

Variation in below-ground carbon fluxes along a *Populus* hybridization gradient

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Summary

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Received: 12 March 2007

Accepted: 23 May 2007

- Here, soil CO₂ efflux, minirhizotron fine root production (FRP), and estimated total below-ground carbon allocation (TBCA) were examined along an elevation and hybridization gradient between two cottonwood species.
- FRP was 72% greater under high-elevation *Populus angustifolia*, but soil CO₂ efflux and TBCA were 62% and 94% greater, respectively, under low-elevation stands dominated by *Populus fremontii*, with a hybrid stand showing intermediate values.
- Differences between the responses of FRP, soil CO₂ efflux and TBCA may potentially be explained in terms of genetic controls; while plant species and hybridization explained variance in carbon flux, we found only weak correlations of FRP and TBCA with soil moisture, and no correlations with soil temperature or nitrogen availability.
- Soil CO₂ efflux and TBCA were uncorrelated with FRP, suggesting that, although below-ground carbon fluxes may change along environmental and genetic gradients, major components of below-ground carbon flux may be decoupled.

Key words: cottonwood, elevation gradient, fine root production, genetics × environment, minirhizotron, root production, soil CO₂ efflux, total below-ground carbon allocation.

New Phytologist (2007) doi: 10.1111/j.1469-8137.2007.02167.x

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Introduction

Below-ground carbon (C) flux is fundamentally important to ecosystem C budgets and may play a dominant role in whole ecosystem C exchange (Valentini *et al.*, 2000; Giardina *et al.*, 2005). Soil temperature, moisture, nitrogen (N) availability, and foundational species genetics (Whitham *et al.*, 2006) may all play important roles in regulating this important ecosystem process. Untangling the relative influences of genetics and environment on components of below-ground C flux is therefore of vital importance for understanding ecosystem responses to global change (Schlesinger, 1999; Knorr *et al.*, 2005) and ecosystem feedbacks (Whitham *et al.*,

2003; Fischer *et al.*, 2004, 2006; Schweitzer *et al.*, 2004), and is a focus of major research and funding efforts in genetics and ecology.

Responses of below-ground C fluxes to environmental variation are complex and potentially idiosyncratic (Giardina *et al.*, 2005). Root respiration may increase with temperature and N availability (Valentini *et al.*, 2000; Burton *et al.*, 2002; but see Giardina & Ryan, 2000) and is generally a large proportion of total below-ground carbon allocation (TBCA) and soil CO₂ efflux (Boone *et al.*, 1998; Valentini *et al.*, 2000; Giardina *et al.*, 2005; C. M. Litton *et al.*, in press). Soil temperature can increase fine root production (FRP; Giardina *et al.*, 2005; C. M. Litton *et al.*, in press), but may not change

genetically controlled patterns in C allocation (King *et al.*, 1999). Fine root production (FRP) may also generally decrease with increasing soil water and N availability (e.g. Pregitzer *et al.*, 1990; Tingey *et al.*, 2005). Plants may respond to low soil moisture by investing more C in FRP (Giardina *et al.*, 2005; but see Cox *et al.*, 2005), but environmental effects on soil CO₂ efflux and TBCA may be less clear because these are the result of C flux among multiple actors (Giardina *et al.*, 2005). At study sites in northern Utah, Schweitzer *et al.* (2004) found greater net N mineralization in low-elevation stands of *Populus fremontii* compared with higher elevation stands of *Populus angustifolia*, which may reduce FRP (Fischer *et al.*, 2006). Because high soil N availability and high soil temperatures may covary at low-elevation sites (Schweitzer *et al.*, 2004), these two variables may also interact to affect root respiration and FRP.

The genetic structure of populations of dominant trees may have a predictable influence on C allocation below-ground. For example, cold-climate genotypes may invest more resources in fine root growth than lower elevation, warmer climate genotypes (Oleksyn *et al.*, 1992; Dickmann *et al.*, 1996; Oleksyn *et al.*, 1999; Reich & Bolstad, 2001; Tateno *et al.*, 2004), reflecting an adaptation to reduced resource conditions associated with shorter growing seasons and low N availability (see Fischer *et al.*, 2006). Although the precise mechanism for this pattern is unclear, it has been consistently found in taxa as diverse as conifers (Oleksyn *et al.*, 1999) and deciduous trees (Dickmann *et al.*, 1996). In a common garden, Fischer *et al.* (2006) found that FRP increased along a natural genetic hybridization gradient from genotypes of low-elevation *P. fremontii* to genotypes of high-elevation *P. angustifolia*, and was positively correlated with foliar condensed tannins. Genetic influences on root exudates and mycorrhizas may also be important (Brundrett, 2002; Phillips *et al.*, 2003), but need not be coupled with FRP as trade-offs between reliance on fine roots vs symbionts may have occurred through evolutionary time (Brundrett, 2002).

Because of this variability in responses of below-ground C fluxes to environment and genetics, approaches that incorporate genetics and environmental gradients are particularly important. Using a model system of cottonwoods in northern

Utah, USA, three C fluxes (soil CO₂ efflux, FRP, and TBCA) were examined in order to measure variation along a genetic and elevation gradient. Extensive genetic work at the study sites (see Martinsen *et al.*, 2001; Whitham *et al.*, 2006) allowed us to address genetic levels of variation associated with hybridization which would be difficult in most studies, and may be comparable with previous work in a nearby common garden environment. Thus, this study examines native riparian forest variation in C flux within a genetic context. The study sites also differed in elevation, which allowed us to evaluate responses along an elevation gradient that is common in riparian ecosystems of the western USA. The primary goal was to evaluate relationships between components of below-ground C flux and soil temperature, soil moisture, soil N availability, and a genetic-hybridization gradient. We originally predicted that there would be differences among stands in all three measures of C flux, where high-elevation trees would have highest root production and TBCA, but not soil CO₂ efflux (Dickmann *et al.*, 1996; Schweitzer, 2002; Fischer *et al.*, 2004, 2006). It was also originally predicted that FRP and TBCA would decrease with increasing moisture and N availability, and soil CO₂ efflux would increase with increasing soil temperature, moisture, and N availability.

Materials and Methods

Study site

Along the Weber River in north-central Utah, USA, higher elevation riparian habitats are dominated by *Populus angustifolia* James, lower elevation riparian habitats are dominated by *Populus fremontii* S. Wats., and in a 13-km hybrid zone at their boundaries both parental species and natural F₁ and backcross hybrids are found (Keim *et al.*, 1989). The degree of hybridization within an individual tree can be accurately characterized using the fraction of species-specific restriction fragment length polymorphism (RFLP) markers of *P. fremontii* found in each tree (see Keim *et al.*, 1989; Martinsen *et al.*, 2001 for details).

Forty-five randomly located 117-m² circular plots divided among three representative stands (Table 1) dominated by *P. fremontii*, *P. angustifolia*, or hybrid (*P. fremontii* × *P. angustifolia*)

Table 1 Selected stand characteristics of the four sites along the Weber River, Utah, USA

Site	Number of plots	Latitude, longitude (decimal°)	Elevation (m)	Stand size (ha)	Maximum canopy height (m)	Mean annual precipitation (mm)	Mean daily air temperature (°C)
<i>Populus fremontii</i> 1	10	41.25, -112.03	1295	0.39	34.5	468	14.6
<i>Populus fremontii</i> 2	3	41.16, -111.98	1341	0.31	34.1	467	13.9
Hybrid	15	41.14, -111.95	1360	0.89	21.7	467	13.9
<i>Populus angustifolia</i>	14	41.04, -111.51	1613	0.65	21.9	435	11.2

Climatic data are 30-yr means from the Western Regional Climatic Data Center (<http://www.wrcc.dri.edu/>). Stand size was estimated from 2003 aerial photos.

trees (i.e. 15 plots each) were established. In all plots, numbers of trees and diameters at 1.4 m height were determined, and biomass was estimated using locally developed allometric equations based on diameter (Fischer *et al.*, 2006). At the start of the study, vandals destroyed minirhizotron observation tubes in five plots in the *P. fremontii* stand, and in one plot in the *P. angustifolia* stand. In order to keep an adequate sample size for all measurements, three extra plots in a second *P. fremontii* stand directly adjacent to the hybrid stand were used (see Table 1, *P. fremontii* stand 2) which reduced the sample size to 13 plots for *P. fremontii*. There was no replacement for the lost *P. angustifolia* plot, reducing the sample size to 14 in this stand, and 42 plots overall. Because the sampling was focused in three stands, pseudoreplication may complicate interpretation of the results. The data should be interpreted cautiously as differences may be attributable to unmeasured biotic or abiotic factors unique to each stand.

Soil moisture (gravimetric (at 105°C for 48 h) from the upper 10 cm of soil) and temperature (measured using a digital soil temperature probe at 7.5 cm depth from the ground surface) were measured once per month at midday in the center (near the minirhizotron and soil CO₂ efflux measurements) of a subset of 10 plots per stand type. Moisture and temperature were predicted to be important because they are major drivers of respiration and N availability, and covary with elevation of the stands (Schweitzer, 2002; Table 1). With two separate field incubations (June to November 2002, and November 2002 to June 2003), annual resin N availability (Hart & Firestone, 1989) was also quantified. Mixed bed ion-exchange resin bags were placed adjacent to each minirhizotron tube at 10 cm depth in the soil. The ion-exchange resin bags consisted of 30 ml (~16 g) of mixed bed ion-exchange resin (Ionac[®] NM-60 H⁺/OH⁻ form type 1 beads; J. T. Baker, Phillipsburg, NJ, USA) in a nylon stocking. Resin was extracted using 100 ml of 2 M KCL and analyzed for ammonium and nitrate (NO₂⁻ + NO₃⁻) N on a Lachat flow-injection analyzer (Lachat Instruments, Loveland, CO, USA).

Each tree in the hybrid-zone plots (15 plots) was assigned a categorical *P. fremontii* RFLP score to allow analysis of C flux in the context of tree genetic composition on a subset of the data. Many trees within these plots have had their RFLP-based genetic status evaluated (see Keim *et al.*, 1989; Martinsen *et al.*, 2001; Wimp *et al.*, 2004 for details). This extensive work has shown that, based on leaf morphology phenotype identification (see Bangert *et al.*, 2005), we can conservatively approximate three categorical classes of the proportion of *P. fremontii* RFLP markers in a given tree by giving *P. fremontii* a score of 1.0, F₁ hybrids a score of 0.5, and both backcross and *P. angustifolia* trees a score of 0.0 (see also Martinsen *et al.*, 2001; Bangert *et al.*, 2005; Fischer *et al.*, 2006). This approach is justified based on > 20 yr of previous genetic work on these two species and their hybrids at these study sites, and the extreme rarity of hybrids intermediate between F₁ and backcross hybrids in the wild (see Martinsen

et al., 2001; Bangert *et al.*, 2005). However, any morphological technique is prone to misinterpretation problems, and this could be a potential source of error in the analyses. This estimation was only used for a limited subset of the analyses within the broader context of the study. The RFLP scores were averaged within a plot to produce an average index of the proportion of *P. fremontii* RFLP markers for each plot (plot RFLP index).

Minirhizotron fine root production

During early May 2002, one acrylic minirhizotron tube (Withington *et al.*, 2003) was installed at the center of each plot to measure fine (≤ 2.0 mm) root production (FRP). Minirhizotron tubes (63.5 mm internal diameter; 3.0 mm wall diameter; 1.0 m length) were installed 0.00–0.55 m deep, at 36° from the horizontal (Johnson *et al.*, 2001). At all sites, soils are classified in the United States Department of Agriculture (USDA) Soil Taxonomical order of Entisols and have loamy sand or sandy loam surface textures. Additionally, these soils are subject to frequent disturbance by flooding (Schweitzer, 2002). Using a trench profile technique (Van Noordwijk *et al.*, 2000) in six 1-m deep pits, it was determined that > 70% of fine roots in the plots occur between 0.0 and 0.4 m (data not shown; see also Johnson *et al.*, 2001).

Image collection began one growing season after tube installation as roots may need time to equilibrate after tube installation (Price & Hendrick, 1998; Joslin & Wolfe, 1999). Every 2 wk from November 2002 to November 2003, images were taken at vertical depths of 0.00–0.12, 0.12–0.24, and 0.24–0.36 m, using a rotating scanner head CI-600 minirhizotron (CID Inc., Vancouver, WA, USA). The scanner-based technology produced a 360°, 0.22 × 0.20 m image of the tube–soil interface at 75 dots per inch (DPI) for analysis. Images were analyzed separately using the program ROOTTRACKER[™] (Duke University, Durham, NC, USA). Each fine root was individually digitally tagged, identified, and monitored for growth, development, death, and disappearance.

The FRP estimates (g production m⁻² of ground area yr⁻¹) were estimated for each tube using the equation

$$\text{Fine root production (g m}^{-2} \text{ yr}^{-1}) = \sum_i \frac{L_i \times D_i}{\text{SRL} \times A_i \times \text{DOF}}$$

(*i*, a given depth of measurement; *L*, the total length of new root production by individual roots measured (m yr⁻¹); *D*, the vertical depth (m) sampled; SRL, median specific root length (m g⁻¹); *A*, the measurement area of each image (m²); DOF, an estimated depth of field of each image (m; Johnson *et al.*, 2001).) A DOF of 0.002 m was assumed based on the maximum fine root diameter (see Johnson *et al.*, 2001). Specific root lengths were directly estimated using elutriated roots (Smucker *et al.*, 1982) from soil cores (0.002 m²,

0.15 m deep) taken from the centers of all plots in the field ($n = 42$) in June 2003. The median SRL was estimated at 28 m g^{-1} , for all tree types, which is similar to other estimates for other temperate forest trees (Pregitzer *et al.*, 2002). The assumption that SRL would be similar among tree types was supported by lack of significant differences among stands in SRL ($n = 10$; $P = 0.26$; also see Fischer *et al.*, 2006) and median root diameter (all roots measured; $P = 0.48$). It was assumed that ash-free root mass was 50% C for comparison of results with soil CO_2 efflux and TBCA (see following sections). Finally, root turnover (yr^{-1}) was estimated by dividing FRP by maximum standing crop (Table 2).

Soil CO_2 efflux

A LI-COR 6200 (Li-Cor, Lincoln, NE, USA) infrared gas analyser (IRGA) with a soil measurement chamber (11.9 l, 27.5 cm diameter, 20 cm tall; Hart & DiSalvo, 2005) was used to estimate soil CO_2 efflux in 30 randomly selected plots (from the 42 minirhizotron plots). The 30 plots were divided between the *P. fremontii* stands (seven plots in stand one and three plots in stand two), the hybrid stand (10 plots), and the *P. angustifolia* stand (10 plots). The IRGA was calibrated and measurements were taken similarly to descriptions in Hart & DiSalvo (2005). Measurements were taken once per month in the same location near the plot center, between 11:00 and 14:00 h from 17 March through 8 November 2003. Once a month, five plots were chosen at random within each stand for measurements every 6 h over a 24-h period to determine diel variation in soil CO_2 efflux. Standard repeated measures analysis of variance (ANOVA) indicated no significant diel variation in any of the plots measured ($P = 0.820$), similar to the finding in another riparian study in California (Hart & DiSalvo, 2005). Estimates were scaled up to annual rates using a procedure similar to that used by Hart & DiSalvo (2005), where direct estimates of flux were multiplied by time between measurements, and winter rates were estimated as the average of the first and last measurements of the year which were taken while the surface soil was frozen. Five low-elevation sites were measured once per month during winter and consistent low values were found during this cold period (data not shown). Accompanying each IRGA measurement, air temperature was measured inside the chamber, and soil temperature and gravimetric soil moisture (see section 'Study site' above) were measured within 10 cm of the chamber.

Total below-ground carbon allocation estimation

Total below-ground carbon allocation was estimated with a method similar to the original approach of Raich & Nadelhoffer (1989), using the difference between estimated litterfall inputs (from 2002) and soil CO_2 efflux to estimate TBCA. This approach relies on a steady-state assumption for

Table 2 General measured characteristics of *Populus* stands along the Weber River, Utah, USA

Stand type	Allometric estimated litterfall ($\text{g m}^{-2} \text{ yr}^{-1}$)	Combined litter from litter traps (g m^{-1})	Stem density (stems ha^{-1})	Tree mass (kg m^{-2})	Fine root production ($\text{g C m}^{-2} \text{ yr}^{-1}$)	Fine root turnover (yr^{-1})	Maximum standing fine root length (m root m^{-2})	Total N (mg g^{-1} resin)	Soil temperature ($^{\circ}\text{C}$)	Soil moisture (%)	Soil temperature range ($^{\circ}\text{C}$)	Soil moisture range (%)
<i>Populus fremontii</i>	578.7 ± 46.4 A	540.3	721 ± 66 A	1284 ± 185 A	111.5 ± 23 A	0.91 ± 0.1 A	44.1 ± 7.3 A	0.24 ± 0.05 A	14.6 ± 0.1 A	10.5 ± 0.7 A	13.5–15.0	2.7–15.7
Hybrid	314.1 ± 43.2 B	331.7	549 ± 77 A	881 ± 209 A	145.6 ± 20.6 AB	1.0 ± 0.1 A	48.5 ± 6.8 A	0.14 ± 0.07 B	15.5 ± 0.7 A	8.6 ± 0.8 A	12.9–19.9	3.7–11.5
<i>Populus angustifolia</i>	414.5 ± 43.2 B	382.5	592 ± 65 A	1322 ± 154 A	191.5 ± 21.3 B	1.4 ± 0.1 B	47.4 ± 7.6 A	0.12 ± 0.02 B	12.1 ± 0.3 B	20.7 ± 1.5 B	10.7–13.8	11.9–27.7

Values are mean \pm standard error for the first four columns. Values for soil temperature and moisture reflect mean growing-season values, and ranges in mean growing-season values among plots within stands. Means followed by different letters are significantly different using an analysis of variance and Tukey HSD test.

soil C unless soil C pools are directly measured. While this steady-state assumption is unlikely to be met in young, accreting stands, it is more likely to be valid in older, mature stands (see Giardina & Ryan, 2002; Giardina *et al.*, 2005 for issues concerning steady-state assumptions). The forests stands used in this study were in the most advanced seral stage for this forest type. Additionally, this assumption may be justified because changes in soil C pools in a single year are much smaller than soil CO₂ efflux and litterfall C fluxes (see Giardina & Ryan, 2002; Giardina *et al.*, 2005). However, caution should be used in interpretation of such TBCA values because of this steady-state assumption and because 1-yr data may not represent longer term changes.

Stem diameter measurements in the plots were used from June 2003 to estimate yearly litterfall using locally developed allometric equations (Fischer *et al.*, 2004; Cox *et al.*, 2005) and assuming that leaf biomass m⁻² minus resorption (~15% fresh leaf mass) was equal to leaf litterfall m⁻². This method provided estimates similar to those for 10 litter traps per stand, collected monthly (Schweitzer *et al.*, 2004; see Table 2). Litter-trap data were unavailable for plot-level comparison because all litter for each stand was combined during collection from traps. Fifty per cent C was assumed for all plant biomass.

Statistical analysis

All analyses were conducted on annual totals and mean growing season values. Four types of analysis were conducted separately: (1) comparisons among stands using ANOVA (42 plots; 30 for IRGA and TBCA measurements); (2) simple linear regression within each stand between environmental variables (mean growing-season soil temperature, gravimetric moisture, and resin N) and FRP (42 plots), soil CO₂ efflux, and TBCA (30 plots); (3) simple linear regression between estimated plot *P. fremontii* RFLP index and C fluxes within hybrid-zone plots where all tree types co-occur (15 plots for FRP; 10 plots for IRGA and TBCA); and finally (4) an information-theoretic approach (Burnham & Anderson, 2002) to evaluate candidate linear models for predicting FRP, soil CO₂ efflux, and TBCA. Briefly, the information-theoretic approach uses maximum likelihood theory and the principle of parsimony to assess the strength of evidence for each model in a candidate set of *a priori* defined models. Akaike's information criterion, adjusted for small sample size (AIC_c), an estimate of model likelihood, Akaike weights (*w_i*), and an evidence ratio computed from these variables were used to simultaneously compare and rank multiple models from a set of *a priori* candidate models (Burnham & Anderson, 2002). Each measure provides an index of the best model given the data, and the evidence ratio gives a comparative 'odds' of the top-ranked model being the best model given the data. All models were single-variable linear models (soil temperature, moisture, N availability or *P. fremontii* RFLP index) except one model that combined temperature and soil moisture.

Models whose ΔAIC (AIC_c relativized to the lowest value) differed by < 2.0 were not considered statistically distinguishable, as is common practice (Burnham & Anderson, 2002). The AIC_c values were calculated from AIC values given in JMP stepwise regression analyses (JMP DISCOVERY statistical package 4.0; SAS Institute Inc., Cary, NC, USA).

Standard ANOVA and least squares regression analysis were used for all comparisons of stands and regression analyses (JMP DISCOVERY statistical package 4.0). An alpha of 0.05 was used to denote significance. A Tukey HSD test was used to separate means when ANOVA results were significant.

Results

General stand characteristics

A selected set of stand characteristics and locations are listed in Table 1. Values for the measured variables litterfall, mean growing season temperature, and mean growing season moisture are reported in Table 2. The higher elevation *P. angustifolia* stand is cooler and receives less precipitation based on 30-yr averages of temperature and precipitation (Table 1). During 2003 this site had cooler soils ($P < 0.001$) and higher soil moisture ($P < 0.001$) than other sites (Table 2). Estimated litterfall differed among stands ($P = 0.001$), and there was higher litterfall in the *P. fremontii* stand than in the other stands.

Comparisons of C flux among stands

On the basis of results from an earlier common garden study (Fischer *et al.*, 2006), it was expected that FRP would be highest in *P. angustifolia* stands and lowest in *P. fremontii* stands, with hybrids having intermediate values. In agreement with these expectations, FRP (g C m⁻² yr⁻¹; Fig. 1a) was highest in the *P. angustifolia* stand and was lowest in the *P. fremontii* stands, and the hybrid stand was intermediate ($P = 0.047$). Ratios of FRP to TBCA are also important to consider, because they depict below-ground investment in fine roots as a proportion of total below-ground flux. The FRP:TBCA ratio was also higher in the *P. angustifolia* stand than in the hybrid and *P. fremontii* stands ($P < 0.001$; Fig. 1b). Fine root turnover (Table 2) was also highest in the *P. angustifolia* stand.

Soil CO₂ efflux showed an opposite pattern among stands compared with FRP, and was lower in the *P. angustifolia* and hybrid stands than in the *P. fremontii* stands ($P = 0.005$; Fig. 1c). Estimated TBCA also showed an opposite trend among stands compared with FRP (Fig. 1d), reflecting the strong influence of soil CO₂ efflux on this variable relative to litterfall (i.e. ΔCO₂ >> Δlitterfall). The highest mean TBCA values were in the *P. fremontii* and hybrid stands, and TBCA was significantly lower in the *P. angustifolia* stand ($P = 0.003$; Fig. 1d).

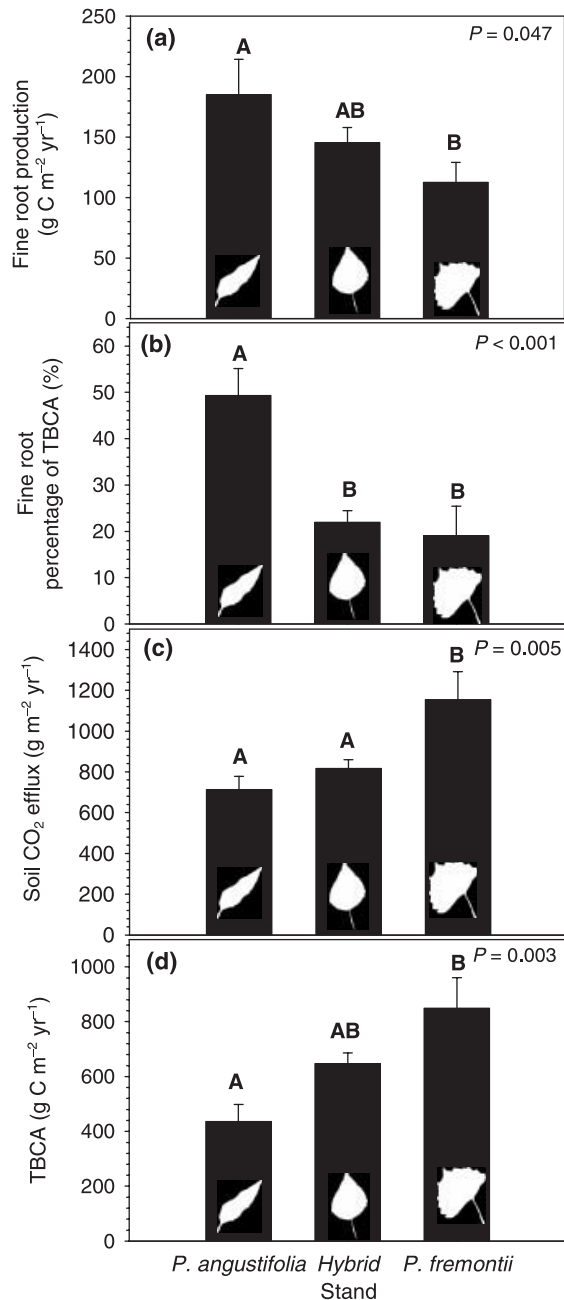


Fig. 1 Carbon (C) flux in *Populus* forests. (a) Fine root production (FRP) for *Populus angustifolia*, hybrid, and *Populus fremontii* stands. (b) FRP expressed as a percentage of total below-ground C allocation (TBCA) for *P. angustifolia*, hybrid, and *P. fremontii* stands. (c) Soil CO₂ efflux for the same stands. (d) TBCA for all stands. Error bars denote 1 standard error. Different letters represent significant differences at $P < 0.05$ from a Tukey's HSD test for multiple comparisons.

Within-stand regressions among environment, genetics, and C flux

Despite a large range within stands in mean growing season temperature, moisture and resin N (Tables 1, 2), C flux

variables were poorly related to mean annual temperature, moisture, and N availability. Fine root production was not significantly related to mean growing-season temperature, soil moisture, or N availability within stands (Table 3). Similarly, fine root turnover was not related to abiotic variables ($P > 0.05$). There were also no significant within-stand regressions between soil CO₂ efflux or TBCA and mean growing-season temperature or N availability within the *P. fremontii* stands, the hybrid stand or the *P. angustifolia* stand (Table 3) when analysed separately. In the *P. angustifolia* stand, soil CO₂ efflux was negatively related to mean growing-season gravimetric soil moisture ($r^2 = 0.42$; $P = 0.025$), but no significant relationship was found in other stands (Table 3).

However, with all stands pooled (Fig. 2), FRP was positively related to mean growing-season soil moisture ($r^2 = 0.11$; $P = 0.05$), but not soil temperature ($P = 0.13$) or resin N ($P = 0.88$). Pooled regressions between soil CO₂ efflux and mean growing-season soil moisture ($P = 0.05$), temperature ($P = 0.69$) and N availability ($P = 0.86$) were not significant. With all plots pooled, TBCA showed a negative relationship with mean growing-season soil moisture ($r^2 = 0.22$; $P = 0.006$), but was not related to soil temperature ($P = 0.199$) or resin N ($P = 0.854$). The ratio of FRP:TBCA was positively related to mean growing-season soil moisture ($r^2 = 0.53$; $P < 0.001$), negatively related to mean growing-season soil temperature ($r^2 = 0.17$; $P = 0.030$), and unrelated to resin N ($P = 0.584$) with stands pooled. Fine root turnover was positively related to soil moisture ($r^2 = 0.22$; $P = 0.01$), negatively related to soil temperature ($r^2 = 0.26$; $P = 0.01$) and unrelated to resin N ($P = 0.685$; data not shown).

In order to help clarify how tree genetics influence C flux, relationships were analyzed between estimated plot RFLP index and C flux variables in the hybrid plots where all tree cross types (*P. fremontii*, *P. angustifolia*, and hybrids) occurred together. In support of genetic controls on FRP and in agreement with a common garden study (Fischer *et al.*, 2006), FRP declined with higher genetic representation of *P. fremontii* (higher plot RFLP index; $r^2 = 0.51$; $P = 0.003$; Fig. 3). No significant relationship was found between either soil CO₂ efflux ($P = 0.896$) or TBCA ($P = 0.387$) and plot RFLP index ($r^2 = 0.58$; $P = 0.017$) among the hybrid plots.

What best predicts below-ground C flux across stands?

Across all stands, model selection analyses suggested general support for genetic controls over FRP, soil CO₂ efflux, and TBCA (Table 4). The analyses indicated that the best factors (treated as individual linear models) for predicting FRP were average growing-season soil moisture and *P. fremontii* RFLP index, based on low AIC_c values. However, the factors soil

Table 3 *P*-values for simple linear regression analyses

Stand type	FRP vs θ	FRP vs T_s	FRP vs N	Soil CO ₂ efflux vs θ	Soil CO ₂ efflux vs T_s	Soil CO ₂ efflux vs N	TBCA vs θ	TBCA vs T_s	TBCA vs N
<i>Populus fremontii</i>	0.10	0.56	0.44	0.94	0.10	0.64	0.91	0.78	0.35
Hybrid	0.46	0.80	0.90	0.28	0.88	0.52	0.71	0.37	0.29
<i>Populus angustifolia</i>	0.92	0.98	0.58	0.03 ($r^2 = 0.42$)	0.09	0.95	0.38	0.12	0.86

Regression analyses were conducted for the variables fine root production (FRP), gravimetric soil moisture (θ), soil temperature (T_s), nitrogen availability (N; ammonium and nitrate/nitrite), soil CO₂ efflux and total below-ground carbon allocation (TBCA) within each stand type ($n = 10$ for all analyses). Where regressions were significant (one case), an r^2 value is included and the value is in bold.

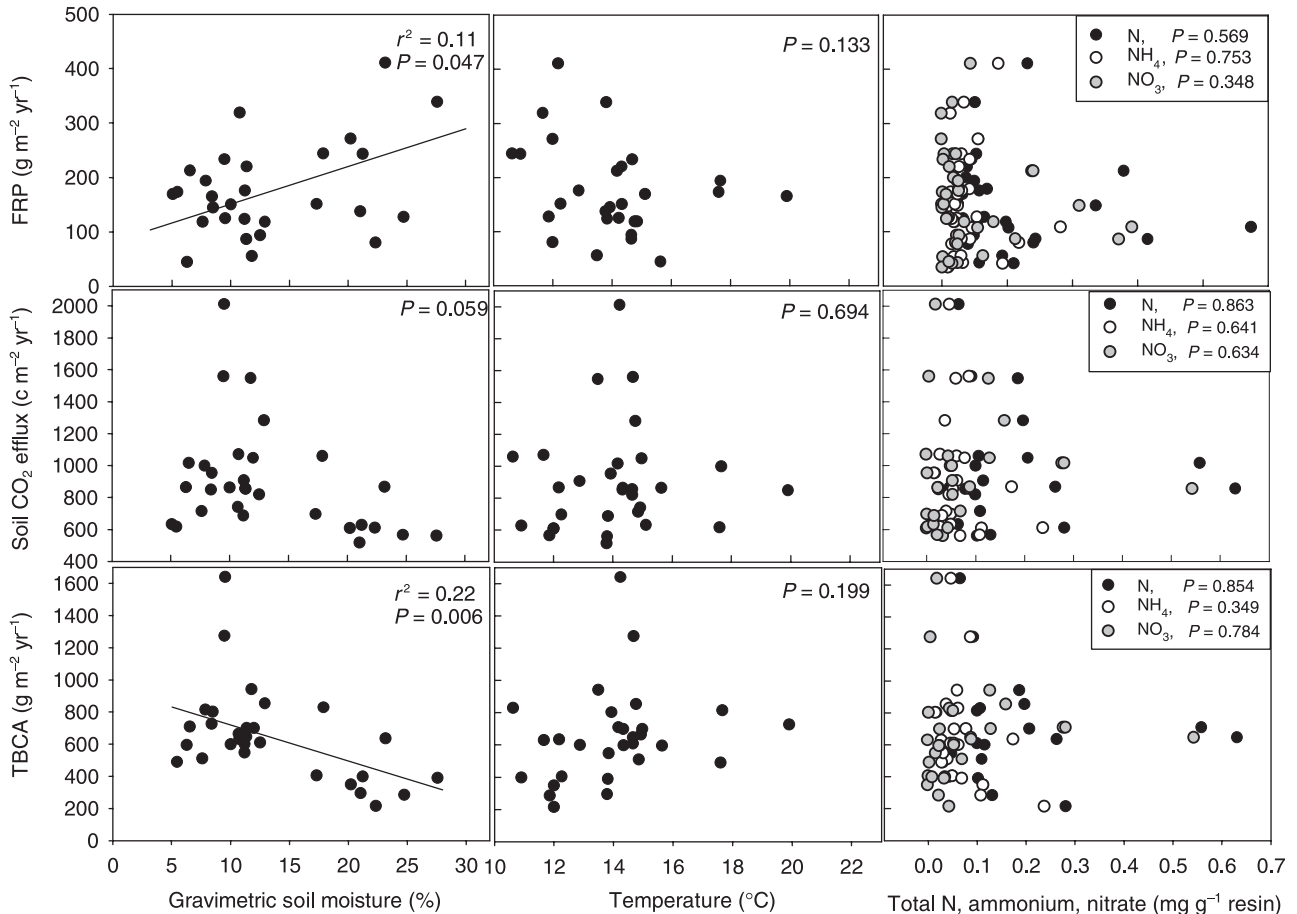


Fig. 2 Scatterplots of fine root production (FRP), soil CO₂ efflux and total below-ground C allocation (TBCA) vs gravimetric soil moisture, soil temperature, and N availability (as measured with ion-exchange resins). N refers to total inorganic N, and measures of nitrate include nitrite. Nonsignificant ($P > 0.05$) linear regression lines are not shown.

moisture and *P. fremontii* RFLP index only were able to describe ~30% each of the explanatory weight of all models and, based on ΔAIC_c values (difference < 2), these two models were statistically indistinguishable from each other. Additionally, the evidence ratio indicated that the intercept (null model) has ~1 : 3 odds of being a better explanatory variable.

The best factor predicting soil CO₂ efflux was the *P. fremontii* RFLP index. This was indicated by the lowest

AIC_c score, a low ΔAIC_c (calculated from AIC_c), and very high weights of evidence (w_i), indicating that this single variable can account for almost 96% of the variation explained by all models. Average growing-season soil moisture had odds of 1 : 57 of being a better explanatory variable, and only accounted for 2% of the explanatory weight of all models (w_i). Estimated TBCA was also best predicted by plant genetics. The *P. fremontii* RFLP index accounted for 62% of the variation explained by all models (w_i) in the prediction

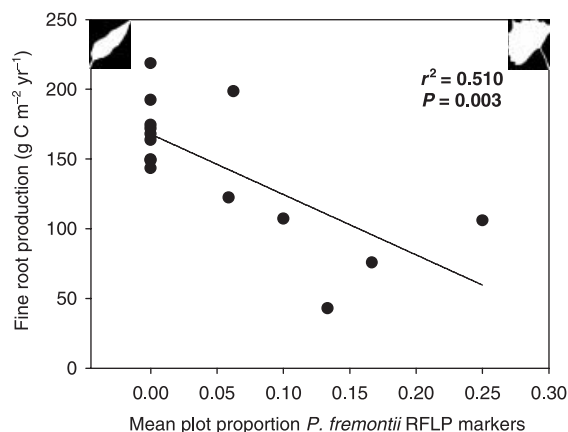


Fig. 3 Fine root production in plots within the hybrid stand ($n = 15$ plots) where all tree types occur vs the estimated mean plot proportion of *Populus fremontii* restriction fragment length polymorphism (RFLP) markers.

of TBCA, and this single-variable model had the lowest AIC_c score. However, soil moisture was indistinguishable from the RFLP index based on ΔAIC_c values, accounted for 24% of the explanatory weight of all models (w_i), and

based on the evidence ratio had ~1 : 3 odds of being a better model.

Relationships among C fluxes

Finally, the stand comparisons indicated that FRP followed an opposite pattern among stand types compared with both soil CO_2 efflux and TBCA. However, no significant statistical relationship was found between soil CO_2 efflux and FRP (Fig. 4a). Similarly, TBCA and FRP were unrelated at the plot level across all stands ($P = 0.792$; Fig. 4b). We did not test for relationships between soil CO_2 efflux and TBCA as TBCA was partially calculated from soil CO_2 efflux and thus was nonindependent. Fine root turnover was unrelated to soil CO_2 efflux ($P > 0.05$; data not shown).

Discussion

The data provide support for: (1) differences in C flux among stand types dominated by genetically different trees; (2) genetic-based predictability of FRP where all tree types occur together; and (3) low single-variable predictability

Table 4 Model selection criteria for selecting the best model predicting respective carbon fluxes of fine root production (FRP), soil CO_2 efflux, and total below-ground C allocation (TBCA)

	AIC_c	ΔAIC_c	Lik model	w_i	Evid. ratio
FRP					
Moisture	224.57	0.00 ^a	1.00	0.32	1.00
RFLP	224.83	0.26 ^{ab}	0.88	0.29	1.14
Temperature	226.19	1.62 ^{ab}	0.45	0.14	2.24
Intercept	226.82	2.24 ^b	0.33	0.11	3.07
Temperature and moisture	226.86	2.29 ^b	0.32	0.10	3.14
Nitrogen	228.95	4.38 ^c	0.11	0.04	8.92
Soil CO_2 efflux					
RFLP	296.92	0.00 ^a	1.00	0.96	1.00
Moisture	305.01	8.09 ^b	0.02	0.02	57.10
Intercept	306.02	9.10 ^{bc}	0.01	0.01	94.47
Temperature and moisture	306.75	9.83 ^{bc}	0.01	0.01	136.05
Temperature	307.93	11.01 ^c	0.00	0.00	245.59
Nitrogen	308.31	11.39 ^c	0.00	0.00	297.17
TBCA					
RFLP	281.45	0.00 ^a	1.00	0.62	1.00
Moisture	283.30	1.85 ^a	0.40	0.24	2.52
Temperature and moisture	285.59	4.14 ^b	0.13	0.08	7.94
Intercept	287.53	6.08 ^{bc}	0.05	0.03	20.94
Temperature	287.90	6.45 ^c	0.04	0.02	25.11
Nitrogen	289.82	8.37 ^d	0.02	0.01	65.68

Row titles reflect the predictive variables in the model. The 'Intercept' model has no predictive variables, and thus functions as a 'null' model. Models are ranked from the best (top) to worst (bottom) model based on ΔAIC_c values (based on Akaike's information criterion for small sample size (AIC_c)) which reflect an index of the amount of information lost when approximating truth with the model. However, as a general rule, models with ΔAIC_c values within 2 of each other are indistinguishable in terms of fit (denoted by the same superscript letters). For example, for the fine root production (FRP) model, 'Moisture' (mean growing-season soil moisture), 'RFLP' (*Populus fremontii* restriction fragment length polymorphism index) and 'Temperature' (mean growing-season soil temperature) are the best models according to all model selection criteria, including the ΔAIC_c values (lowest), the likelihood value for the best model (Lik model; 1.0), the Akaike weight of evidence (w_i ; closest to 1), and the evidence ratio (Evid. ratio); the 'Intercept' model has a 1 : 3 chance of being better than 'Moisture', given the data.

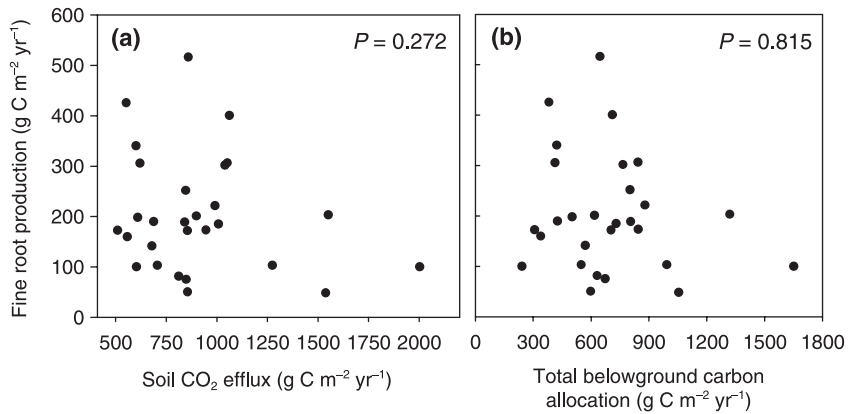


Fig. 4 (a) Fine root production vs soil CO₂ efflux, and (b) total below-ground carbon allocation (TBCA) pooled across all stands.

of below-ground C flux based on abiotic factors. Also, although genetics and hybridization may be an important control on below-ground C flux, FRP and soil CO₂ efflux changed in opposite directions along the gradient, and were uncorrelated.

Differences in C flux among *Populus* stand types is important because it may reflect diversity in ecological interactions of a foundation species (Ellison *et al.*, 2005). Additionally, small genetic or environmental differences may have large impacts on important flux rates that help to determine ecosystem C budgets. For example, high investment in FRP vs more labile C pools may increase soil C storage over longer time periods (Harrison *et al.*, 2004; Fischer *et al.*, 2006). The finding that different but superficially similar ecosystems (i.e. cottonwood forests) can in fact have large differences in C flux and below-ground allocation means that changes in climate, changing species ranges, habitat fragmentation and reduced population size (i.e. resulting in genetic drift), and the introduction of genetically modified organisms may have significant impacts on C cycling.

Our data are consistent with genetic control of FRP. Three lines of evidence support this assertion. First, stand-level patterns in FRP were consistent with those found in a common garden study (Fischer *et al.*, 2006), where FRP predictably declined as *P. fremontii* RFLP marker representation increased, and FRP was 75% greater under *P. angustifolia* and backcross hybrid canopies. In the current study, across greater environmental heterogeneity and in natural *Populus* stands, FRP was 72% higher in the *P. angustifolia*-dominated stand than in the *P. fremontii* stands and the hybrid stand was intermediate. Secondly, within the hybrid stand where all cross types grow side by side and environmental effects were greatly reduced, FRP declined with increasing estimated genetic representation of *P. fremontii* in forest plots. Finally, although a single environmental variable (soil moisture) was weakly correlated with FRP across all stands (Fig. 2), a model selection technique indicated that this factor was statistically indistinguishable from genetic factors (Table 4). These lines of evidence also held true for ratios of FRP to TBCA.

It was predicted that soil temperature, soil moisture, and N availability would all strongly influence FRP, soil CO₂ efflux, and TBCA. Nearly the opposite pattern was found, where no significant relationships with soil temperature, only weak relationships with soil moisture, and no relationship between C fluxes and N availability were found. However, the *P. fremontii* plots had nearly twofold higher soil CO₂ efflux compared with the *P. angustifolia* plots (Fig. 1c), and this increase matches the prediction that warmer soils will have higher soil CO₂ efflux (Boone *et al.*, 1998; Burton *et al.*, 2002; Ryan & Law, 2005). Lack of direct correlations among temperature and FRP, soil CO₂ efflux and TBCA could be a result of poor temporal resolution in the soil temperature measurements, and future, more detailed studies may provide better insight into temperature controls at local scales. Soil moisture was a predictor of both FRP and TBCA when all sites were combined, and of soil CO₂ efflux in the *P. angustifolia* stand. However, the reasons for these relationships are unclear, and the results may have been confounded by covarying genetic effects (for example, *Populus* genetics may also determine transpiration rate; see Fischer *et al.*, 2004). The expectation was that soil CO₂ efflux would increase with increasing soil moisture, but the results did not support this prediction. Instead, it was found that across all stands TBCA decreased with increasing soil moisture while fine root production increased and, in at least one stand, soil CO₂ efflux declined with increasing soil moisture. Reduced TBCA associated with high moisture availability is consistent with resource allocation theory (Bloom *et al.*, 1985), but increases in FRP with increasing soil moisture are not. Additionally, the plot-level measurements of soil moisture were not significant predictors of FRP or TBCA within stands. Higher soil N availability in *P. fremontii* plots could also alter C flux, as other studies have predicted (Pregitzer *et al.*, 1990; Burton *et al.*, 2002; Schweitzer *et al.*, 2004), but no statistical support was found for N-availability effects on C flux. In fact, the highest fine root turnover was found where N availability was lowest (Table 2), in contrast to other studies (e.g. Nadelhoffer, 2000), where it was found that root turnover and production

may increase with N. The lack of statistical significance with environmental variables within stands in these data could also be a result of low sample sizes ($n = 10\text{--}15$) or low precision of measurements, and future studies may clarify these results.

Our findings indicate that below-ground C allocation and flux may be affected by changes in the above-ground genetic structure of dominant trees. Genetic controls of soil CO₂ efflux and TBCA were stronger than measured environmental controls in all model selection comparisons. This suggests that genetics are an important regulator of below-ground C flux. This is especially important because it means that shifting ranges and altered genetics of foundation species (Krueper *et al.*, 1993; Ellison *et al.*, 2005) could strongly affect below-ground C flux. If we find predictable patterns of genetic influence related to elevation or environmental gradients, then this significantly improves the ability to predict ecosystem-level responses to changing species ranges and genetic pollution. For example, if low-elevation genotypes have higher TBCA, then migration of these genotypes to higher elevations with climate change may result in increased TBCA at high elevations. However, unmeasured biotic and abiotic differences between stands could confound some of the results, and neither soil CO₂ efflux nor TBCA was correlated with plot RFLP index in the hybrid-zone plots when data for these plots were analyzed alone. Current common garden studies on soil CO₂ efflux (N.R. Lojewski *et al.*, Northern Arizona University, unpublished) may clarify these patterns.

Opposite, but uncorrelated, trends among the stands for FRP vs soil CO₂ efflux and TBCA were likely a reflection of multiple controls on components of below-ground C flux, and potentially support differential influences of genetics on below-ground C fates. Below-ground C allocation is complex and dynamic, and includes significant contributions to root respiration, coarse root production, symbioses, and rhizodeposition, while only a portion is allocated to fine root growth (Eissenstat & Yanai, 1997; Burton *et al.*, 2002; C. M. Litton *et al.*, in press). Controls over FRP and soil CO₂ efflux may be decoupled because environmental conditions (e.g. temperature, moisture, and N availability) differentially affect components of TBCA (e.g. structural C pools, exudates/mycorrhizal associations, and respiration), or because separate genetic controls affect partitioning of components of below-ground C differently. These two explanations are clearly not mutually exclusive.

Overall, the results highlight four important concepts: (i) large differences can exist in C flux between apparently similar stands with different genetic representation; (ii) FRP in particular may be sensitive to the genetic structure of dominant trees; (iii) key environmental parameters such as average soil temperature, moisture, and soil N availability are not always the strongest predictors of soil C flux, and may be trumped by genetic factors; and (iv) even between similar stands, soil CO₂ efflux and FRP may be decoupled, and in fact FRP may change in an opposite direction compared with TBCA and

soil CO₂ efflux in response to environmental and genetic gradients. The very factors that may reduce FRP (e.g. high soil resource availability) could also increase proportional below-ground allocation to root maintenance respiration, mycorrhizas, and rhizodeposition. Both environmental and genetic controls may be involved in the decoupling of important components of C flux, and these should be investigated in future studies to elucidate the impact of genetic and global change on below-ground C pools and fluxes.

Acknowledgements

We would like to thank the Ogden Nature Center for the provision of facilities and the US National Science Foundation for financial support through grants DEB-0078280 and DEB-0425908. We would like specifically to thank Nathan Lojewski for extensive field work. We also thank Pam Cox, Julius Cantella, Bob Ivens, Piper Townsend, Greg Cox, Jen Schweitzer, Joe Bailey, Paul Selmants, Gina Wimp, Allen Haden, Dylan Weber, Axhel Muñoz, Amanda Thompson, Amala Posey, Dave Baumley and members of the Evergreen Field Ecology, Hart, Lindroth, and Whitham laboratories for field assistance and for providing comments on earlier versions of this paper. We would also like to thank Richard Norby and three anonymous reviewers for suggesting significant improvements to the original manuscript.

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