

# Competitive relationships of *Andropogon gerardii* (Big Bluestem) from remnant and restored native populations and select cultivated varieties

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## Summary

1. Although genetic differentiation among plant populations is well known, its relevance for preserving the integrity of native ecosystems has received little attention. In a series of competition experiments with *Andropogon gerardii* Vitman, a dominant species of the North American Tallgrass Prairie, plant performance was related to seed provenance and restoration activities.

2. Glasshouse experiments showed plant performance to be a function of seed source. Differential target plant performance relative to competitor identity was observed when plant performance was assessed across a range of competitor densities. Local and non-local plants were larger when competing against non-local plants relative to the local and cultivar plants, while cultivar plants were consistently larger than local and non-local plants regardless of competitor identity or density. The consistency of cultivar performance could reflect directional selection during cultivar development for consistently high fecundity, vigorous vegetative growth and resistance to pathogens.

3. In a field experiment, non-local plants were half the size of local and cultivar plants, supporting recognition of seed provenances of *A. gerardii* based on differences in plant performance among source populations observed in the glasshouse study, and previous genetic analyses of the same populations.

4. This study establishes that seed provenance and restoration activities influence the competitive ability of a dominant species which, in turn, may affect plant community structure and potential ecosystem function.

*Key-words:* ecological genetics, grass competition, glasshouse and field experiments, tallgrass prairie

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## Introduction

Ecosystem properties are strongly influenced by the characteristics of the dominant species (Gibson *et al.* 1999b; Grime 1999). If competition is an important determinant of plant community structure (Tilman 1988), then the competitive ability of the dominant species will affect the entire community. Previous grassland studies have investigated competitive interactions in relation to disturbance (Knapp *et al.* 1999); fungal associations (Hartnett *et al.* 1993; Anderson, Hetrick & Wilson 1994; van der Heijden *et al.* 1998); nutrient heterogeneity (Casper & Jackson 1997; Farley & Fitter 1999; Casper, Cahill & Jackson 2000); and productivity gradients (Foster 1999; Suding & Goldberg 1999; Tilman

1993; Rajaniemi, Allison & Goldberg 2003). The few studies that have included genetic components have focused on competitive interactions among genotypes within a population, or genotypes from populations of different successional stages (Aarssen 1988; Taylor & Aarssen 1990; Cheplick & Salvadori 1991; Sugiyama & Nakashima 1991; Turkington 1994; Cheplick 1997). However, few studies have considered both competitive abilities and genetic relationships as they relate to seed provenance (Gustafson, Gibson & Nickrent 2002).

Differences in intraspecific competitiveness among seed provenances or cultivated varieties of the dominant species used to recreate/restored plant communities may affect community dynamics. Maladapted genotypes may reduce fecundity, germination rates and survivorship, thus negatively affecting population dynamics directly through reduced fitness and indirectly by crossing with native ecotypes (Newman & Pilon 1997; Etterson & Shaw 2001; Gustafson *et al.* 2002). Cultivated varieties of a dominant plant species, however, may

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pose a different threat to the entire ecosystem. Direct effects on ecosystem properties have been observed with higher photosynthetic rates of *Andropogon gerardii* Vitman cultivars relative to local plants (Skeel & Gibson 1996) and indirectly with reduced net nitrification rates under a cultivar of *Panicum virgatum* L. relative to local plants (Baer 2001). Traits selected during cultivar development could directly affect intra- and interspecific competitive dynamics within a community, as well as altering the genetic composition of the local genotype through introgression (Gustafson, Gibson & Nickrent 2001; Pywell *et al.* 2003).

In this study we used a matched series of glasshouse and field experiments to investigate plant performance of a dominant species (*A. gerardii*) from local remnant and restored tallgrass prairies, two cultivated varieties (cultivars), and a non-local seed provenance population. *Andropogon gerardii* is a dominant grass of the North American tallgrass prairie (Risser *et al.* 1981) that exhibits extensive phenotypic and genetic variability throughout its range (McMillan 1959; Gustafson, Gibson & Nickrent 1999). We expected competitive abilities to be different among seed sources because the maternal populations of *A. gerardii*, and their seed cohorts, used in our competition studies have been shown to be genetically different (Gustafson 2000; Gustafson, Gibson & Nickrent 2004). Competition among seedlings was investigated because several studies have indicated that the early establishment stage is when this species is most sensitive to competition (Foster 1999; Suding & Goldberg 1999), and restoring/recreating North American grasslands is typically accomplished by broadcasting seed. We used a combination of glasshouse and field experiments to address the following two questions regarding *A. gerardii* from local and non-local seed provenances and select cultivated varieties: (1) Are there differences in plant performance among the different seed provenances? and (2) Do these differences reflect local adaptation: (local > non-local); grassland conservation activities (restored > remnant); or directional selection during cultivar development (cultivar > non-cultivar seed provenances).

## Materials and methods

### PLANT MATERIAL

*Andropogon gerardii* (hereafter referred to by genus) seeds were collected from 100–300 randomly chosen individuals at each of the following Illinois grasslands: DeSoto Railroad Prairie (remnant: 37°51' N, 89°14' W); Wheelock Railroad Prairie (remnant: 41°40' N, 90°15' W); Mason County State Nursery (restored: 40°19' N, 89°54' W); and Fermi National Laboratory (restored: 41°50' N, 88°15' W). These sites are classified as tallgrass prairies and represent some of the largest grasslands in Illinois (Robertson 2001). We defined a remnant as a site that has not been ploughed; restored sites are characterized by a history of row-crop pro-

duction and subsequent replanting with seeds from local remnant grasslands. Seeds from a non-local remnant were obtained from the 3487 ha tallgrass prairie Konza Prairie Biological Station (39°05' N, 96°35' W), Kansas. Seeds of two cultivated varieties (cultivars), Roundtree (Jackson County, Iowa) and Pawnee (Pawnee County, Nebraska) were purchased from Sharp Brothers Seed Company (Clinton, MO, USA). Cultivars were included in this study because traits selected during development (e.g. quick establishment, vigorous vegetative growth, high seed production) may confer a competitive advantage over local genotypes, and because these cultivars have been used extensively in grassland restoration projects, roadside plantings, and as native forage in North America (USDA, NRCS 2002). Seeds were stored at 4 °C until needed. Seeds of each population were mixed, germinated and grown under glasshouse conditions for 3 weeks.

### GLASSHOUSE EXPERIMENTS

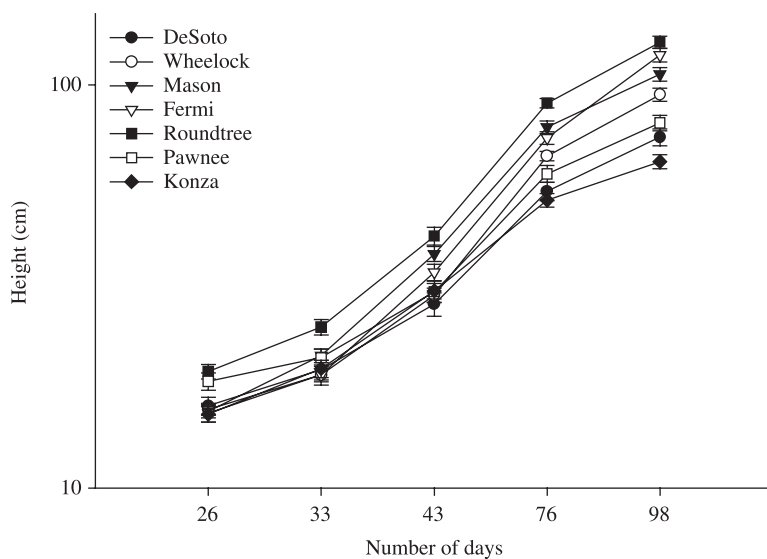
Two glasshouse experiments were conducted using two different experimental designs. First, a full factorial diallel design was used to test for differences in plant biomass among multiple local (Illinois) remnant, restored and cultivar populations. This experiment consisted of six replicates for all possible combinations of seven populations, two plants per pot, with one designated as the target and the other the associate (6 replicates × 7 target × 7 associate = 294 pots). This design provides a useful tool for screening the source population effect on the outcome of competition (Gibson *et al.* 1999a; Connolly, Wayne & Bazzaz 2001). Plants of approximately the same size were planted equidistant from each other and from the side of 16.5 cm diameter round pots containing a soil-less potting medium, and watered as needed for 98 days. The maximum height of each plant was recorded at roughly 1-week intervals. At the end of the experiment maximum height, number of tillers, number of flowering culms and number of leaves were recorded. Plants were harvested, separated into shoot and root systems and dried for 48 h at 80 °C. Measures of height, tillers, leaves and number of flowering culms were positively correlated with biomass. Therefore we used plant biomass to assess plant performance.

The second glasshouse experiment was a full factorial partial additive (target–neighbour) design that was used to assess the response of an individual (target) to an increasing number of associates (neighbours), using local (Wheelock Railroad Prairie, IL) and non-local (Konza Prairie, KS) seed provenances, and one cultivar (Roundtree). This design tests whether different densities alter the competitive hierarchy among the three seed sources and overcomes some of the limitations of the diallel experiment, but at the expense of investigating fewer populations (Gibson *et al.* 1999a). There were three replicates from all possible target–neighbour combinations with four neighbour densities

(3 replicates  $\times$  3 target  $\times$  3 neighbour  $\times$  4 densities = 108 pots). The target seedling and neighbour seedlings (0, 1, 2, 4) of approximately the same size were planted equidistant from one another and from the inside surface of the pots (potting medium and watering regime as in experiment 1). The maximum height of plants was measured at 50, 78, 87 and 101 days after starting the experiment. Plants were harvested after 101 days and processed as above.

#### FIELD EXPERIMENT

A vegetation-removal experiment was established (22 May 1998) in an old-field community in Jackson County, Illinois (37°37' N, 89°17' W), dominated by *Festuca arundinacea* Shreb., *Andropogon virginicus* L., *Dactylis glomerata* L. and *Poa pratensis* L. A randomized block design was used with six replicates of all combinations of vegetation removal ( $\pm$ ) and the same three source populations used in the target–neighbour experiment (6 replicates  $\times$  2 vegetation removal levels  $\times$  3 populations = 36 experimental units). The removal treatment was established by clipping at ground level and removing all living and dead plant material in a 0.5 m<sup>2</sup> circular plot, 7 days before establishing the experiment. The unmanipulated control plots were established at the same time. An *Andropogon* plant was transplanted into the centre of each plot and monitored for 100 days, with removal plots weeded. Maximum plant height and number of flowering culms were measured at 1-month intervals. The final dry shoot biomass was determined after 100 days, which corresponds to peak anthesis in late August.



**Fig. 1.** Maximum *Andropogon gerardii* height (log mean  $\pm$  1 SE) in the intraspecific diallel glasshouse experiment: circles, remnant (DeSoto, Wheelock); triangles, restored (Mason, Fermi); squares, cultivars (Roundtree, Pawnee); diamond, non-local remnant (Konza); x axis, number of days since establishing the experiment.

#### DATA ANALYSIS

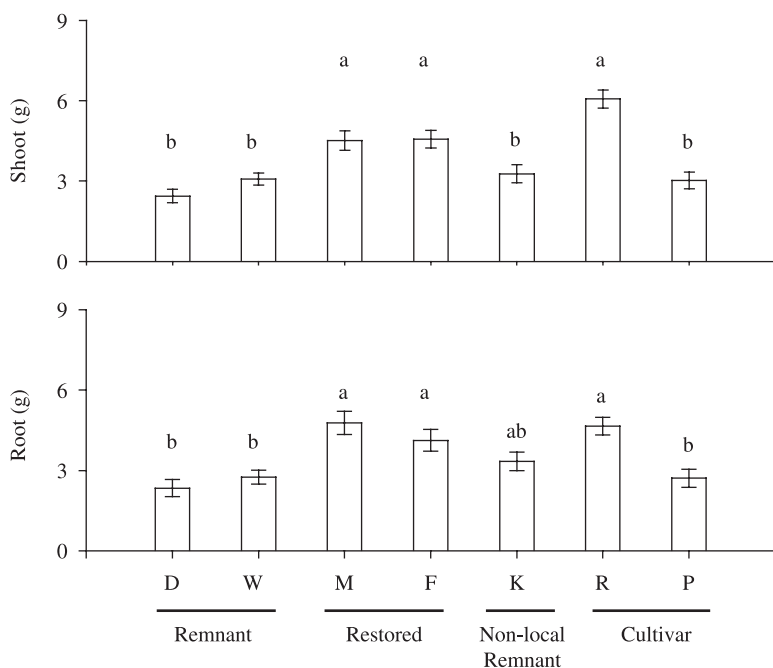
Populations used in these experiments were not randomly selected, hence target and associate treatments were considered fixed effects. The diallel glasshouse experiment was analysed using a two-way fixed-effects ANOVA to test for differences in plant biomass (total, shoot and root) among the seven populations. Total biomass responses were similar to shoot biomass, so here we present only shoot and root biomass. The target–neighbour glasshouse experiment was analysed using a two-way analysis of covariance (ANCOVA) with plant biomass as a function of target, associate and the interaction, with total neighbour biomass as the covariate (Goldberg & Scheiner 2001). The field experiment was analysed using a randomized-block two-way ANOVA with two treatments: source population (three levels) and removal (two levels). Because the blocks were defined arbitrarily with no visible difference in vegetation, slope and soil substrate, it is reasonable to assume no block  $\times$  treatment interaction. Therefore the null hypothesis would be: no effect of the treatment in any block, with the block main effect being tested with the  $MS_{residuals}$  (Newman, Bergelson & Grafen 1997). Repeated-measures ANOVA (RMANOVA) was conducted on the mean maximum height from the diallel (two-way), target–neighbour (three-way), and field experiments (two-way block design). All analyses were performed on log-transformed *Andropogon* biomass (+1) using a general linear model, REGWQ means separation procedure, and lsmean procedures in SAS (SAS Institute Inc., Cary, NC, USA). The number of flowering culms were correlated with diallel ( $r = 0.69$ ,  $P < 0.0001$ ), target–neighbour ( $r = 0.73$ ,  $P < 0.0001$ ), and field experiment ( $r = 0.85$ ,  $P < 0.0001$ ), and gave the same response pattern as biomass measures, hence we present biomass results.

#### Results

##### GLASSHOUSE EXPERIMENTS

In the diallel experiment, RMANOVA of the maximum height of *Andropogon* showed a significant time  $\times$  target effect ( $F_{24,880} = 34.9$ ,  $P < 0.01$ ). Rank order among populations was fairly well established by 76 days with Roundtree plants as the tallest, and the non-local remnant (Konza) plants as the shortest (Fig. 1). The only exception to this established ranking was the two restored populations (Mason and Fermi) which switched rank after  $\approx 80$  days.

There were significant target population effects on shoot ( $F_{6,219} = 10.4$ ,  $P < 0.01$ ) and root ( $F_{6,219} = 7.6$ ,  $P < 0.01$ ) biomass, but no effect of associate plant identity or target  $\times$  associate interaction ( $P < 0.05$ ). Regardless of the seed provenance of their association, target plants from the two restored populations (Mason and Fermi) and the Roundtree cultivar were larger than those from the two local remnant populations



**Fig. 2.** *Andropogon gerardii* target plant performance from local (DeSoto, D; Wheelock, W; Mason, M; Fermi, F) and non-local remnant (Konza, K) grasslands, and two cultivated varieties (Roundtree, R; Pawnee, P). Values represent mean  $\pm$  1 SE; different letters denote significant differences ( $P < 0.05$ ).

and the Pawnee cultivar (Fig. 2). *Andropogon* plants from Konza Prairie, the non-local remnant, produced less shoot biomass than Mason, Fermi and Roundtree plants, but root biomass was not different (Fig. 2).

RMANOVA of maximum height from the target-neighbour experiment revealed significant time  $\times$  target ( $F_{6,210} = 3.9$ ,  $P < 0.01$ ), time  $\times$  density ( $F_{9,210} = 3.3$ ,  $P < 0.01$ ), and time  $\times$  target  $\times$  density interactions ( $F_{18,210} = 1.9$ ,  $P < 0.05$ ). Roundtree and Wheelock plants were smaller when grown with any competing plants, but the size of Konza plants was reduced with the addition of two or four competing plants (Fig. 3). In addition to the observation of differential plant height as a function of competitor density, Roundtree plants were approximately twice as tall as Wheelock and Konza plants (Fig. 3).

Differential target biomass relative to neighbour identity was indicated by significant target  $\times$  neighbour interactions (Table 1). Wheelock and Konza target plants were larger when competing with Konza neigh-

**Table 1.** ANCOVA analysis of *Andropogon gerardii* performance as a function of seed source, with total biomass of neighbouring plant(s) as covariate

Source	Shoot	Root
Target	$F_{2,95} = 67.4^{***}$	$F_{2,95} = 40.1^{***}$
Neighbour	$F_{2,95} = 10.8^{***}$	$F_{2,95} = 5.3^{**}$
Target $\times$ neighbour	$F_{4,95} = 1.9$	$F_{4,95} = 2.8^*$
Covariate	$F_{1,95} = 30.3^{***}$	$F_{1,95} = 56.2^{***}$

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ .

hours than with the Wheelock and Roundtree neighbours (Fig. 4). Roundtree target plants, however, were typically larger when competing with Wheelock and Konza neighbours relative to the plant's performance against itself. Target plant biomass generally increased from Konza ( $0.59 \pm 0.33$  g) to Wheelock ( $0.71 \pm 0.32$  g) to Roundtree ( $1.07 \pm 0.32$  g), with differential biomass as a function of competing plant identity and density.

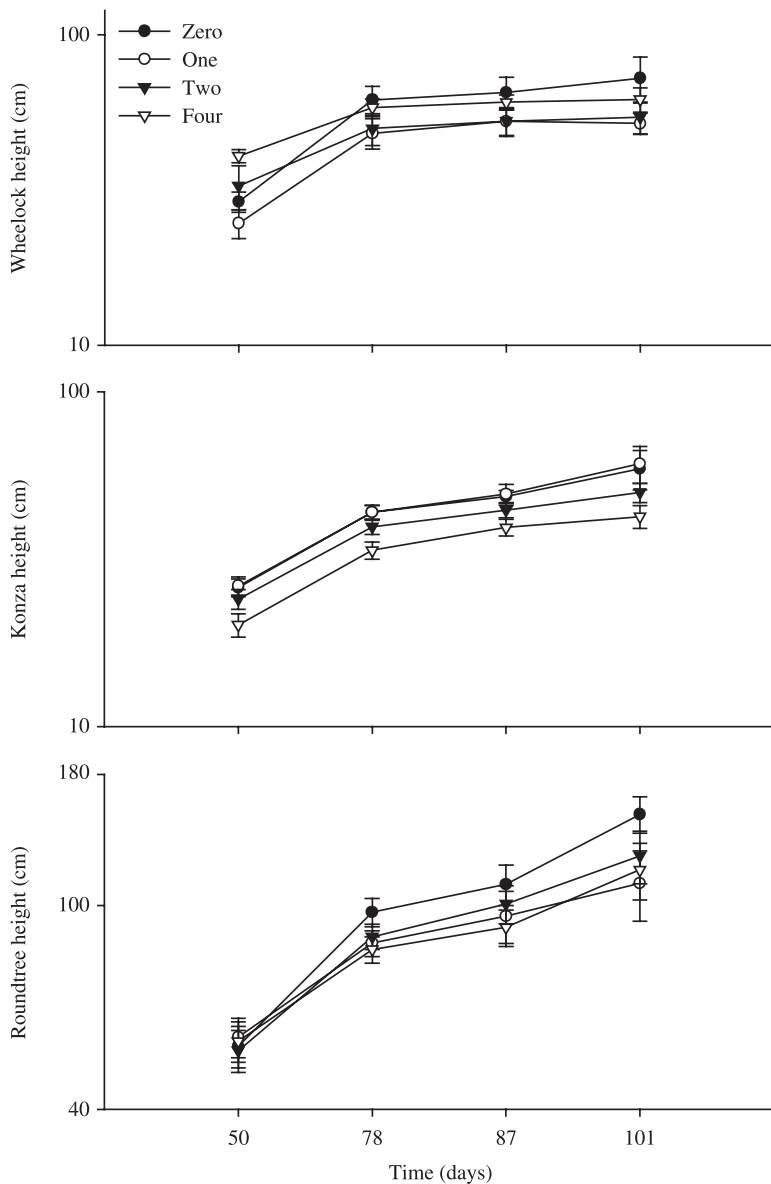
## FIELD EXPERIMENT

Maximum height RMANOVA showed significant target effects ( $F_{6,70} = 3.1$ ,  $P < 0.05$ ). Konza (non-local remnant) plants were significantly shorter ( $P < 0.05$ ) than Wheelock (local remnant) and Roundtree (cultivar) plants 22 days after establishment in the field, and these differences remained throughout the growing season (Fig. 5). *Andropogon* shoot biomass was significantly ( $F_{2,25} = 6.6$ ,  $P < 0.05$ ) reduced when competing with surrounding old-field vegetation (Fig. 6). While the Wheelock and Roundtree plants generally produced more shoot biomass than Konza plants, with or without the surrounding vegetation, there were no significant target or target  $\times$  removal treatment effects (Fig. 6).

## Discussion

Our results indicate differences in *Andropogon* performance and competitiveness related to seed provenance and restoration activities. Under glasshouse and field conditions *Andropogon* from non-local provenances were consistently smaller than the local provenance plants, which supports the long-held belief that plant populations are adapted to their local environmental conditions (Turesson 1922). These results are consistent with previous field research that found non-local *Andropogon* from its western range (Nebraska, USA) was consistently smaller than local Illinois plants when grown in a restored tallgrass prairie established in the early 1970s (Gustafson *et al.* 2001). The temporal consistency of these results during several experiments (from the first measurements made on seedlings through flowering) substantiates the inferences that we make (Gibson 2003).

Restored grassland communities contribute to the conservation of natural areas by countering urban expansion and habitat fragmentation, as well as by contributing to the ecological and genetic variation of individual plant species. *Andropogon* plants from the restored grasslands, which were established with seed from multiple local remnants, and the Roundtree cultivar were consistently larger than plants from local and non-local seed provenances. Two possible, but not exclusive, explanations of this enhanced plant performance are (1) heterosis resulting from crossing among divergent genotypes used to restore the plant community; or (2) introgression from the *Andropogon* cultivars that have been used for forage and erosion control throughout the North American Great Plains since the



**Fig. 3.** Mean maximum height of *Andropogon gerardii* from Wheelock, Konza and Roundtree populations as a function of number of competitors (0, 1, 2, 4 plants). Values represent log means ( $\pm 1$  SE).

1950s. Genetic analyses of these *Andropogon* populations indicated no difference in genetic diversity between remnant and restored populations, and the restored populations were more genetically similar to other restored populations than they were to local remnant populations or cultivars (Gustafson 2000; Gustafson *et al.* 2004). In the genetic analysis, restored *Andropogon* populations grouped according to the identity of the restoration practitioners rather than the location of nearby remnant populations (within  $\approx 100$ – $150$  km). The specific location of these seed donor populations was either not documented, as is common with community-based conservation activities, or unavailable. It was not possible to conduct genetic analyses of the populations used as seed sources for the restored populations, thus we could not test empirically heterosis or cultivar introgression, or identify a robust local genotype. It

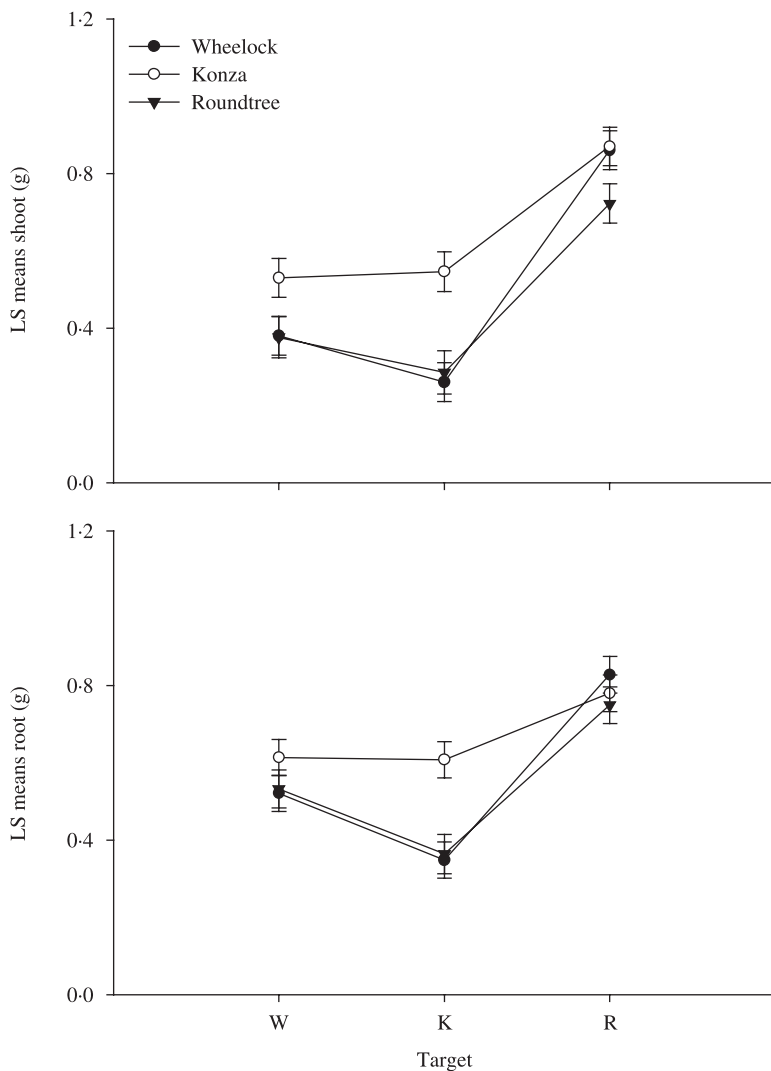
was clear, however, that restoration activities and practices do influence the genetic and ecological attributes of this dominant species and, potentially, the entire plant community.

Interspecific competition by the dominant species may affect floristic diversity, especially in restored plant communities. In a study comparing species composition of remnant and adjacent restored grasslands established with dominant species cultivars, Kindscher & Tieszen (1998) found that remnant sites contained more species than the restored sites, and species richness decreased with distance from remnant communities. They attributed this lack of species establishment to the inability of later successional species to disperse into the restored plant community. Factors other than propagule dispersal, however, are important in the development of plant communities (Eriksson & Jakobsson 1998; Jones & Hayes 1999; Rand 2000; Verheyen & Hermy 2001; Campbell, Rochefort & Lavoie 2003). The inability of the later successional species to become established in the restored grassland may relate to the absence of keystone herbivores that create open sites and disperse seeds (Knapp *et al.* 1999) and/or, as our results suggest, competitive factors associated with the use of grass cultivars.

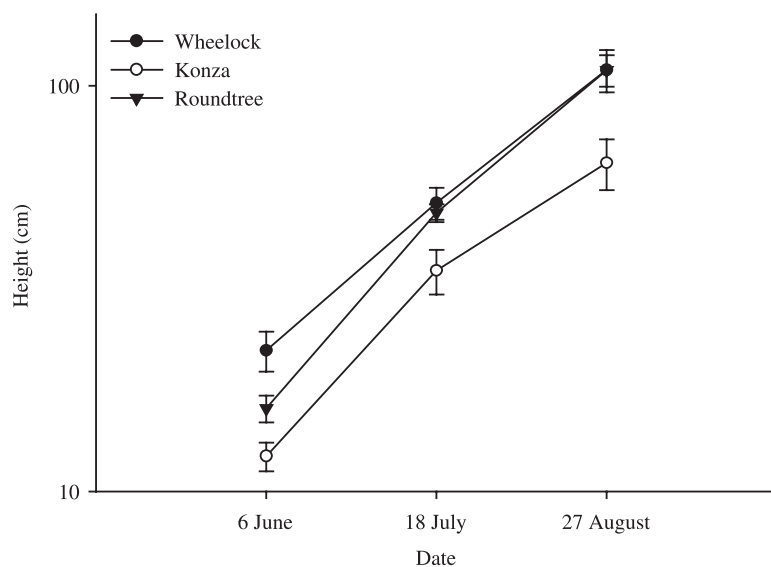
Genetic identity (seed source), rather than genetic diversity, is a better predictor of *Andropogon* performance under glasshouse and field conditions, which supports the notion that local adaptations can occur within widespread, genetically diverse, dominant species (Knapp & Rice 1996; Gustafson *et al.* 2002). This is one of the first reports that we are aware of to test directly competitive effects of different seed sources used in habitat restoration. Despite limitations (a single density for the diallel experiment; reduced number of populations for the target–neighbour experiment; field data from a single season), this study indicates that non-local seed sources may be unsuitable for use in local restoration/conservation projects. Unsuitable sources include non-local native donors (e.g. our Konza population) and cultivars. Any differences in competitive ability among populations of the dominant species, such as seed source (as shown here) or genetic diversity (Booth & Grime 2003), can affect population and community dynamics (Gibson *et al.* 1999a; Grime 1999; Schwartz *et al.* 2000). Therefore understanding the ecological and genetic dynamics of the dominant species may be the best approach to understanding plant community dynamics.

### Acknowledgements

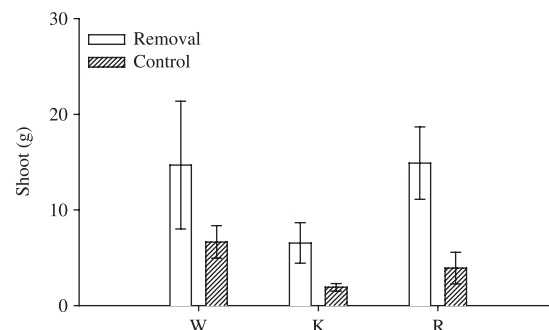
We thank the site managers for providing access and site information, Konza Prairie Biological Station and Joe Ely for collecting the Konza seed, and Dave Horvath for Mason County seed. We also thank Brenda Casper and two anonymous reviewers for comments on a previous version of the manuscript, and Jerry Van Sambeek and the US Forest Service for glasshouse



**Fig. 4.** *Andropogon gerardii* target plant biomass as a function of neighbour plant identity and total neighbour plant(s) biomass as covariate. Values are lsmeans ( $\pm 1$  SE) of log-transformed total biomass ( $x + 1$ ). Wheelock, W; Konza, K; Roundtree, R.



**Fig. 5.** Maximum *Andropogon gerardii* height from Wheelock (W), Konza (K) and Roundtree (R) populations grown in an old-field vegetation-removal experiment. 1998 field experiment: values represent means ( $\pm 1$  SE) after 22 (6 June), 60 (18 July), and 100 (27 August) days since planting.



**Fig. 6.** *Andropogon gerardii* biomass of local (Wheelock, W), non-local (Konza, K) and cultivar (Roundtree, R) target plants grown with (control) or without (removal) surrounding vegetation. Values are means  $\pm 1$  SE.

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