 m² with a 1·5 m buffer between plots. Each 1 m² plot was lined with 12-mil heavy plastic buried 36 cm into the soil profile to inhibit rhizome connections among the experimental plots and plots were arrayed in a random grid. Monoculture plots contained six individuals (i.e. clones) of a single *S. altissima* genotype. Diversity plots contained six individuals, one each of six randomly selected genotypes, with no two plots containing identical combinations of genotypes to avoid sampling effects or the influence of particularly high yielding genotypes in mixture compared to monoculture plots (Wardle 1999). In a fully factorial design, monoculture and diversity plots were subject to one of four nutrient treatments: (i) control (no nutrient amendment), (ii) nitrogen (N) amendment (10 g m⁻² year⁻¹), (iii) phosphorus (P) amendment (10 g m⁻² year⁻¹) and (iv) P and N amendment (P = 5 g m⁻² year⁻¹ and N = 5 g m⁻² year⁻¹). Plots were fertilized following established 'NutNet' protocols to enable comparisons with other fertilization experiments (Borer *et al.* 2014). Each genotype was replicated in two monoculture plots and included in three diversity plots for a total (N) of 80 monoculture and 12 diversity plots.

MEASUREMENTS OF ECOSYSTEM STRUCTURE AND FUNCTIONS

Ecosystem structure

To determine the main and interactive effects of genotypic variation, intraspecific diversity and soil nutrients on ecosystem structure, we quantified leaf area index (LAI) and above-ground plant biomass on each of the treatment plots. We measured LAI with a line-integrating ceptometer (Decagon Accupar, Decagon Devices, Pullman, WA, USA) that records canopy photosynthetically active radiation (PAR) interception by quantifying PAR above and below the plant canopy. We took four PAR measurements (two above and two below the plant canopy) per experimental plot and then averaged them for each of the three measurement times during the growing season. To determine above-ground biomass, we used an already established allometric equation ($y = 0·010$ $x + 1·055$, $R^2 = 0·83$, $P < 0·0001$, Breza *et al.* 2012) with both stem diameter and height as predictors of above-ground biomass for June, July and August 2010. In September, we destructively harvested plot-level above-ground biomass by clipping all individuals at ground level. We oven-dried all above-ground biomass for each plot at 65 °C for c. 48 h and then weighed it to determine biomass.

Ecosystem function

To determine the effects of variation in genotype identity, intraspecific diversity and soil nutrients on ecosystem functions, we quantified soil and whole ecosystem carbon (CO_2) and water (H_2O vapour) exchange. Soil CO_2 efflux was measured using a LI-6400 infrared gas analyser (Li-Cor Inc., Lincoln, NE, USA) placed over installed PVC collars (80 cm² in area, 5 cm in height) in the soil (one PVC collar per plot). Measurements were taken monthly between 10·00 and 15·00 h. We estimated net ecosystem of exchange carbon (NEE; μmols CO_2 m⁻² s⁻¹) and water (ET; μmols H_2O m⁻² s⁻¹) at the plot level monthly by recording the flux of carbon dioxide (CO_2) and water vapour (H_2O) from each *Solidago* monoculture and diversity plot using a Li-COR 7500 infrared gas analyser (Li-Cor Inc.). We placed a portable chamber (0·49 m² in area and 0·37 m³ in volume) covered with semi-transparent polyethylene material over each experimental plot and recorded [CO_2] and [H_2O] for c. 120 s (Arnone & Obrist 2003; Huxman *et al.* 2004; Potts *et al.* 2006). Finally, we determined ecosystem water use efficiency (eWUE), by calculating the ratio of NEE and ET. We recorded NEE and ET measurements between the hours of 11·00 and 14·00 h on a clear, sunny day to ensure maximum ecosystem-level photosynthetic activity.

STATISTICAL ANALYSES

To determine the main and interactive effects of time with our treatments, we ran a series of repeated-measures analysis of variance (RMANOVA) for ecosystem structure (LAI and ANPP) and ecosystem function (NEE, ET, eWUE, soil CO_2 efflux) response variables. We then followed up RMANOVAS with two 2-way ANOVA models to determine the main and interactive effects of plant genotype × nutrients and genotypic diversity × nutrients on ecosystem structure (LAI and ANPP) and associated functions (NEE, ET, eWUE, soil CO_2 efflux) at each time point during the growing season. We used Tukey's HSD means separation test (α = 0·05) to identify which treatment means significantly differed from one another. We applied the appropriate transformations to any response variable not fitting a normal distribution. We also performed a series of eight linear regressions to determine the relationship between ecosystem structure (LAI and ANPP) and functions (NEE and ET) across monocultures vs. diversity plots. We used JMP 11 (SAS Institute Inc., Cary, NC, USA) for all of our statistical analyses.

In addition to the parametric analyses described above, we also tested whether there were non-additive effects of genotypic diversity compared to expectations based on monocultures. The non-additivity analysis reveals whether the mixture plots have higher or lower trait values than expected given their genotype composition. Plant traits used in this analysis included height, stem diameter, biomass, leaf length, leaf width and leaf area. We did not analyse plot-level ecosystem functions because these cannot be expressed as individual-level values and thus cannot be drawn at random to reconstitute mixture plots. Using peak-growing season (August) values for traits directly related to biomass (biomass, height and stem diameter), we first reconstituted each mixture plot by drawing individuals from the appropriate monoculture plots. In other words, if a mixture plot contains genotypes 1 through 6, we would draw one individual from monoculture plots from genotype 1, and then one individual from genotype 2, and so on through genotype 6. Then, we calculated the mean trait value across all the reconstituted mixture plots. We repeated this process 1000 times, sorted the mean trait values from lowest to highest and generated a 95% confidence interval spanning the 25th to 75th values. If the observed trait value for the mixture plots fell outside the null confidence interval, we concluded that there was a non-additive effect of genotypic diversity on that trait.

Analysis of selection and complementarity effects

In mixture plots, any differences between expected and observed values of plant traits can be expressed as an additive combination of selection and complementarity effects (Loreau and Hector

2001). Selection effects capture whether changes of the relative traits (e.g. biomass) of genotypes in mixtures are non-randomly correlated with those genotypes' traits in monoculture. For example, a selection effect would arise when one of the genotypes in a mixture is very productive in monoculture and that productive genotype also dominates the mixture. Complementarity effects capture any change in the average relative yield in mixture compared with monocultures and thus represent whether genotypes perform better or worse or the same in mixtures relative to monocultures. We calculated selection and complementarity effects for each mixture plot. It is important to recognize that selection and complementarity effects provide no evidence of a significant effect of genotypic diversity; thus, interpreting selection and complementarity is generally more meaningful when the non-additivity analysis produces significant results.

Results

PLANT GENOTYPE, GENOTYPIC DIVERSITY AND NUTRIENT ADDITION IMPACTS ON ECOSYSTEM STRUCTURE AND FUNCTION OVER TIME

ANPP, LAI, NEE, ET and eWUE differed across time in monoculture plots and diversity plots (Tables S1 and S2, Supporting Information); yet, all variables peaked in September and exhibited the lowest values in July. However, interactions between time × plant genotype, time × diversity, time × nutrients and time × genotype × diversity × nutrients did not significantly influence ecosystem structure (ANPP, LAI) or function (NEE, ET, eWUE) (Tables S1 and S2).

PLANT GENOTYPE EFFECTS ON ECOSYSTEM STRUCTURE AND FUNCTION

Plant genotype effects on ecosystem structure remained consistent across time, but inconsistently scaled up to influence ecosystem functions. Variation in plant genotype identity strongly influenced ANPP, both within and across time (Table 1). ANPP ranged from 664 to 917 g m^{-2} across plant genotypes at the end of the study (Fig. S1). LAI did not vary across genotypes at any of the examined time periods (Fig. S1). On the other hand, ecosystem functions were inconsistently influenced by plant genotypes with carbon dynamics only affected by variation in genotype early in the growing season and water dynamics only influenced by genotypic variation later in the growing season.

The influence of plant genotype on soil CO_2 efflux, NEE, ET and eWUE differed across months. Individual *Solidago* genotypes varied in NEE in July (−1·43 to −35·31 µmol CO_2 m^{-2} s^{-1}), August (−8·13 to −26·44 µmol CO_2 m^{-2} s^{-1}) and seasonally (−9·59 to −22·69 µmol CO_2 m^{-2} s^{-1}), but not in September (Fig. S2). ET only varied significantly among plant genotypes in August (3·85–10·72 mmol H_2O m^{-2} s^{-1}), September (0·81–5·94 mmol H_2O m^{-2} s^{-1}) and seasonally (3·49–7 mmol H_2O m^{-2} s^{-1}), but not in July (Fig. S2). eWUE varied significantly across *Solidago* genotypes only in July

(0·94–3·69 µmol CO_2:mmol H_2O m^{-2} s^{-1}) and August (1·71–3·68 µmol CO_2:mmol H_2O m^{-2}s^{-1}), (Fig. S2). Finally, plant genotype only influenced soil CO_2 efflux in July (0·70–15·46 µmol CO_2 m^{-2} s^{-1}).

PLANT GENETIC DIVERSITY EFFECTS ON ECOSYSTEM STRUCTURE AND FUNCTION

Solidago genotypic diversity had minimal impacts on ecosystem structure and function. The only statistically significant impacts of genotypic diversity on ecosystem structure and function were early in the growing season. For instance, LAI was 58% greater in monoculture plots compared to diversity plots early in the growing season, but these effects became insignificant later in the in the growing season. Surprisingly, plant genotypic diversity did not affect ANPP (Table 2).

Genotypic diversity plots had 38% and 43% greater NEE (greater CO_2 uptake) and eWUE (greater carbon uptake per unit water loss), respectively, compared to monoculture plots in July. However, similar to diversity impacts on ecosystem structure, this effect became insignificant as the growing season progressed (Table 2). Soil CO_2 efflux and ET did not differ among monoculture and diversity plots. Diversity effects also did not influence the measured ecosystem functions seasonally (averaged across time) (Table 2).

The non-additivity analysis revealed only one difference between the expected and observed values among diversity plots (Fig. S3); specifically, stem diameters were smaller than expected. However, after accounting for multiple comparisons using a false discovery rate of 0·05 (Verhoeven, Simonsen & McIntyre 2005), none of the traits, including stem diameter, showed significant non-additivity.

SOIL NUTRIENT EFFECTS ON ECOSYSTEM STRUCTURE AND FUNCTION

Surprisingly, nutrient addition inconsistently influenced few of the ecosystem functions we measured and did not influence ecosystem structure. The only significant effect of nutrient addition was on soil CO_2 efflux in September (Tables 1 and 2). Phosphorus addition increased soil CO_2 efflux by c. 30% relative to control and nitrogen addition plots in September. There were no interactions between plant genotype and soil nutrient additions (Table 1) or diversity and soil nutrient additions on the ecosystem structure and function variables we measured (Table 2).

LINKING ECOSYSTEM STRUCTURE AND FUNCTION ACROSS TREATMENTS

ANPP, not LAI, was a good predictor of ecosystem functions across monoculture and diversity treatments over the growing season. ANPP accounted for 66% ($P = 0.008$)

Table 1. Two-way ANOVA results testing for the main and interactive effects of plant genotype and nutrient amendments on ecosystem structure (LAI, Biomass) and functions (NEE, ET, EWUE, Soil H_2O and CO_2 efflux) in July, August, September and seasonally

Source	July F	July P	August F	August P	September F	September P	Seasonal F	Seasonal P
Leaf area index								
Nutrients	1·24	0·30	0·41	0·66	0·23	0·80	0·84	0·44
Genotype	1·51	0·19	0·88	0·55	1·39	0·24	1·27	0·29
Nutrients × Genotype	0·77	0·70	0·73	0·74	0·65	0·82	0·76	0·71
Biomass (g m^{-2})								
Nutrients	1·51	0·24	0·08	0·92	0·88	0·42	0·56	0·64
Genotype	**13·40**	**<0·01**	**8·81**	**<0·01**	**3·41**	**0·01**	**15·09**	**<0·01**
Nutrients × Genotype	1·56	0·14	1·39	0·21	0·34	0·98	1·26	0·26
Net Ecosystem CO_2 Exchange (μmol CO_2 m^{-2} s^{-1})								
Nutrients	0·89	0·42	1·28	0·22	0·23	0·79	0·92	0·41
Genotype	**2·39**	**0·05**	**4·26**	**<0·01**	0·6	0·77	**2·36**	**0·05**
Nutrients × Genotype	0·34	0·99	1·77	0·09	0·46	0·95	0·47	0·94
Ecosystem Transpiration (mmol H_2O m^{-2} s^{-1})								
Nutrients	1·73	0·20	1·24	0·30	0·33	0·72	1·15	0·33
Genotype	0·73	0·66	**2·92**	**0·02**	0·31	0·94	**2·66**	**0·03**
Nutrients × Genotype	0·69	0·78	1·38	0·22	0·39	0·96	1·31	0·27
Ecosystem Water Use Efficiency (μmol CO_2 per mmol H_2O)								
Nutrients	0·30	0·75	0·57	0·57	0·27	0·76	0·75	0·48
Genotype	**2·56**	**0·04**	**5·82**	**<0·01**	0·48	0·86	0·62	0·75
Nutrients × Genotype	0·33	0·99	1·07	0·42	0·77	0·70	0·58	0·87
Soil CO_2 Efflux (μmol CO_2 m^{-2} s^{-1})								
Nutrients	1·47	0·25	1·87	0·18	**5·91**	**0·01**	**3·09**	**0·06**
Genotype	**2·34**	**0·05**	1·31	0·29	1·41	0·25	1·78	0·14
Nutrients × Genotype	1·29	0·29	1·11	0·40	0·56	0·87	1·36	0·24

Statistically significant results shown in bold.

Table 2. Two-way ANOVA results testing for the main and interactive effects of intraspecific diversity and nutrient amendments on ecosystem structure (LAI, Biomass) and functions (NEE, ET, eWUE, Soil H_2O and CO_2 efflux) in July, August, September and seasonally

July			August			September			Seasonal		
Source	F	P	Source	F	P	Source	F	P	Source	F	P
Leaf area index											
Nutrients	2·20	0·12	Nutrients	0·18	0·83	Nutrients	0·48	0·62	Nutrients	0·31	0·74
Diversity	**3·64**	**0·06**	Diversity	0·43	0·52	Diversity	1·09	0·30	Diversity	2·41	0·13
Nutrients × Diversity	0·74	0·48	Nutrients × Diversity	0·96	0·39	Nutrients × Diversity	0·38	0·69	Nutrients × Diversity	0·27	0·76
Biomass (g m^{-2})											
Nutrients	0·73	0·49	Nutrients	0·51	0·60	Nutrients	0·43	0·65	Nutrients	0·91	0·44
Diversity	0·00	1·00	Diversity	0·07	0·80	Diversity	0·05	0·82	Diversity	0·78	0·38
Nutrients × Diversity	0·18	0·84	Nutrients × Diversity	0·98	0·38	Nutrients × Diversity	0·18	0·83	Nutrients × Diversity	0·76	0·52
Net Ecosystem CO_2 Exchange (μmol CO_2 m^{-2} s^{-1})											
Nutrients	1·64	0·20	Nutrients	0·06	0·94	Nutrients	0·09	0·91	Nutrients	1·17	0·32
Diversity	**3·37**	**0·07**	Diversity	1·83	0·18	Diversity	1·56	0·22	Diversity	<0·01	0·95
Nutrients × Diversity	0·65	0·53	Nutrients × Diversity	0·72	0·49	Nutrients × Diversity	0·54	0·59	Nutrients × Diversity	0·28	0·75
Ecosystem Transpiration (mmol H_2O m^{-2} s^{-1})											
Nutrients	1·89	0·16	Nutrients	0·02	0·98	Nutrients	0·27	0·76	Nutrients	1·25	0·29
Diversity	0·81	0·37	Diversity	1·29	0·26	Diversity	0·05	0·83	Diversity	0·08	0·78
Nutrients × Diversity	2·19	0·12	Nutrients × Diversity	0·77	0·47	Nutrients × Diversity	0·14	0·87	Nutrients × Diversity	1·58	0·22
Ecosystem Water Use Efficiency (μmol CO_2 per mmol H_2O)											
Nutrients	2·22	0·12	Nutrients	0·12	0·89	Nutrients	1·17	0·32	Nutrients	0·005	0·99
Diversity	**5·74**	**0·02**	Diversity	0·1	0·75	Diversity	0	0·95	Diversity	0·25	0·62
Nutrients × Diversity	1·01	0·37	Nutrients × Diversity	0·1	0·90	Nutrients × Diversity	0·28	0·75	Nutrients × Diversity	0·16	0·85
Soil CO_2 Efflux (μmol CO_2 m^{-2} s^{-1})											
Nutrients	1·32	0·28	Nutrients	0·59	0·18	Nutrients	**3·69**	**0·03**	Nutrients	1·61	0·21
Diversity	1·57	0·22	Diversity	0·30	0·29	Diversity	1·85	0·18	Diversity	0·75	0·39
Nutrients × Diversity	0·14	0·87	Nutrients × Diversity	0·22	0·40	Nutrients × Diversity	1·96	0·15	Nutrients × Diversity	0·07	0·93

Statistically significant results shown in bold.
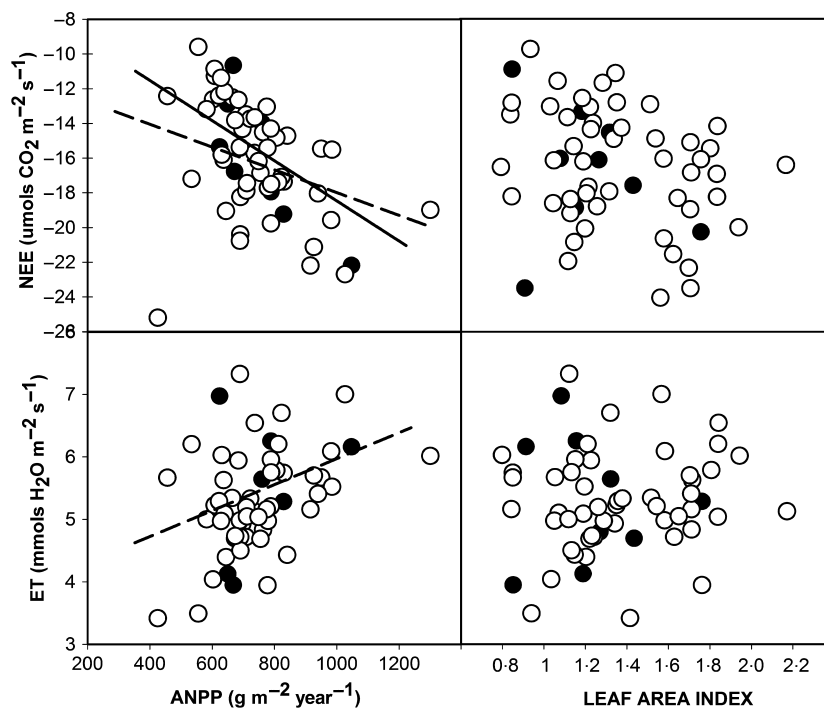
Fig. 1. Linear regressions quantifying the relationships between NEE, ET and ANPP and LAI. ANPP, not LAI, influenced NEE across mixture and monoculture plots. Solid and dashed regression lines indicate mixture and monoculture plots, respectively. Black symbols represent mixture, while white symbols represent monoculture treatments.

and 51% ($P < 0.001$) of the total variation in NEE across diversity and monoculture plots, respectively (Fig. 1, Table S3). Further, while variation in ANPP across diversity and monoculture plots predicted NEE (e.g. ecosystem CO_2 dynamics), only variation in monoculture plot ANPP predicted water dynamics. ANPP accounted for 25% ($P = 0.001$, $R^2 = 0.16$) of the total variation in ET in monocultures only, whereas ANPP effects across diversity plots were not significant (ET $P = 0.33$, $R^2 = 0.13$) (Fig. 1, Table S3). Finally, LAI accounted for very little of the variation in ecosystem functions ($0.0003 > R^2 < 0.05$) and its relationship was never significant ($P > 0.05$) (Fig. 1, Table S3).

Discussion

Our study contributes to the growing body of research that explores how variation in plant genotype influences ecosystem function (Whitham 2006; Wymore *et al.* 2011). Overall, we found that genotypic variation, as well as genotypic diversity, influenced ecosystem structure and function in our constructed *Solidago* plots. However, in contrast to previous work, we found weak direct and no significant interactive effects of soil nutrient level on the structure and function of our experimental ecosystems (Johnson *et al.* 2008; Crutsinger *et al.* 2013). The influence of genotype on ecosystem structure remained constant across the growing season, but its influence on function varied over time. Overall, variation in plant genotypic identity was related to carbon dynamics early but not late in the growing season (coefficient of variation (CV) July = 44.3, CV September = 21.6), while the opposite was true for water dynamics (CV July = 18.9, CV September = 27.9).

PLANT GENOTYPE INFLUENCES ANPP AND ASSOCIATED ECOSYSTEM-LEVEL CARBON AND WATER DYNAMICS

Our work supports findings that plant genotype can alter plant carbon and water dynamics in both woody and herbaceous ecosystems (e.g. Madritch & Hunter 2003; Breza *et al.* 2012). At our site, genotype explained c. 44% (model R^2) of the total variation in water and carbon fluxes. However, the influence of genotype varied across the growing season; a pattern that likely emerged because genotypes vary in their growth rates over the growing season (Breza *et al.* 2012). When a greater proportion of genotypes in the population grow faster early in the growing season than other genotypes, a differential demand for CO_2 among genotypes would emerge early, but not late, in the season. Additionally, later in the season all genotypes stop growing to allocate carbon towards reproduction, a pattern highlighted by the first day of flowering data (Breza *et al.* 2012; Burkle *et al.* 2013). Thus, the variation in reproduction across genotypes may begin to alter carbon and water dynamics to a larger extent to affect growth rates earlier rather than later in the growing season (Breza *et al.* 2012; Burkle *et al.* 2013). This pattern is evident in our data; early in the growing season (e.g. June to July) above-ground biomass across plant genotypes increased by 23-fold, whereas later on in the growing season growth rates slowed and above-ground biomass only increased by 35% (Fig. S1; e.g. from July to August). Temporal variation in plant growth can be indicative of changes in plant physiology, phenology, resource availability and/or of negative plant–soil feedback increasing over time (Bazzaz 1996; Pendergast, Burke & Carson 2013; Jones 2014). Interestingly, in our study plant genotype had a

larger influence on water dynamics at the peak of the growing season. Thus, as soil moisture became more limiting at the peak of the growing season, genotypic variation in water use efficiency emerged. Given that global changes may alter genotypic distributions of plants across systems as well as seasonal water availability (Fisher *et al.* 2014), our data suggest that these genotypic and environmental changes may scale up to influence the seasonal dynamics of ecosystem carbon and water balance (Enquist *et al.* 2015).

COMMUNITY GENOTYPIC DIVERSITY MINIMALLY IMPACTS ECOSYSTEM STRUCTURE AND FUNCTION

Our study indicates that plant genotype, rather than genotypic diversity per se, strongly drives ecosystem function; a pattern also observed in other studies (Madritch, Donaldson & Lindroth 2006; Crutsinger, Sanders & Classen 2009; but see Madritch & Hunter 2002). Niche complementarity (i.e. niche partitioning and facilitation) (Hooper *et al.* 2005) and selection effects (Huston 1997; Wardle 1999; Loreau & Hector 2001) may drive previously observed positive relationships between species diversity and community structure (i.e. ANPP, LAI), and ecosystem function (i.e. Hooper *et al.* 2005). Here, complementarity effects dominated, but they were not consistently positive (negative complementarity effects might be more appropriately called competition effects, but this distinction is not often made). Because complementarity effects were both positive and negative, there was no detectable effect of diversity on biomass (Figs S3 and S4). This mix of positive and negative complementarity suggests a mixture of facilitative and competitive interactions between genotypes in mixture plots and is unsurprising given that there was no non-additive effect of diversity on any plant trait (after accounting for multiple comparisons). Selection effects were weak and unrelated to the magnitude of complementarity effects, suggesting that covariance between a genotype's traits in monoculture and that same genotype's traits in mixtures was of little importance. However, greater facilitation (e.g. positive feedbacks) within genotypes may increase productivity in monocultures, enhancing ecosystem structure such as above-ground net primary productivity (Bever, Westover & Antonovics 1997; Bever *et al.* 2010). To further explore these patterns, future work should tease apart the relative influence of niche complementarity mechanisms, facilitation vs. niche partitioning, on how genotypic diversity influences the functioning of ecosystems.

SOIL NUTRIENTS DID NOT INTERACT WITH PLANT GENOTYPE OR GENOTYPIC DIVERSITY TO AFFECT ECOSYSTEM STRUCTURE AND FUNCTION

Contrary to our prediction, there was no overall effect of soil nutrients and soil nutrients did not interact with plant genotype or genotypic diversity to influence any of the processes we measured. The lack of nutrient effects was surprising given that grasslands are generally strongly nitrogen limited (Elser *et al.* 2007; Gruner *et al.* 2008; Borer *et al.* 2014). However, we should note that we did not directly measure soil nitrogen or phosphorus availability; hence, it is possible that fertilization did not impact productivity as a result of a lack of limitation by either nutrient in our study system. Prior work in old fields close to this study site also found no evidence for N limitation of primary productivity with high rates of fertilization (Blue *et al.* 2011; Wright *et al.* 2014); thus, another factor, such as soil water availability, must limit productivity in this ecosystem. Similarly, in a contrasting ecosystem, marine seagrass productivity was generally not influenced by the interaction among genotype, genotypic diversity and nutrient availability (Thomas *et al.* 2011). However, the opposite patterns were found in a pine forest, where respiratory CO_2 fluxes in *Pinus taeda* clones varied in their response to soil nitrogen fertilization (Stovall, Seiler & Fox 2013). Clearly, there is divergence in the response of ecosystems to nutrient additions, genotype and genotypic diversity. Extant ecosystem properties such as nutrient constraints and soil physical properties as well as differences in nutrient use efficiencies among study organisms and overall differences in plasticity across taxa may explain the variation among studies. Experiments that cross the genotype identity of plants with different nutrient constraints across a broad nutrient gradient would begin to tease apart the divergence in research results across these contrasting ecosystems.

ANPP PREDICTS THE NET ECOSYSTEM EXCHANGE OF CARBON AND WATER ACROSS MONOCULTURE AND DIVERSITY PLOTS

Not surprisingly, ANPP was correlated with NEE and ET (Baldocchi 2008) in our experiment. More productive genotypes had higher rates of net ecosystem water and carbon exchange. Similar to other studies (Wilsey & Polley 2004), this effect was detectable in the diversity plots for seasonal NEE of CO_2, but not for ET. Diversity plots with lower and higher ANPP showed similar ranges in ecosystem function (e.g. ET values). A possible explanation for the lack of relationship between ANPP and ET in the diversity plots is that the diversity plots in our experiment had a narrower range of ANPP (e.g. 600–1000 g m^{-2}) than the monoculture plots (e.g. 400–1300 g m^{-2}).

Variation in biodiversity can also influence ANPP, LAI and whole ecosystem CO_2 uptake (Hooper *et al.* 2005). Generally speaking, in previous studies that manipulated plant biodiversity the number of species in a plot were positively associated with an increase in ANPP, LAI (Tilman, Wedin & Knops 1996) and NEE (Wilsey & Polley 2004). Surprisingly, we did not find a significant relationship between genotypic diversity and LAI. We also found no relationship between LAI and the ecosystem functions we measured, but we did find a relationship between function and ANPP. One potential reason for this discrepancy may be that ANPP integrates stems and leaves that collectively influence ecosystem functions, whereas LAI only

incorporates leaf area. One common explanation for the positive effect of interspecific diversity is that trait differences among species increase ANPP, LAI and NEE (Hooper *et al.* 2005). In our system, key traits that predicted ANPP (but not LAI) were stem diameter and plant height. In fact, the relative importance of genotype and diversity can shift depending on context (species diversity example: Tilman, Lehman & Thomson 1997). The observed lack of variation in productivity across diversity treatments is likely due to statistical averaging, through which mixing many genotypes in one plot moderates the effects of genotypes with extreme traits values or contributions to ecosystem processes. In our case, extreme genotypes exhibited the highest and lowest values for both ecosystem structure and function variable values and mixing these genotypes in the diversity treatments likely muted the overall impacts of diversity on ecosystem structure and function.

There is a growing appreciation that within-species variation can have as large an impact on communities and ecosystems as among-species variation (Crutsinger *et al.* 2006). Arguably, this should not be surprising; from an evolutionary standpoint, genotype variation is roughly a smaller-scale version of species variation, and the fact that species variation affects communities and ecosystems is considered unremarkable. Global changes such as nitrogen deposition and warming are shaping the distribution and function of plant genotypes in the landscape (Treseder & Vitousek 2001; Madritch, Donaldson & Lindroth 2006). Our data show that variation in plant genotype can alter important ecosystem carbon and water dynamics. Thus, global change driven shifts in genotypes on the landscape may scale up to alter important ecosystem processes. Exploring how variation in genotype identity is influenced by global change and how those changes may influence the exchange of carbon and water with the atmosphere is an important next step in this line of research.

Acknowledgements

Data accessibility

Data deposited in the SHAREOK Repository: http://dx.doi.org/10.15763/grd.tbp2010.

References

Arnone, J.A. & Obrist, D. (2003) A large daylight geodesic dome for quantification of whole-ecosystem CO₂ and water vapour fluxes in arid shrublands. *Journal of Arid Environments*, **55**, 629–643.

Baldocchi, D. (2008) 'Breathing' of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany*, **56**, 1–26.

Bazzaz, F.A. (1996) *Plants in Changing Environments: Linking Physiological, Population, and Community Ecology*. Cambridge University Press, Cambridge, UK.

Bever, J.D., Westover, K.M. & Antonovics, J. (1997) Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology*, **85**, 561–573.

Bever, J.D., Dickie, I.A., Facelli, E. *et al.* (2010) Rooting theories of plant community ecology in microbial interactions. *Trends in Ecology and Evolution*, **25**, 468–4688.

Blue, J.D., Souza, L., Classen, A.T., Schweitzer, J.A. & Sanders, N.J. (2011) The variable effects of soil nitrogen availability and insect herbivory on aboveground and belowground plant biomass in an old-field ecosystem. *Oecologia*, **167**, 771–780.

Borer, E.T., Seabloom, E.W., Gruner, D.S. *et al.* (2014) Herbivores and nutrients control grassland via light limitation. *Nature*, **508**, 517–520.

Breza, L.C., Souza, L., Sanders, N.J. & Classen, A.T. (2012) Within and between population variation in plant traits predicts ecosystem functions associated with a dominant plant species. *Ecology and Evolution*, **2**, 1151–1161.

Burkle, L.A., Souza, L., Genung, M.A. & Crutsinger, G.M. (2013) Plant genotype, nutrients, and G × E interactions structure floral visitor communities. *Ecosphere*, **4**, 1–20.

Cardinale, B.J., Duffy, J.E., Gonzales, E. *et al.* (2012) Biodiversity loss and its impact on humanity. *Science*, **486**, 59–67.

Cornelissen, J.H.C., Lavorel, S., Garnier, E. *et al.* (2003) A handbook of protocols for standardized and easy measurements of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.

Crutsinger, G.M., Sanders, N.J. & Classen, A.T. (2009) Comparing intra- and inter-specific effects on litter decomposition in an old-field ecosystem. *Basic and Applied Ecology*, **10**, 535–543.

Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C. & Sanders, N.J. (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, **313**, 966–968.

Crutsinger, G.M., Reynolds, W.N., Classen, A.T. & Sanders, N.J. (2008) Disparate effects of plant genotypic diversity on foliage and litter arthropod communities. *Oecologia*, **158**, 65–75.

Crutsinger, G.M., Gonzalez, A.L., Crawford, K. & Sanders, N.J. (2013) Local and latitudinal variation in abundance: the mechanisms shaping the distribution of an ecosystem engineer. *Peer Journal*, **1**, e100.

De Deyn, G.B., Cornelissen, H.C. & Bardgett, R.D. (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, **11**, 516–531.

Díaz, S., Kattge, J. & Cornelissen, J.H.C. *et al.* (2016) The global spectrum of plant form and function. *Nature*, **529**, 167–177.

Elser, J.J., Bracken, M.E. & Cleland, E.E. *et al.* (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, **10**, 1135–1142.

Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webbjj, C.T., Henderson, A., Sloat, L.L. & Savage, V.M. (2015) Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. *Advances in Ecological Research*, **52**, doi: 10.1016/bs.aecr.2015.02.001

Fisher, D.G., Chapman, S.K., Classen, A.T., Gehring, C.A., Grady, K.C., Schweitzer, J.A. & Whitham, T.G. (2014) Marschner review: plant genetic effects on soils under climate change. *Plant and Soil*, **379**, 1–19.

Genung, M.A., Bailey, J.K. & Schweitzer, J.A. (2012) Welcome to the neighbourhood: interspecific genotype by genotype interactions in *Solidago* influence above- and belowground biomass and associated communities. *Ecology Letters*, **15**, 65–73.

Genung, M.A., Lessard, J.P., Brown, C.B. *et al.* (2010) Non-additive effects of genotypic diversity increase floral abundance and abundance of floral visitors. *PLoS ONE*, **5**, e8711.

Gross, R.S. & Werner, P.A. (1983) Relationships among flowering phenology, insect visitors, and seed-set of individuals- experimental studies on 4 co-occurring species of goldenrod (Solidago, Compositae). *Ecological Monographs*, **53**, 95–117.

Gruner, D.S., Smith, J.E., Seabloom, E.W. *et al.* (2008) A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecology Letters*, **11**, 740–755.

Halverson, K., Heard, S.B., Nason, J.D. & Stireman, J.O. (2008) Origins, distribution, and local co-occurrence of polyploid cytotypes in *Solidago altissima* (Asteraceae). *American Journal of Botany*, **95**, 50–58.

Hooper, D.U., Chapin, F.S., Ewel, J.J. *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N. & Vellend, M. (2008) Ecological consequences of genetic diversity. *Ecology Letters*, **11**, 609–623.

Huston, M.A. (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, **110**, 449–460.

Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts, D.L. & Schwinning, S. (2004) Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, **141**, 254–268.

Johnson, M.T.J. & Agrawal, A.A. (2005) Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). *Ecology*, **86**, 874–885.

Johnson, M.T.J., Lajeunesse, M.J. & Agrawal, A.A. (2006) Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters*, **9**, 24–34.

Johnson, M.T.J., Dinnage, R., Zhou, A. & Hunter, M.D. (2008) The importance of plant genetic variation for competition among plant species. *Journal of Ecology*, **96**, 947–955.

Jones, H.G. (2014) *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology*. Cambridge Press, Cambridge, UK.

Kattge, J., Diaz, S., Lavorel, S. *et al.* (2011) TRY – a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.

Lojewski, N.R., Fischer, D.G., Bailey, J.K., Schweitzer, J.A., Whitham, T.G. & Hart, S.C. (2012) Genetic components to belowground carbon fluxes in a riparian forest: a common garden approach. *New Phytologist*, **29**, 1133–1142.

Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72–76.

Maddox, G.D. & Root, R.B. (1987) Resistance to 16 diverse species of herbivorous insects within a population of goldenrod, *Solidago altissima*-genetic variation and heritability. *Oecologia*, **72**, 8–14.

Madritch, M., Donaldson, J.R. & Lindroth, R.L. (2006) Genetic identity of *Populus tremuloides* litter influences decomposition and nutrient release in a mixed forest stand. *Ecosystems*, **9**, 528–537.

Madritch, M.D. & Hunter, M.D. (2002) Phenotypic diversity influences ecosystem functioning in an oak sandhills community. *Ecology*, **83**, 2084–2090.

Madritch, M.D. & Hunter, M.D. (2003) Intraspecific litter diversity and nitrogen deposition affect nutrient dynamics and soil respiration. *Oecologia*, **136**, 124–128.

Pendergast, T.H., Burke, D.J. & Carson, W.P. (2013) Belowground complexity drives aboveground dynamics: a test of the soil community feedback model. *New Phytologist*, **197**, 1300–1310.

Potts, D.L., Huxman, T.E., Scott, R.L., Williams, D.G. & Goodrich, D.C. (2006) The sensitivity of ecosystem carbon exchange to seasonal precipitation and woody plant encroachment. *Oecologia*, **150**, 453–463.

Semple, J.C. & Cook, R.E. (2006) *Flora of North America North of Mexico*. Oxford University Press, New York, NY, USA.

Souza, L., Weltzin, J.F. & Sanders, N.J. (2011) Differential effects of two dominant plant species on community structure and invasibility in an old-field ecosystem. *Journal of Plant Ecology*, **4**, 123–131.

Souza, L., Bunn, W.A., Simberloff, D., Lawton, R.M. & Sanders, N.J. (2011a) Biotic and abiotic influences on native and exotic richness relationship across spatial scales: favourable environments for native species are highly invasible. *Functional Ecology*, **25**, 1106–1112.

Souza, L., Weston, D.J., Sanders, N.J., Karve, A., Crutsinger, G.M. & Classen, A.T. (2011b) Variation from individuals to ecosystems in the response to climatic warming: a test with *Solidago altissima*. *Ecosphere*, **2**, 1–14.

Stovall, J.P., Seiler, J.R. & Fox, T.R. (2013) Respiratory C fluxes and root exudation differ in two full-sib clones of *Pinus taeda* (L.) under contrasting fertilizer regimes in a greenhouse. *Plant and Soil*, **363**, 257–271.

Thomas, F., Abbott, J.M., Steinberg, C., Balk, M., Williams, S.L. & Stachowicz, J.J. (2011) Plant genotype and nitrogen loading influence seagrass productivity, biochemistry, and plant-herbivore interactions. *Ecology*, **92**, 1807–1817.

Tilman, D., Lehman, C.L. & Thomson, K.T. (1997) Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 1857–1861.

Tilman, D., Wedin, D. & Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**, 718–720.

Treseder, K.L. & Vitousek, P.M. (2001) Potential ecosystem-level effects of genetic variation among populations of *Metrosideros polymorpha* from a soil fertility gradient in Hawaii. *Oecologia*, **126**, 266–275.

Verhoeven, K.J.F., Simonsen, K.L. & McIntyre, L.M. (2005) Implementing false discovery rate control: increasing your power. *Oikos*, **108**, 643–647.

Wardle, D.A. (1999) Is "sampling effect" a problem for experiments investigating biodiversity-ecosystem function relationships? *Oikos*, **87**, 403–407.

Whitham, T.G., Bailey, J.K., Schweitzer, J.A. *et al.* (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics*, **7**, 510–523.

Whitham, T.G., Young, W.P., Martinsen, G.D. *et al.* (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology*, **84**, 559–573.

Wilsey, B.J. & Polley, H.W. (2004) Realistically low species evenness does not alter grassland species-richness-productivity relationships. *Ecology*, **85**, 2693–2700.

Wise, M.J. & Abrahamson, W.G. (2008) Ducking as a means of resitance to herbivory in tall goldenrod, *Solidago altissima*. *Ecology*, **89**, 3275–3281.

Wright, P., Cregger, M.A., Souza, L., Sanders, N.J. & Classen, A.T. (2014) The effects of insects, nutrients, and plant invasion on community structure and function above- and belowground. *Ecology & Evolution*, **4**, 732–742.

Wymore, A.S., Keeley, A.T., Yturralde, K.M., Schroer, M.L., Propper, C.R. & Whitham, T.G. (2011) Genes to ecosystems: exploring the frontiers of ecology with one of the smallest biological units. *New Phytologist*, **191**, 19–36.

Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Fig. S1. Plant genotype variation in total aboveground biomass and leaf area index in July, August, and September.

Fig. S2. Plant genotype variation in NEE, ET, WUE, and Soil CO_2 efflux in July, August, and September.

Fig. S3. Analysis of non-additivity for height, stem diameter, and biomass measured in August.

Fig. S4. Analysis of selection and complementarity for height, stem diameter, and biomass measured in August.

Table S1. Results from a repeated measures analysis of variance (RMANOVA) testing for the effects of time, time × nutrients, time × genotype, time × genotype × nutrients on ANPP, LAI, NEE, ET, and EWUE.

Table S2. Results from a repeated measures analysis of variance (RMANOVA) testing for the effects of time, time × nutrients, time × diversity, time × diversity × nutrients on ANPP, LAI, NEE, ET, and eWUE.

Table S3. Parameter estimates for the linear regressions that estimated relationships between ecosystem structure (ANPP and LAI) and ecosystem functions (NEE, ET, EWUE).