Plant responses to competition and soil origin across a prairie–forest boundary

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Summary

1 The distribution of different plant growth-forms may be caused by interactions among plants. Previous studies show that prairie and forest vegetation have different competitive effects and also influence both resource availability and soil community structure.

2 I used a field experiment to distinguish between short-term competitive effects and the long-term effects of vegetation on soils. Soil cores were reciprocally transplanted between prairie and forest sites. Seedlings of a grass (*Bouteloua gracilis*) and a shrub (*Elaeagnus commutata*) were planted into these cores and grown with or without neighbours.

3 Soil origin did not significantly alter the survival, growth or responses to competition of either transplant species. *Bouteloua* and *Elaeagnus* growth was suppressed by neighbours to about the same extent in prairie, but only *Bouteloua* growth was suppressed in forest, resulting in a significant interaction between environment and competition. All except one of the interactions involving soil origin were not significant, suggesting that plant-soil feedbacks did not modify the effects of competition or environment.

4 The results suggest that environment and competition have much larger influences on the performance of juvenile plants in the field than does soil origin. Further work is needed to determine the relative importance of resource competition and soil community effects on plant performance among species and study systems.

Key-words: *Bouteloua gracilis*, competition, *Elaeagnus commutata*, forest, grass, growth, indirect effects, plant-soil feedback, prairie, reciprocal transplant experiment, shrub

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Introduction

Variation in competitive ability may determine the distribution and abundance of species along environmental gradients (Walter 1985; Tilman 1988; Keddy 1990; Barton 1993), but the extent to which such variation determines the location and persistence of boundaries between different vegetation types is poorly understood (Walter 1985; Keddy 1989). For example, competitive response ability (*sensu* Goldberg 1990) often varies with successional stage or along environmental gradients, but not in a predictable way (Silvertown & Dale 1991; Goldberg 1996; Wilson 1999; D. A. Peltzer & S. D. Wilson, unpublished data). Species distribution may be less influenced by the effects of competition between species than by other, indirect interactions (e.g. Holt 1984; Miller 1994; Wootton 1994; Strong 1997) or, alternatively, competitive responses may be affected by factors such as soil-type.

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Plants affect both soil resources and soil communities, and plant-induced changes in soils may affect plant performance. There are abundant data on the effects of both plants on soil and soil on plants in terrestrial vegetation (e.g. Shipton 1977; Wedin & Tilman 1990; van der Putten *et al.* 1993; Binkley 1995; Wardle *et al.* 1999), but relatively few studies have considered these interactions as feedbacks (but see Bever *et al.* 1997; Aerts 1999). Negative feedbacks are important because they may allow for species coexistence and community stability (Levins 1974; DeAngelis *et al.* 1986; Mills & Bever 1998). For example, the mechanism of negative feedback causing the maintenance of species diversity and ecosystem stability is thought to be resource competition (Grace & Tilman 1990; Tilman & Pacala 1993; Chapin *et al.* 1996).

Plant-soil feedbacks in natural vegetation include those mediated by the effects of root-feeding nematodes in Dutch dune slacks (van der Putten *et al.* 1993; van der Putten & Peters 1997), and by fungal pathogens in north-eastern US old fields (Bever 1994; Mills & Bever 1998). Empirical evidence and models show that both positive and negative plant-soil feedbacks can drive

species-level replacements (Bever *et al.* 1997), supporting the idea that this may drive succession and promote species coexistence in natural vegetation (Kaye & Hart 1997; Watkinson 1998). However, few studies have determined whether plant-soil feedbacks occur at the level of plant growth-forms or vegetation types (but see Pastor *et al.* 1984).

Aspen parkland, which includes patches of both forest and prairie vegetation, is an excellent system to examine interactions between plants and soils. The soil microbial community is dominated by fungi in forest but by bacteria in prairie (Ingham *et al.* 1985; McGonigle 1995). Furthermore, woody species in temperate zones are typically ectomycorrhizal whereas grasses are usually endomycorrhizal (Harley & Smith 1983; Allen 1991; Brundrett 1991). Forest vegetation increases the abundance and patchiness of soil moisture and available nitrogen within 4 months (Wilson & Kleb 1996; Kleb & Wilson 1997). Thus, in order for prairie to invade forest, or for forest to invade prairie, juvenile plants must not only compete for resources with the resident vegetation, but must also establish in soil communities that may not contain appropriate mutualists. I determined whether soils under prairie and forest vegetation modify interactions among plants using factorial combinations of reciprocal soil transplants and vegetation removals to separate the effects of competition from soil origin. I asked whether: (i) grasses and woody plants respond differently to competition in prairie and forest, (ii) the outcome of competition depends on soil origin, and (iii) plant-soil feedbacks occur between prairie and forest.

Variation in plant-soil feedbacks was examined by measuring the performance of transplants in 'home vs. away' (*sensu* Bever 1994) soil origins. If there is no net plant-soil feedback, soil origin will not affect transplant performance whereas positive feedback will be indicated if species perform best in 'home' soils (i.e. woody plants in forest soil and grasses in prairie soil) and negative feedback if they perform best in 'away' soils.

Materials and methods

STUDY SITE

I worked at White Butte Recreation Area (50–28′ N, 104–22′ W), 18 km east of Regina (Sask., Canada) where the vegetation consists of discrete patches of aspen forest and mixed-grass prairie. The forest canopy is formed by *Populus tremuloides* Michx. with an understorey of snowberry (*Symphoricarpos occidentalis* Hook.), raspberry (*Rubus idaeus* L. var. *aculeatissimus* Regel & Tiling) or meadowsweet (*Spirea alba* Du Roi) and individuals of the shrub wolfwillow (*Elaeagnus commutata* Bernh. *ex* Rybd.) are scattered among the ground layer of the grasses *Poa* spp. and *Agropyron* spp. Prairie is dominated by *Agropyron* spp., *Bouteloua gracilis* (HBK) Lag., *Carex* spp., *Koelaria macrantha* (Ledeb.) J. A. Schultes f., *Poa* spp., *Stipa comata* Trin. & Rupr. and

Selaginella densa Rydb, but also contains small patches of the shrubs *Rosa acicularis* Lindl., *Symphoricarpos* and *Elaeagnus* (nomenclature follows Looman & Best 1987). The climate is continental with mean daily temperatures of –17 °C in January and 19 °C in July (Environment Canada 1993). The mean annual precipitation is 384 mm, mainly falling from May to September. Parent soils for both forest and prairie vegetation at White Butte are regosols on silty sand (Agriculture Canada 1992). Soils under forest have more available N and moisture than soils under prairie during the growing season (see Table 1 in Li & Wilson 1998). There are no differences in topography or soil texture between forest and prairie (D. Peltzer, unpublished data).

EXPERIMENTAL TREATMENTS

Treatments were applied to two 20 m × 20 m plots located at each of three sites separated by at least 500 m in each vegetation type. Soil and target plants were manipulated on a 8 × 8 sampling grid (64 subplots on a 1 m grid). Forest and prairie soils were collected in early May 1997 and 1998 using plastic tubes (10 cm diameter, 15 cm deep). Although these tubes are relatively small, they contain an appropriate volume of soil (*c*. 1.2 L) for measuring plant seedling responses over a growing season; the use of larger tubes is not logistically feasible. After collection, all plants in the tubes were sprayed with a systemic herbicide (3% glyphosate solution, trade name 'RoundUp') to ensure that the soil moved between environments did not contain any non-target plants. Tubes from each soil origin (prairie or forest) were placed randomly into experimental plots located in adjacent forest and prairie sites (soil destination). To increase the generality of the results, reciprocal soil transplants were carried out at three sites, each separated by *c*. 500 m.

I applied a 'no neighbours' (NN) competition treatment to one plot at each site and 'all neighbours' (AN) the other. For the NN treatment in forest, all aspen stems rooted with 5 m from the plots were cut and understorey grasses and shrubs were clipped at the soil surface. In prairie, neighbours were removed by applying a 3% glyphosate solution within a 20 cm radius of each tube. Tubes were left in the ground to eliminate root competition from neighbours as well as any effects they may have on soil resource levels and patchiness over a growing season (Kleb & Wilson 1997). Although tubes were open at the bottom, roots of transplanted seedlings did not grow into the surrounding soils within one growing season. Shading was eliminated by clipping resprouting neighbour shoots within a 30 cm radius twice monthly during the growing season.

For the AN treatment, tubes were removed immediately after transplanting, leaving the soil core flush with the soil surface; this controlled for the effects of disturbance. Neighbouring vegetation was left intact.

Decaying neighbour roots left inside the tubes are a source of carbon that may alter N availability to transplants. However, work by McLellan *et al.* (1995) suggests

that leaving decaying roots in place is unlikely to alter the growth of transplant species significantly. For example, nutrient mineralization from the dead roots of prairie grasses is small relative to immobilization: Seastedt (1988) found that 86–94% of N remained in grass roots after 1 year of decomposition in the field. This suggests that any increase in transplant growth in neighbour removal treatments is most likely caused by the removal of N uptake by neighbours (see discussion in Wilson & Tilman 1995), particularly since similar effects of root decay are expected in both NN and AN treatments.

Roots would be severed around transplanted seedlings in the AN competition treatment, possibly giving target plants an advantage compared with naturally establishing seedlings in intact vegetation. This is not a problem for comparing AN effects among sites and other experimental treatments, but it may underestimate the total effects of competition in the field. One way to reduce this effect is to plant seedlings several weeks after the competition treatments are applied, as was done in this study.

TARGET PLANTS

Seedlings of *Bouteloua gracilis*, a common C_4 perennial tussock grass, were grown from commercial seed sown in plastic pots (2.5 cm diameter, 12 cm deep) containing a 1 : 6 mixture of sterilized local soil (mix of forest and prairie soils) : peat moss. Seedlings were thinned to one plant per pot at germination and grown in a glasshouse under natural light and without fertiliser. Plants were watered daily to field capacity. A common native shrub (*Symphoricarpos occidentalis* Hook.), found in both forest and prairie, was initially selected for study and grown from root cuttings in 1997, but these cuttings did not survive in the field. For the 1998 experiment, another common native shrub, *Elaeagnus commutata* Bernh. *ex* Rybd., was grown from seed as for *Bouteloua*. *Bouteloua* was chosen as a representative grass species because of its widespread distribution in mixed grass prairie and *Elaeagnus* as the woody species because it is found scattered throughout prairie and forest edges in the region. Seedlings for both species can be grown relatively easily from local seed, and although neither species is obligately mycorrhizal, mycorrhizae are known to increase drought tolerance and P uptake in *Bouteloua* (Allen *et al*. 1981) and *Frankia* causes N fixation in *Elaeagnus* (Paschke 1997).

Seedling shoot mass (g) was estimated using regression equations. *Bouteloua*: shoot mass in grams = $(0.000577 \times TTL + 0.02682015)^2$, $R^2 = 0.98$, $P < 0.001$, $n = 30$, where TTL = total tiller length in mm; *Elaeagnus*: shoot mass in grams = $(0.00331 \times ht + 0.062167)^2$, $R^2 = 0.93$, $P < 0.001$, $n = 30$, where ht = seedling height in millimetres. The sizes of all seedlings were measured before they were transplanted in late May in each year. All seedlings were treated twice with the fungicide Benomyl in early May prior to planting to eliminate soil fungi (both pathogenic and symbiotic).

Seedlings were acclimated outside for 1 week prior to planting, during which time they were watered daily. One seedling was planted in the centre of each transplanted soil core during late May. Seedlings were immediately given 250 mL of water and shaded for 10 days using opaque plastic (30 cm × 40 cm). Seedlings that died within 3 weeks of planting were replaced. Shoots of all living seedlings were harvested, dried (70 °C, 2 days) and weighed in mid-September.

Ten replicate tubes were established for each of the 16 possible combinations of environment (forest or prairie), soil origin (forest or prairie), competition (NN or AN) and species (*Bouteloua* or *Elaeagnus*) at each of three sites (total of 480 tubes). Competition treatments were blocked within each site × environment combination to give a replicated split-plot design with environment × competition combinations forming the main plot factor and species and soil origin as split-plot factors. In 1997, only results for *Bouteloua* were used ($n = 240$) because of complete shrub mortality.

The relative growth rate (RGR) of each transplant was calculated as: RGR = $(\ln M_f - \ln M_i)/d$, where M_f is the final shoot mass, M_i is the initial shoot mass, and d is the number of days between biomass measurements. Competition intensity (CI), the proportional reduction in transplant growth caused by neighbours, was calculated as: CI = $(RGR_{NN} - RGR_{AN})/RGR_{NN}$, where RGR_{NN} and RGR_{AN} are the growth rates for transplants in NN and AN competition treatments, respectively (Wilson & Keddy 1986; Peltzer 1999). Prior to calculation of CI, a constant value was added to growth rates to eliminate negative values of RGR (i.e. the lowest seedling performance was set to 0). This technique avoided spurious large positive values of CI caused by negative growth rates in some AN competition treatments, i.e. an artefact of subtracting a negative number in the numerator of the equation. Positive values of CI are then evidence for competition whereas negative values of CI indicate facilitation.

Such single-season removal experiments are appropriate for determining variation in competitive response abilities (*sensu* Goldberg 1990) for at least two reasons. First, over longer periods (> 1 years), species may reach the carrying capacity of the experimental unit and this may occur sooner for fast-growing species than for slow. They may then appear to be less influenced by competition, complicating comparisons among species with respect to competitive response ability. Second, competitive responses appear to be consistent among years. Single-season experiments repeated among years found no significant variation in competitive responses among years (e.g. Wilson & Tilman 1993, 1995; Peltzer *et al*. 1998).

RESOURCE AVAILABILITY

The short-term effects of vegetation on resource levels were measured over each growing season. Nitrogen availability was measured using nylon resin bags (3 cm × 3 cm) containing 2 g of wet mixed-bed ion exchange resin

(AG 501-X8, Bio-Rad, Hercules, CA, USA) having 1.0 mmol g^{-1} of both anion and cation exchange capacity. This represents a sevenfold excess over ion equivalents in soil mass flow, litter leachate and precipitation, ensuring that the resin did not become saturated over the course of the experiment and all ions would therefore be retained (Köchy & Wilson 1997). Resin bags were washed in 2 M NaCl and rinsed with double-distilled water to wash out N accumulated during fabrication and processing.

One resin bag was buried 5 cm deep in each transplanted soil core and at N five randomly located locations within each experimental plot at the time of seedling transfer (late May), and removed during harvest (mid September). After air drying, bags were extracted in 30 mL of 2 M NaCl solution. Available nitrogen was determined after converting ammonium and nitrate fractions to ammonia, with an ion selective electrode (Orion model 95–12, Boston, MA) and corrected for values obtained for 10 unused bags. Extraction of bags loaded with known concentrations of NH$_4$Cl and KNO$_3$ recovered *c.* 92.3% of loaded N. N availability (expressed as total N flux (sum of nitrate and ammonium) in µg N resin bag^{-1} day^{-1}) was corrected for this recovery rate (i.e. dividing N content by 92.3%).

Soil moisture was measured twice monthly using lysimeters randomly located in each plot ($n = 5$ per plot). Lysimeters were identical to transplant tubes except that the bottom was covered by polyethylene mesh (1 mm) to allow for water throughflow while retaining soil, and contained only soil from prairie. It was assumed that seasonal differences in lysimeter mass (sum of tube + soil + water masses) were caused by fluctuations in soil moisture. Water content was calculated by subtracting dry weight (determined by drying at 80 °C for 3 days at end of experiment).

Light penetration was measured in June and August in 1997 and monthly in 1998 in the same locations as lysimeters ($n = 5$ per plot) using a 1×40 cm long integrating light probe (Sunfleck ceptometer, Decagon, Pullman, WA, USA). One measurement was made 10 cm above the vegetation and a second at the soil surface. Because light could not be measured above the vegetation in forest AN plots, measurements of incident light were taken at least 20 m outside the forest canopy. Light penetration to the soil surface was calculated as the proportion of light above the vegetation.

DATA ANALYSIS

Transplant survivorship at the end of the growing season was tested among treatments and their interactions with likelihood ratio chi-square tests using logistic regression (JMP version 3.2, SAS Institute 1997). Unless otherwise stated, all analyses reported are for the larger 1998 data set.

Differences in growth among environments, competition treatments, soil origins and species were examined using split-plot ANOVA. Environment, competition, soil origin and species were treated as fixed effects and site

was treated as a random factor. Log transformations prior to data analysis improved the normality and homoscedasticity of the data (Zar 1984).

Two interactions are of particular interest in this analysis. First, a significant interaction among the factors soil origin, competition and species would suggest that forest and prairie soils modify the effects of competition on growth differently between species. Second, a significant interaction among the factors soil origin, environment and species would suggest that forest and prairie soils alter the effect of environment on growth differently between transplant species.

The influence of environment and soil origin on species competitive responses (measured as competition intensity, CI) and of N availability was examined using split-plot ANOVA. A significant interaction between soil origin and species would suggest that plant-soil feedbacks modify competitive responses differently between species. Differences in light penetration and soil moisture among environments and competition treatments were compared using repeated-measures ANOVA (Stevens 1992; von Ende 1993). Because there were no differences between results from univariate repeated-measures ANOVA and MANOVA, only results from ANOVA are presented.

Results

SURVIVORSHIP

Survivorship of both species was similar in forest and prairie environments (Fig. 1, Table 1, no significant main effect of environment). Competition significantly decreased survivorship (Table 1, overall mean (± SE) was: 83.5 ± 3.4% in AN vs. 95.0 ± 2.0% in NN, $n = 120$). A significant interaction between competition and environment was caused by neighbours reducing survival more in prairie than in forest (Fig. 1). Neither soil nor any of its interactions were significant, suggesting that transplants survived equally well in soils from prairie or forest. *Elaeagnus* had lower survivorship in prairie than in forest, and both were lower than for *Bouteloua*, which had *c.* 90% survivorship in both environments (significant interaction between species and environment, Table 1).

Results in 1997 for *Bouteloua* differed in that they showed no effect of competition but did vary with soil origin (Fig. 1, logistic regression: competition effect: $\chi^2_{(1)} = 1.40$, $P = 0.237$, soil origin: $\chi^2_{(1)} = 5.80$, $P = 0.016$).

GROWTH

Growth, like survival, was similar between forest and prairie environments (Fig. 2, split-plot ANOVA: main effect of environment: $F_{1,2} = 3.38$, $P = 0.207$). Neighbours strongly suppressed growth, and to about the same extent in both environments (competition: $F_{1,2} = 177.49$, $P = 0.005$; environment–competition interaction: $F_{1,2} = 1.14$, $P = 0.397$).
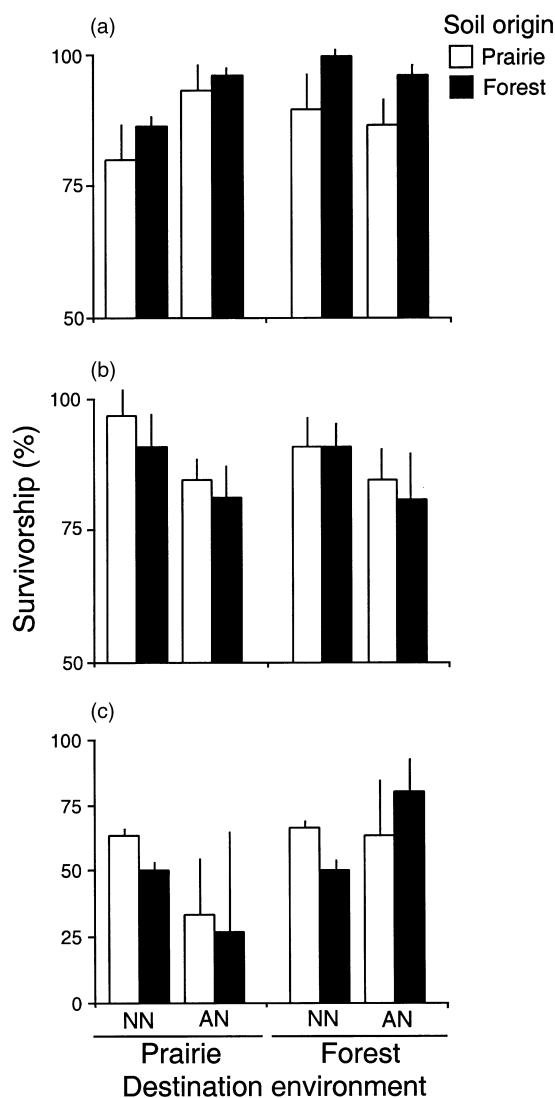
Fig. 1 Survivorship (mean + 1 SD) of a grass, *Bouteloua*, in 1997 (a) and 1998 (b), and a shrub, *Elaeagnus*, in 1998 (c), after one growing season. NN, neighbours removed; AN, neighbours intact. (See Table 1 for statistical results.)

Soil origin again had little effect although there was a significant interaction among soil origin, competition and species ($F_{1,290}$ = 5.65, P < 0.001). This interaction was caused by forest soils enhancing growth of *Bouteloua* in NN plots, but reducing it in AN plots whereas for *Elaeagnus* growth in AN plots was lower in prairie soils and similar in both soil types in NN plots (Fig. 2).

A significant three-way interaction among species, environment and competition ($F_{1,290}$ = 4.76, P = 0.029) was caused by the reduction due to neighbours being greater in prairie than in forest for *Elaeagnus* but not for *Bouteloua* (Fig. 2).

Large differences in growth among species may obscure the effects of environment and soil origin, and therefore I also conducted separate ANOVAs on each species. The only difference seen in the single-species ANOVA for *Bouteloua* was a significant interaction between soil origin and competition ($F_{1,205}$ = 4.64, P < 0.032)

Table 1 Likelihood ratios and $P > \chi^2$ for the influence of environment (E), competition (C), soil origin (O) and species (Sp) on transplant survival in 1998 (Fig. 1)

Source	d.f.	Likelihood ratio chi-square[a]	$P > \chi^2$
E	1	0.12	0.732
C	1	10.46	0.001
E × C	1	5.57	0.018
O	1	3.23	0.073
O × E	1	2.16	0.141
O × C	1	2.28	0.131
O × E × C	1	0.88	0.346
Sp	1	81.74	0.000
Sp × E	1	7.98	0.005
Sp × C	1	5.80	0.016
Sp × E × C	1	0.09	0.769
Sp × O	1	1.70	0.192
Sp × E × O	1	0.61	0.434
Sp × C × O	1	0.25	0.619
Sp × E × C × O	1	3.30	0.069
Full model negative log likelihood 221.25			

[a]Likelihood ratio tests are calculated as twice the difference of the log likelihoods between the full model and the model without the tested effect(s) present.

due to a greater effect of neighbours in soils from forest. When *Elaeagnus* alone was considered, growth was significantly lower in prairie than in forest ($F_{1,205}$ = 18.89, P < 0.048) and environment interacted with competition because neighbours reduced growth to a greater extent in prairie than in forest ($F_{1,2}$ = 27.65, P < 0.034).

Overall, growth is most strongly affected by competition and to a lesser extent environment, but soil origin has little impact on growth.

COMPETITION INTENSITY

Competition intensity was similarly positive in both environments and in soil from both origins (Fig. 3, neither effect nor their interaction significant). There was a significant species effect ($F_{1,119}$ = 10.54, P = 0.002) and species–environment interaction ($F_{1,119}$ = 4.11, P = 0.045) because *Elaeagnus* was less affected by neighbours in forest. No other interactions were significant.

RESOURCE AVAILABILITY

Soil N availability was significantly higher in NN plots than in AN plots and in soil from prairie than in soil from forest, but environment had no effect. Neighbours reduced N to a greater extent in forest than in prairie (environment × competition: $F_{1,2}$ = 5.07, P = 0.025). Higher N fluxes were observed in soils from forest when soil was moved to prairie than when soil was moved to other sites in forest, resulting in a significant interaction between soil origin and environment (Fig. 4, $F_{1,360}$ = 37.61, P < 0.001). Soil origin did not alter the effects of neighbours on N availability (soil origin × competition and soil origin × competition × species not significant).
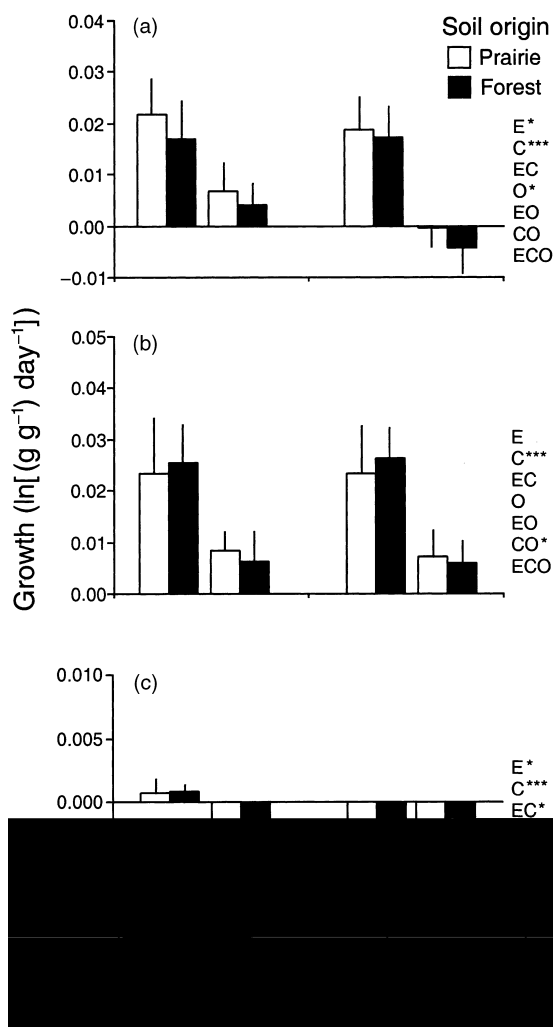
Fig. 2 Growth rates (mean + 1 SD) of *Bouteloua* in 1997 (a) and 1998 (b), and *Elaeagnus* in 1998 (c) during one growing season. Treatments as in Fig. 1. Significance of ANOVA for effects of E, environment; C, competition; O, soil origin; and their interactions: *$P < 0.05$; ***$P < 0.001$.
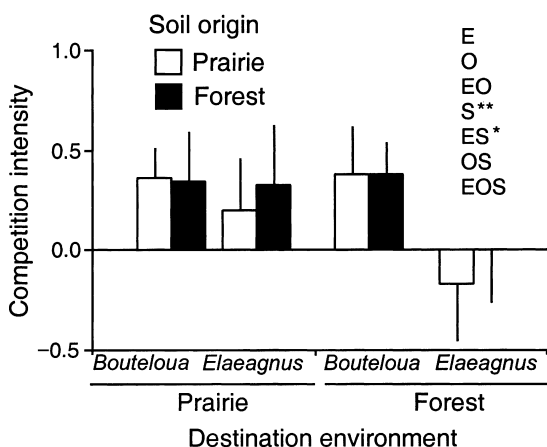

Fig. 3 Competition intensity (mean + 1 SD) for two species during 1998. Treatments as in Figs 1 and 2, ANOVA: †$P < 0.10$; **$P < 0.01$.
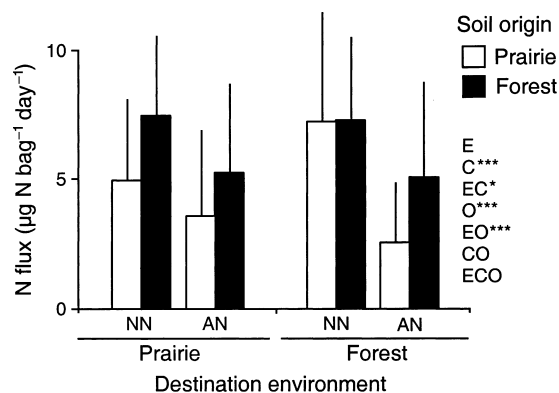

Fig. 4 Soil N flux (mean + 1 SD) in 1998 measured using ion-exchange resin bags. Treatments as in Figs 1 and 2, ANOVA: *$P < 0.05$; ***$P < 0.001$.
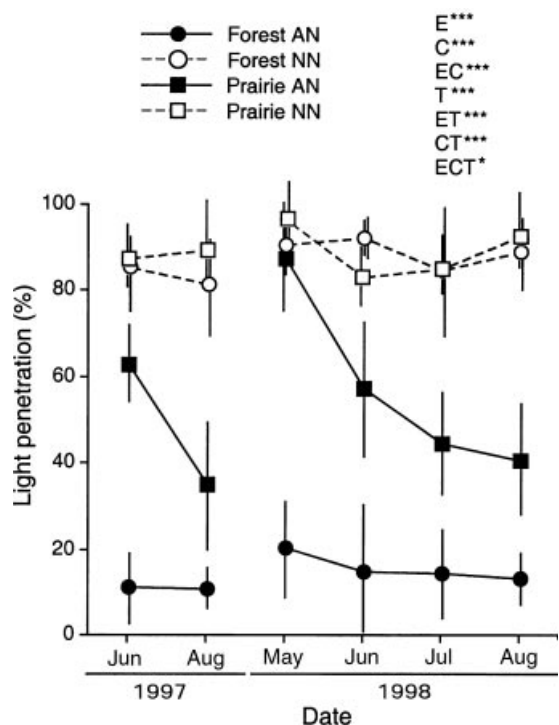

Fig. 5 Seasonal light penetration (mean percentage of incident light). Vertical lines represent ± 1 SD of the mean. Treatments as in Figs 1 and 2, repeated-measures ANOVA includes the effects of T, time: *$P < 0.05$; ***$P < 0.001$.

Light penetration was reduced in forest and by competition (Fig. 5). Neighbour removals increased light penetration to a greater extent in forest (Fig. 5). Light penetration decreased throughout the growing season in AN plots, particularly in prairie.

Overall, soil moisture was nearly twice as high in forest as in prairie, but was not altered by competition suggesting that neighbours did not significantly alter water availability (Fig. 6). However, neighbours significantly reduced soil moisture, particularly during mid-summer (July and August) (time × competition: $F_{12,41} = 3.99$, $P < 0.001$). This seasonal effect of neighbours on soil
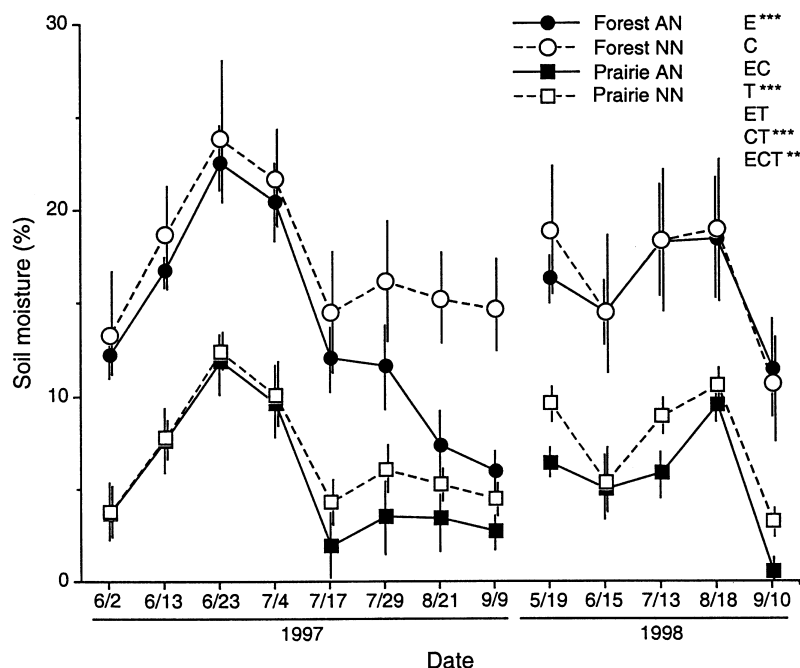
Fig. 6 Soil moisture (mean percentage) measured in weighing lysimeters ($n = 5$ replicates per plot). Vertical lines represent ± 1 SD of the mean. Treatments as in Figs 1 and 2, repeated-measures ANOVA includes the effects of T, time: **$P < 0.01$; ***$P < 0.001$.

moisture was stronger in forest than in prairie (time $\times$ environment $\times$ competition: $F_{12,41} = 4.33$, $P < 0.001$).

Discussion

The results suggest that competition between grasses and trees is more important than plant-soil feedbacks in determining the performance of plants. Although *Bouteloua* grew significantly faster in soils from prairie than from forest in the first year of the study (Fig. 2, 1997 growth), soil origin did not alter survivorship (Fig. 1, Table 1), the effects of neighbours on growth (Fig. 2), or the intensity of competition experienced by either *Bouteloua* or *Elaeagnus* (Fig. 3). On the other hand, competition significantly reduced the growth of both species in prairie and forest environments (Fig. 2, NN vs. AN).

These results contrast with previous studies that have observed negative plant-soil feedbacks, for example, for survival of a composite forb and the growth of three grasses (Bever 1994). However, for two of the grasses, *Panicum sphaerocarpon* was a stronger competitor than *Danthonia spicata* across all soil communities (Bever 1994) suggesting that the lack of soil effects on competitive ability (Fig. 3) may be more general.

Transplant performance was assessed in soil originating (or 'cultured') under forest or prairie vegetation. Any feedbacks observed could be caused by several agents, including resources, mutualists or pathogens. The soil microbial community was not examined here because the aim was to separate the effects of vegetation on resources from persistent differences in soils between forest and prairie. More detailed knowledge of the soil

microbial community and fauna would, however, enrich our understanding of the mechanisms underlying plant-soil feedbacks. Soil mutualists and pathogens may operate simultaneously, and this may result in no net feedback being observed, as seen for the growth of a native prairie grass (*Andropogon gerardii*) (Hetrick & Wilson 1989). Soil pathogens and mutualists may also accumulate through time, as occurs in many agricultural systems (Shipton 1977), dune slacks (van der Putten *et al*. 1993, 1997) and old fields (Bever 1994; Mills & Bever 1998), or may alter the germination, growth and recruitment of juvenile plants via responses to fungal mutualists (Eissenstat & Newman 1990; Allen 1991; Smith *et al*. 1998) or pathogens (Harman 1983; Burdon 1987). The role of soil communities in the recruitment of juvenile plants in natural vegetation is largely un-explored, but may have important consequences for restoration efforts, the maintenance of species richness in communities and the occurrence of discrete boundaries between vegetation types by altering the regeneration niche of species (*sensu* Grubb 1977).

There are many unresolved questions about the role of plant-soil feedbacks and their importance in natural vegetation. For example, how do plants vary in their effects on and responses to changes in soil community composition? Are plant-soil feedbacks less important in more productive systems where soil mutualists or pathogens may contribute less to variation in species performance than in relatively unproductive systems (Burdon 1987; Grime 1993)? Several recent reviews and studies have shown that below-ground interactions in the soil community can strongly influence above-ground processes (Bever *et al*. 1997; Laakso & Setälä 1999; Wardle

1999; Wardle *et al.* 1999). Clearly, there is a need to examine plant-soil feedbacks among systems to understand their general importance in plant communities.

COMPETITION

Competition greatly reduced the performance of transplants in both prairie and forest (Figs 2 & 3). For *Bouteloua*, growth and competition intensity were similar in prairie and forest whereas for *Elaeagnus*, growth was lower and competition intensity was higher in prairie. Competition was less intense between woody plants than it was either between herbaceous species, or between herbaceous and woody plants. This result is consistent with previous studies of tree–grass competition at large spatial scales (Peltzer & Wilson, in press), and in a common garden experiment (Li & Wilson 1998). These studies support the hypothesis that woody plants suppress herbaceous species more than other woody species, resulting in the formation of woody plant clusters through facilitation (Yarranton & Morrison 1974; see discussions by Archer *et al.* 1988; Archer 1990; Belsky 1994).

Including soil communities explicitly into field competition experiments is a largely unexplored avenue of research (Watkinson 1998). Results from several competition experiments in pots or microcosms suggest that soil microbes can alter plant competitive ability. For example, in a competition experiment between two grasses, *Lolium perenne* and *Holcus lanatus*, either root competition or mycorrhizae alone gave an advantage to *H. lanatus*. However, the effects were synergistic, with the combination conferring a much greater advantage of *H. Lanatus* over *L. perenne* (Fitter 1977). Reducing the abundance of mycorrhizae using fungicide strongly decreased the competitive ability of one prairie grass, *Andropogon gerardii*, but not of a second grass, *Elymus canadensis* (Hartnett *et al.* 1993). Many native rangeland species are mycorrhizal obligates, but invasive plants in these systems are not; invasive species may therefore alter the soil community by decreasing the abundance of the mycorrhizae on which native plants depend (Goodwin 1992; Marler *et al.* 1999). Although there is strong evidence that soil communities can alter plant competitive ability, at least in highly controlled pot experiments, the performance of juvenile plants in this field experiment was affected much more by competition than by soil origin.

Acknowledgements

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