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Effects of Smooth Brome (Bromus inermis) Invasion on Tallgrass Prairie.

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Effects of Smooth Brome (*Bromus inermis*) Invasion on Tallgrass Prairie

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THESIS ACCEPTANCE

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ABSTRACT

Effects of Smooth Brome (*Bromus inermis*) Invasion on Tallgrass Prairie

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Data collected in 1984 and 2000 along a 65 m-long *roadside-to-prairie* gradient were compared to quantify smooth brome (*Bromus inermis*) invasion into a native, tallgrass prairie in eastern Nebraska and to assess the effect of this expansion on prairie composition and diversity. Smooth brome expanded 15 meters further into tallgrass prairie during the 16 years of the study while also increasing cover an average of 8%. Overall, species diversity (H') decreased from 1.04 to 0.95 along the entire road-prairie gradient during this time although the decrease was significant ($P \leq 0.10$) at only three of the five distances from the road that were sampled. Thirteen species declined significantly, including porcupine grass (*Stipa spartea*) (−23%), Indian grass (*Sorghastrum nutans*) (−12%), and prairie phlox (*Phlox pilosa*) (−8%); sideoats grama (*Bouteloua curtipendula*), averaging 2% in 1984, was absent in 2000. Despite these decreases, there was a subset of species that increased, some native and some non-native, of which many were strongly rhizomatous. Four native species that increased significantly were stiff sunflower (*Helianthus rigidus*) (+25%; from 0% in 1984), prairie goldenrod (*Solidago missouriensis*) (+8%), false sunflower (*Heliopsis helianthoides*) (+7%) and clammy ground cherry (*Physalis heterophylla*) (+5%). Field bindweed (*Convolvulus arvensis*), a non-native species also increased significantly (+5%). Canopy

cover of New Jersey tea (*Ceanothus americanus*) (4% cover), a woody, prairie species, and gray-green wood sorrel (*Oxalis dillenii*) (<0.5% cover), a non-native herb, were unchanged over time. In combination, these results suggest an overall decline in species diversity between 1984 and 2000, either in response to increases in smooth brome or coincident with conditions that favor its increase. The rate of decline varies among species. The net effect of these responses extended over time would be a tallgrass prairie characterized by a lower diversity than can be accounted for by fragmentation effects alone and one that supports a greater proportion of non-native species. While these results do not prove conclusive cause-effect relationships between smooth brome encroachment and tallgrass prairie diversity, they do provide sufficient cause for concern when considering both threats to native tallgrass prairie ecosystems and means by which to address these concerns.

INTRODUCTION

The tallgrass prairie of eastern central North America once extended from Saskatchewan south to Texas, incorporating 58 million ha. Of this ecosystem less than 99% remains (Samson and Knopf 1994), a direct consequence of cultivation and urban expansion in conjunction with more subtle changes occurring with alteration of historic factors, such as fire and large-herbivore grazing. The result today is a fragmented ecosystem of many isolated, small remnants embedded in a matrix of non-native habitats. Prairie remnants are particularly subject to degradation and loss of native diversity for many reasons among which is encroachment of undesirable species as has been reported for Fescue (*Festuca*) Prairie (Grilz *et al.* 1994), Mixed Prairie (Nernberg and Dale 1997), and Tallgrass Prairie (Blankespoor and May 1996, Blankespoor and Larson 1994, Boettcher and Bragg 1989). Invasion by non-indigenous plants, in particular, is potentially irreversible and problematic to native ecosystems (Gordon 1998, Wein *et al.* 1992). Of the many species known to encroach into native prairies, smooth brome (*Bromus inermis*) is one of concern, particularly in the central and northern tallgrass prairie where cool conditions characterize portions of the growing season.

Smooth brome is a cool-season, sod-forming, long-lived perennial that reproduces from seeds and that also spreads by creeping rhizomes. This species was introduced into the United States in 1884 from Hungary and has been widely used both as a forage crop and for plantings along roadsides, fence lines, and railroad right-of-ways where its dense root system is useful in limiting erosion and other disturbances (KSU Cooperative Extension Service 1986). In general, smooth brome advances in a front as rhizomes expand into previously unoccupied areas from their point of origin, such as from a roadside planting. The rate at which the smooth brome advances depends on various factors, including soil moisture, texture, and chemistry, as well as plant species composition (Blankespoor and May 1996). In addition to its aggressive growth characteristic, smooth brome seeds have a high germination rate, allowing this species to take advantage of suitable environmental conditions such as short periods of precipitation. Thus, smooth brome seeds can easily establish patches within the interior of prairies from which they then expand rhizomatously

Smooth Brome Control

One concern of land managers is that substantial smooth brome encroachment into native prairies will ultimately affect native flora (Grilz *et al.* 1994, Blankespoor and Larson 1994, Nernberg and Dale 1997). Thus, due to its presumed adverse effects on tallgrass prairie, various types of management have been studied to assess those best able to prevent or slow smooth brome establishment. Management considerations have included the use of fire, herbicides, and mowing (Masters *et al.* 1992, Blankespoor and Larson 1994, Grilz and Romo 1994,1995, Willson and Stubbendieck 1996, Bragg *et al.* 1999, Willson and Stubbendieck 2000). All types of management, however, are likely to have similar effects on other plants with similar phenology, including native species. Whether this consequence is of importance depends on the specific management objective of the site.

Fire Management

In general, burning alone is not sufficient to ensure smooth brome control (Nagel *et al.* 1994); rather it is the season of burning that is critical. Fire applied too early in the spring, for example, encourages smooth brome (Willson and Stubbendieck 1995) whereas burning during late spring is better able to affect some control (Blankespoor and Larson 1994, Willson and Stubbendieck 2000). In addition to season of burn, the frequency with which fire is applied is a factor affecting differential responses of smooth brome. For example, Bragg *et al.* (1999), in a 12-year-study, found that only annual spring burns, and, to a lesser extent, annual summer burns, effectively reduced smooth brome, results supported also by Willson and Stubbendieck (1997). In the 1999 study, quadrennial burns, irrespective of season of treatment, all resulted in an increase in smooth brome cover at the expense of warm-season native grasses such as big bluestem (*Andropogon gerardii*). These results suggest that the phenological stage of smooth brome is critical in explaining the response of this species to burning. For example, Willson and Stubbendieck (1997) showed that the best time to affect smooth brome adversely is during tiller elongation, heading, and flowering, whereas a burn earlier than these stages stimulates the growth of tillers (Willson and Stubbendieck 1995).

Herbicide Management

Although correctly timed burns affect some degree of control over smooth brome, they do not always produce optimum results. Thus, the application of herbicides, in conjunction with fire, has been evaluated. Grilz and Romo (1995), in their study on a fescue prairie, reported poor smooth brome control with burning alone, but when a late spring burn was followed by the application of glyphosate, smooth brome was effectively controlled. Herbicide application in the absence of fire has also been evaluated to some extent. For example, applying atrazine in late spring has been shown to suppress the growth of smooth brome and increase that of warm-season native species in tallgrass prairie (Masters *et al.* 1992, Willson and Stubbendieck 1996, Willson and Stubbendieck 2000).

Mowing Management

Mowing is a common practice on tallgrass remnants, although its effect on smooth brome has received limited attention and results have been inconsistent. For example, Old (1969) reported that a single mowing and raking in late April adversely affected that year's growth of smooth brome, Willson and Stubbendieck (1996) found no such effect under similar conditions. Similarly, while annual mowing was not addressed, Bragg *et al.* (1999) found that quadrennial mowing in the spring, summer, and fall resulted in an increase in smooth brome. These inconsistent results suggest the need for further study analysis, particularly on season and frequency of treatment.

Study Objective

Many factors are known to affect plant communities over time including general effects of fragmentation (e.g. *species relaxation*; Saunders *et al.* 1991) and management (e.g. see Bragg *et al.* 1999). Any or all of these may play a role in changes observed. This study, however, is intended to explore possible relationships between smooth brome encroachment and the response of other species and community characteristics (e.g.

diversity). However, it is not designed to show conclusively a cause-and-effect relationship.

While the invasive nature of smooth brome has been documented, its effects on native, tallgrass prairie species composition and diversity remain unclear. Given this, my study took advantage of data collected in the early 1980's to compare with those collected in 2000 to assess the degree of smooth brome invasion into a native tallgrass prairie and the impact of this invasion on species composition and diversity. My hypotheses are (1) that smooth brome has increased significantly, (2) that this increase has significantly diminished native tallgrass species diversity, and (3) that the degree of effect between years is greater in areas most recently invaded by smooth brome.

METHODS

My study was conducted at Stolley Prairie, a 10 ha native tallgrass prairie situated approximately 15 km northwest of Omaha, Nebraska (41°16' N, 96°11' W). An original survey of the site in 1979 showed domination by the warm-season grass, big bluestem (*Andropogon gerardii*), with porcupine grass (*Stipa spartea*), the dominant cool-season species (Boettcher and Bragg 1989). Since 1980, the site has been managed with Spring burns every 3-4 years. Annual temperatures in the region range from 30C in July to -12C in January. Average precipitation is 760 millimeters with 74% occurring between April and September. Soil of the site is a Marshall silty clay loam of the Mollisol Soil Order (Bartlett 1975).

Initial vegetation studies were conducted at the site from 1981-1986 in permanently marked plots with the objective being to evaluate the effect of fire season and frequency on tallgrass prairie species composition and diversity (Bragg 1991). The present study re-evaluated these plots, and compared the species composition in 2000 with that of 1984 in order to assess expansion of smooth brome into the prairie and changes in plant composition. The data for 1984 were selected over other years available because (1) this was the most recent year in which all 15 plots had been evaluated and (2) this was long enough after the last treatment-year to mask differential effects of fire on the plots.

The fifteen, 10 by 10-m plots, established in 1981 and re-evaluated in 2000, were arranged in a 3-row by 5-column grid (5 columns of 3 plots each). Column 1 plots were situated approximately 90 m into the prairie. This column of plots was most distant from the road along which smooth brome was assumed to have been planted an unknown number of years before. Column 5 plots were situated approximately 25 m from the road and thus were the closest to the source of smooth brome. Columns 2-4 were spaced approximately 15 m apart at intermediate distances from the road. Within each plot, a 10-meter transect was permanently marked with metal end-poles. Ten 30 by 50-cm microplots were systematically situated at 1-meter-intervals along the transect. In 2000, species composition was evaluated in each microplot using the same procedures followed in 1984. This involved recording the canopy cover for general microplot parameters (i.e. grasses, forbs, woody plants, bare soil and litter) and for individual species. Canopy cover procedures were adapted from Daubenmire (1959) using 9 canopy categories: 0 = absent, 1 = <1%, 2 = 1-5%, 3 = 5-25%, 4 = 25-50%, 5 = 50-75%, 6 = 75-95%, 7 = 95-99%, and 8 = >99%. Species nomenclature follows the Great Plains Flora Association (1986).

For 2000, data were collected in both Spring and Fall. However, when comparing 2000 data to that of 1984, only the Fall data were used since that was the only season for which data were collected in both years. For the purpose of analyzing 2000 data alone, Spring and Fall data were combined into one data set (combination data = combo), with the highest cover value for the year recorded for each species. This procedure was intended both to assess a species at the time of its highest cover and also to include those species seen primarily in the spring.

Analyses of species among distances for each year were conducted using ANOVA procedures. The parametric ANOVA was used, since it is considered sufficiently robust to indicate differences even when assumptions of parametric tests are only approximately met (Zar 1999). The non-parametric Student-Neuman-Kuels Multiple Comparison Test was used to compare differences among the distances from the road (i.e. Columns 1-5) for each of 1984 and 2000. A 2-factor *t*-Test was used to indicate significant differences between years. Statistically significant differences in species diversity between 1984 and 2000 were also calculated using Shannon-Wiener Diversity Index values (H') following procedures described in Zar (1999). H' is a dominance-concentration index of Alpha-diversity that, in this study, was based on canopy cover values for each species. *Species Richness (S)*, the sum of all species in an area, was used for descriptive comparisons among distances and years.

RESULTS AND DISCUSSION

Fifty-eight species were identified in 1984 and 2000 combined, of which 49 were native (Table 1). The general results of this study show that smooth brome cover has increased within the prairie and that this invasion has had a greater effect on individual species than on overall native species diversity.

Smooth Brome Invasion

As hypothesized, smooth brome extended further into Stolley Prairie in 2000 than in 1984 (Fig. 1). The overall, gradual decline in cover from the road into the prairie is consistent with that expected of movement through rhizome extension into an unoccupied area from a source location along the road. Smooth brome's appearance approximately 15 m further into the prairie in 2000 than in 1984 suggests an annual average rate of advance of approximately 1 m/yr, although this is likely to vary depending on the environmental conditions in each year (Blankespoor and May 1996).

In addition to advancing into the prairie, canopy cover of smooth brome increased an average of 8% between 1984 and 2000 throughout the study area, although significant increases ($P \leq 0.05$) were noted for only three of the five distances from the road (Fig. 1). Logical explanations, however, can be inferred for those lacking significance. For Distance 5 (closest to the road), it is likely that smooth brome had already maximized its use of easily accessed niche space in 1984 so that further, significant increases were unlikely during the time period of the study. At Distance 3, smooth brome cover in 1984 was nearly as high as in 2000. This high cover in a prairie-interior location is consistent with that expected with seedling establishment in advance of the rhizomatous front, as

Table 1. Mean canopy cover (%) ± Standard Error (SE) of community parameters and individual species for Fall 1984 and Fall 2000. For those species where spring canopy cover was greater than fall cover, combined data (= *Combo*) are also listed. See text for details on these calculations. ** = introduced or non-native species; tr = ≤ 0.5% cover; -- = data not collected. Superscripts following SE indicate significant differences at $P \leq 0.05$ among the distances according to the Student-Newman-Keuls Multiple Comparison Test. ANOVA *P*-Values indicate results from single factor ANOVA tests among distances.

Species or Community Parameter	Year/Season	Distance from Road (5 = closest to the road) 1	2	3	4	5	ANOVA P-Values
Total Cover	1984 Fall	99±0.5	99±0.5	99±0.5	99±0.1	100±0.0	0.6945
	2000 Fall	100±0	100±0	99±0.7	100±0	100±0	0.0875
Green Biomass	1984 Fall	98±0.7	99±0.5	99±0.5	99±0.1	100±0.0	0.4064
	2000 Fall	99 ± 0.1^{A}	99 ± 0.1^{A}	98 ± 0.7^{A}	99 ± 0.1^{A}	96 ± 1.5^{B}	0.0012
Litter	1984 Fall	58 ± 7.6^{B}	64 ± 7.4^{B}	94 ± 1.3^{A}	55 ± 6.0^{B}	65 ± 6.3^{B}	<.0001
	2000 Fall	99±0.5	99±0.5	92±3.7	99±0.5	99±0.5	0.0131
Soil	1984 Fall	$16\pm3.2A^{B}$	21 ± 5.6^{BC}	6 ± 2.7^{C}	9 ± 2.8^{AB}	13 ± 2.9^{A}	0.0369
	2000 Fall	1 ± 0.5^{B}	1 ± 0.5^{B}	6 ± 2.7^{A}	0^{B}	0^{B}	0.0044
Grass	1984 Fall	99±0.5	99±0.5	99±0.5	99±0.2	98±1.2	0.9184
	2000 Fall	99 ± 0.1^{A}	99 ± 0.1^{A}	98 ± 0.7^{AB}	99 ± 0.2^{AB}	99 ± 0.2^{B}	0.0265
Forb	1984 Fall	16 ± 3.0^{B}	35 ± 4.6^{AB}	27 ± 3.5^{AB}	41 ± 3.4^{A}	30 ± 4.2^{AB}	0.0002
	2000 Fall	51 ± 5.7^{B}	37 ± 5.8^{C}	84 ± 2.7^{A}	61 ± 5.5^{B}	59 ± 4.4^{B}	<.0001
Woody	1984 Fall	12 ± 3.9^{B}	13 ± 4.2^{AB}	20 ± 4.9^{AB}	30 ± 4.9^{A}	18 ± 4.9^{AB}	0.0527
	2000 Fall	0	0	3±2.8	0	0	0.4097
Achillea millefolium	1984 Fall	1±0.5	tr	tr	5±2.5	tr	0.0101
Yarrow	2000 Fall	0	0	0	1±0.5	0	0.4097
Amorpha canescens	1984 Fall	6±2.1	7±2.2	6±2.4	13±3.3	12±4.0	0.1854
Lead plant	2000 Fall	2±1.4	3±1.4	2±0.8	4±2.9	8±3.0	0.2638

Table 1. Mean canopy cover (%) ± Standard Error (SE) of community parameters and individual species for Fall 1984 and Fall 2000. For those species where spring canopy cover was greater than fall cover, combined data (= *Combo*) are also listed. See text for details on these calculations. ** = introduced or non-native species; tr = ≤ 0.5% cover; -- = data not collected. Superscripts following SE indicate significant differences at $P \leq 0.05$ among the distances according to the Student-Newman-Keuls Multiple Comparison Test. ANOVA *P*-Values indicate results from single factor ANOVA tests among distances.

Species or Community Parameter	Year/Season	Distance from Road (5 = closest to the road) 1	2	3	4	5	ANOVA P-Values
Andropogon gerardii	1984 Fall	$82±2.4^{B}$	$74±4.7^{B}$	$76±4.0^{B}$	$73±4.2^{B}$	$92±1.6^{A}$	0.0012
Big bluestem	2000 Fall	$73±5.2^{A}$	$81±4.7^{A}$	$41±6.9^{B}$	$69±5.2^{A}$	$82±4.3^{A}$	<.0001
Andropogon scopaius	1984 Fall	1±0.5	2±1.4	0	0	0	0.0776
Little bluestem	2000 Fall	0	0	0	0	0	1.0000
Anemone cylindrica	1984 Fall	tr	1±0.5	4±3.1	0	0	0.4671
Candle anemone	2000 Fall	0	0	0	0	0	1.0000
Asclepias syriaca	1984 Fall	0	0	1±0.5	0	0	0.4097
Common milkweed	2000 Fall	1±0.7	3±1.5	2±1.4	1±0.5	0	0.2389
Aster ericoides	1984 Fall	$4±1.5^{A}$	0^{B}	0^{B}	$2±2.1^{B}$	$3±1.7^{AB}$	0.2528
White aster	2000 Fall	$1±0.5^{B}$	0^{B}	tr^{B}	$1±0.7^{AB}$	$1±0.7^{A}$	0.2099
Aster laevis	1984 Fall	0	0	0	0	0	1.000
Smooth blue aster	2000 Fall	0^{B}	0^{B}	0^{B}	$5±2.7^{A}$	0^{B}	0.0073
Aster sericeus	1984 Fall	0	0	0	tr	0	0.4097
Silky Aster	2000 Fall	0	0	0	0	0	1.0000
Bouteloua curtipendula	1984 Fall	$7±3.3^{A}$	$2±0.9^{AB}$	$1±0.5^{B}$	$1±0.7^{AB}$	$1±0.5^{AB}$	0.0114
Sideoats grama	2000 Fall	tr	tr	0	0	0	0.4635

Table 1. Mean canopy cover (%) ± Standard Error (SE) of community parameters and individual species for Fall 1984 and Fall 2000. For those species where spring canopy cover was greater than fall cover, combined data (= *Combo*) are also listed. See text for details on these calculations. ** = introduced or non-native species; tr = ≤ 0.5% cover; -- = data not collected. Superscripts following SE indicate significant differences at $P \leq 0.05$ among the distances according to the Student-Newman-Keuls Multiple Comparison Test. ANOVA *P*-Values indicate results from single factor ANOVA tests among distances.

Species or Community Parameter	Year/Season	Distance from Road (5 = closest to the road) 1	2	3	4	5	ANOVA P-Values
Bromus inermis	1984 Fall	0^{B}	1 ± 0.5^{B}	10 ± 4.2^{B}	4 ± 3.3^{B}	9 ± 3.2^{A}	0.0413
**Smooth brome	2000 Fall	6 ± 1.9^{B}	14 ± 2.9^{A}	12 ± 2.9^{A}	17 ± 2.4^{A}	15 ± 3.1^{A}	0.0710
	Spring	12 ± 3.9^{B}	18 ± 3.4^{AB}	16 ± 3.1^{AB}	27 ± 5.0^{A}	23 ± 4.9^{AB}	0.0831
	Combo	12 ± 3.9^{B}	21 ± 3.4^{A}	19 ± 3.5^{A}	29 ± 4.7^{A}	26 ± 4.7^{A}	0.0403
Bromus japonicus	1984 Fall	3 ± 1.1^{A}	0^{B}	0^{B}	0^{B}	0^{B}	<.0001
**Japanese brome	2000 Fall	0	0	0	0	0	1.0000
Carduus nutans	1984 Fall	0	0	1±1.3	0	0	0.4097
**Musk thistle	2000 Fall	0	0	0	0	0	1.0000
Carex spp	1984 Fall	11±2.4	10±1.9	11±2.1	12±2.4	14±2.1	0.7130
Sedge	2000 Fall	tr^{A}	tr^{AB}	tr^{B}	tr^{AB}	1 ± 1.2^{B}	0.3962
Ceanothus americanus	1984 Fall	0^{B}	2 ± 2.1^{AB}	9 ± 4.1^{A}	6 ± 3.1^{AB}	3 ± 2.9^{AB}	0.1430
New Jersey Tea	2000 Fall	0^{B}	0^{B}	8 ± 3.3^{A}	6 ± 3.6^{AB}	2 ± 2.1^{AB}	0.0681
Chenopodium spp.	1984 Fall	tr	0	0	0	0	0.4097
**Lamb's quarters	2000 Fall	0	0	tr	0	0	0.0875
Cirsium altissimum	1984 Fall	1±0.5	0	0	0	0	0.3741
Tall thistle	2000 Fall	0	1±0.5	0	0	0	0.4097

Table 1. Mean canopy cover (%) ± Standard Error (SE) of community parameters and individual species for Fall 1984 and Fall 2000. For those species where spring canopy cover was greater than fall cover, combined data (= *Combo*) are also listed. See text for details on these calculations. ** = introduced or non-native species; tr = ≤ 0.5% cover; -- = data not collected. Superscripts following SE indicate significant differences at $P \leq 0.05$ among the distances according to the Student-Newman-Keuls Multiple Comparison Test. ANOVA *P*-Values indicate results from single factor ANOVA tests among distances.

Species or Community Parameter	Year/Season	Distance from Road (5 = closest to the road) 1	2	3	4	5	ANOVA P-Values
Convolvulus arvensis	1984 Fall	0	0	0	0	0	1.000
**Field bindweed	2000 Fall	tr^{B}	$3±1.0^{AB}$	$8±2.4^{A}$	$2±0.8^{AB}$	$2±0.9^{AB}$	0.0006
	Spring	1±0.7	4±1.5	6±1.7	2±1.4	3±1.0	0.1472
	Combo	$1±0.7^{B}$	$5±1.6^{B}$	$10±2.3^{A}$	$4±1.5^{B}$	$3±1.1^{B}$	0.0012
Conyza canadensis	1984 Fall	$1±0.2^{AB}$	tr^{B}	0^{B}	$2±0.8^{A}$	$1±0.5^{B}$	0.0213
Mare's tail	2000 Fall	0	0	0	0	0	1.0000
Desmanthus illinoensis	1984 Fall	0	0	0	0	0	1.000
Illinois tickclover	2000 Fall	0	0	tr	0	0	0.4097
Dichanthelium acuminatum	1984 Fall	0	1±0.5	0	0	0	0.4097
Dichanthelium	2000 Fall	0	0	0	0	0	1.0000
Dichanthelium oligosanthes	1984 Fall	3±1.0	5±1.5	9±2.5	3±0.9	2±0.8	0.0178
Scribner dichanthelium	2000 Fall	$1±0.7^{AB}$	$1±0.7^{AB}$	$1±0.2^{A}$	tr^{B}	$1±0.5^{AB}$	0.5006
Dichanthelium wilcoxianum	1984 Fall	$5±1.6^{A}$	$1±0.5^{B}$	tr^{B}	0^{B}	$1±0.5^{B}$	<.0001
Wilcox dichanthelium	2000 Fall	0	0	0	0	0	1.0000
Echinacea angustifolia	1984 Fall	0	1±0.5	0	0	1±0.5	0.5595
Purple cone flower	2000 Fall	0	0	0	0	0	1.0000
Elymus canadensis	1984 Fall	1±0.7	5±1.9	6±1.9	8±2.8	1±0.7	0.0224
Canada Wild Rye	2000 Fall	2±1.4	3±1.8	tr	1±0.7	1±0.5	0.2597

Table 1. Mean canopy cover (%) ± Standard Error (SE) of community parameters and individual species for Fall 1984 and Fall 2000. For those species where spring canopy cover was greater than fall cover, combined data (= *Combo*) are also listed. See text for details on these calculations. ** = introduced or non-native species; tr = ≤ 0.5% cover; -- = data not collected. Superscripts following SE indicate significant differences at $P \leq 0.05$ among the distances according to the Student-Newman-Keuls Multiple Comparison Test. ANOVA *P*-Values indicate results from single factor ANOVA tests among distances.

Species or Community Parameter	Year/Season	Distance from Road (5 = closest to the road) 1	2	3	4	5	ANOVA P-Values
Equisetum laevigatum	1984 Fall	4 ± 1.8^{A}	1 ± 0.5^{AB}	3 ± 1.5^{AB}	1 ± 0.5^{AB}	0^{B}	0.0574
Horsetail	2000 Fall	tr	tr	tr	tr	tr	0.6139
Erigeron strigosus	1984 Fall	tr	tr	0	1±0.5	tr	0.1490
Daisy fleabane	2000 Fall	0	0	0	0	0	1.0000
Euphorbia corollata	1984 Fall	6 ± 1.9^{B}	14 ± 3.7^{A}	6 ± 2.4^{B}	4 ± 1.8^{B}	3 ± 1.4^{B}	0.0128
Flowering Spurge	2000 Fall	7 ± 2.9^{AB}	6 ± 1.3^{A}	7 ± 2.4^{B}	14 ± 3.5^{AB}	6 ± 2.1^{AB}	0.2010
Eupatorium rugosum	1984 Fall	0	0	0	0	0	1.0000
White snakeroot	2000 Fall	0^{A}	0^{A}	1 ± 0.5^{A}	0^{A}	1 ± 0.5^{A}	0.5425
Hedeoma hispida	1984 Fall	tr	0	0	0	0	0.4097
Rough false pennyroyal	2000 Fall	0	0	0	0	0	1.0000
Helianthus annuus	1984 Fall	tr	0	0	0	0	0.4097
Common sunflower	2000 Fall	0	0	0	0	0	1.0000
Heliopsis helianthoides	1984 Fall	2 ± 2.1^{B}	4 ± 1.4^{A}	1 ± 0.5^{B}	9 ± 3.7^{A}	tr^{B}	0.0134
False sunflower	2000 Fall	4±1.8	11±3.6	14±3.6	13±3.5	8±3.4	0.1582
Helianthus rigidus	1984 Fall	0	0	0	0	0	1.0000
Stiff sunflower	2000 Fall	23 ± 5.3^{B}	17 ± 4.8^{B}	59 ± 4.7^{A}	14 ± 3.8^{B}	12 ± 2.8^{B}	<.0001
Koeleria pyramidata	1984 Fall	0	0	0	1±0.7	tr	0.1130
Junegrass	2000 Fall	0	0	0	0	0	1.0000

Table 1. Mean canopy cover (%) ± Standard Error (SE) of community parameters and individual species for Fall 1984 and Fall 2000. For those species where spring canopy cover was greater than fall cover, combined data (= *Combo*) are also listed. See text for details on these calculations. ** = introduced or non-native species; tr = ≤ 0.5% cover; -- = data not collected. Superscripts following SE indicate significant differences at $P \leq 0.05$ among the distances according to the Student-Newman-Keuls Multiple Comparison Test. ANOVA *P*-Values indicate results from single factor ANOVA tests among distances.

Species or Community Parameter	Year/Season	Distance from Road (5 = closest to the road) 1	2	3	4	5	ANOVA P-Values
Kuhnia eupatorioides	1984 Fall	0^{B}	$3±1.7^{A}$	$1±0.5^{AB}$	$1±0.5^{AB}$	tr^{AB}	0.1339
False boneset	2000 Fall	tr	0	0	0	0	0.4097
Lactuca spp	1984 Fall	0	0	0	0	0	1.0000
Lettuce	2000 Fall	0	0	1±0.5	0	0	0.2582
Linum rigidum	1984 Fall	$1±0.5^{C}$	$2±1.3^{BC}$	0^{C}	$8±2.2^{A}$	$9±3.0^{AB}$	0.0003
Compact stiffstem flax	2000 Fall	0	0	0	0	0	1.0000
Lysimachia ciliata	1984 Fall	0	0	0	0	0	1.0000
Fringed loosestrife	2000 Fall	$1±0.7^{A}$	0^{B}	0^{B}	0^{B}	0^{B}	0.0507
	Spring	2±0.8	1±0.7	0	0	0	0.0535
	Combo	$3±1.0^{A}$	$1±0.7^{B}$	0^{B}	0^{B}	0^{B}	0.0021
Melilotus spp.	1984 Fall	0	0	0	0	tr	0.4097
**Sweet clover	2000 Fall	0	0	tr	0	0	0.4097
Oxalis dillenii	1984 Fall	tr	tr	tr	tr	tr	0.2437
**Gray-green wood sorrel	2000 Fall	0	0	tr	tr	0	0.3824
	Spring	1±0.5	0	tr	tr	0	0.5088
	Combo	1±0.5	0	tr	tr	0	0.5184
Phlox pilosa	1984 Fall	$3±1.0^{C}$	$9±2.5^{B}$	$14±2.8^{AB}$	$14±2.5^{A}$	$6±1.5^{AB}$	0.0009
Prairie phlox	2000 Fall	$1±0.5^{B}$	$1±0.5^{B}$	$3±1.0^{A}$	$1±0.2^{AB}$	tr^{B}	0.0013
	Spring	1±0.5	1±0.5	2±0.8	1±0.5	tr	0.2534
	Combo	$1±0.7^{B}$	$1±0.7^{B}$	$4±1.1^{A}$	$2±0.5^{A}$	tr^{B}	0.0070

Table 1. Mean canopy cover (%) ± Standard Error (SE) of community parameters and individual species for Fall 1984 and Fall 2000. For those species where spring canopy cover was greater than fall cover, combined data (= *Combo*) are also listed. See text for details on these calculations. ** = introduced or non-native species; tr = ≤ 0.5% cover; -- = data not collected. Superscripts following SE indicate significant differences at $P \leq 0.05$ among the distances according to the Student-Newman-Keuls Multiple Comparison Test. ANOVA *P*-Values indicate results from single factor ANOVA tests among distances.

Species or Community Parameter	Year/Season	Distance from Road (5 = closest to the road) 1	2	3	4	5	ANOVA P-Values
Physalis heterophylla	1984 Fall	1±0.5	1±1.5	2±1.3	2±1.4	0	0.5231
Clammy ground cherry	2000 Fall	$7±2.7^{AB}$	$2±1.4^{B}$	$13±3.0^{A}$	$5±1.9^{B}$	$7±2.6^{AB}$	0.0355
	Spring	5±2.2	0	2±0.9	1±0.7	1±0.7	0.0686
	Combo	$9±3.1^{AB}$	$2±1.4^{B}$	$13±3.0^{A}$	$5±1.9^{B}$	$7±2.6^{AB}$	0.0441
Poa pratensis	1984 Fall	$46±4.9^{C}$	$58±5.9^{BC}$	$67±4.6^{AB}$	$75±3.9^{A}$	$58±4.6^{BC}$	0.0005
**Kentucky bluegrass	2000 Fall	--	--	--	--	--	--
	Spring	$59±6.8^{A}$	$54±6.3^{A}$	$41±6.9^{B}$	$56±6.0^{A}$	$43±5.6^{A}$	0.1650
	Combo	$59±6.8^{A}$	$54±6.3^{A}$	$41±6.9^{B}$	$56±6.0^{A}$	$43±5.6^{A}$	0.1650
Potentilla arguta	1984 Fall	0	1±0.5	0	0	0	0.4097
Tall cinquefoil	2000 Fall	0	0	0	0	0	1.0000
Ratibida pinnata	1984 Fall	0	0	0	0	0	1.0000
Grayhead priarie coneflower	2000 Fall	0	tr	0	3±2.8	0	0.4176
Rhus glabra	1984 Fall	0	0	0	0	0	1.0000
Smooth sumac	2000 Fall	0	0	3±2.8	0	0	0.4097
Rosa arkansana	1984 Fall	$2±1.3^{B}$	$7±3.6^{B}$	$6±3.3^{B}$	$18±4.6^{A}$	$3±2.4^{B}$	0.0060
Prairie wild rose	2000 Fall	--	--	--	--	--	--
	Spring	2±1.4	5±2.1	9±3.9	6±1.9	1±0.5	0.0792
	Combo	2±1.4	5±2.1	9±3.9	6±1.9	1±0.5	0.0792
Rudbeckia hirta	1984 Fall	$3±1.1^{AB}$	$3±1.1^{AB}$	$1±0.7^{B}$	$12±3.1^{A}$	$5±2.1^{AB}$	0.0013
Black-eyed susan	2000 Fall	0	0	0	0	0	1.0000

Table 1. Mean canopy cover (%) ± Standard Error (SE) of community parameters and individual species for Fall 1984 and Fall 2000. For those species where spring canopy cover was greater than fall cover, combined data (= *Combo*) are also listed. See text for details on these calculations. ** = introduced or non-native species; tr = ≤ 0.5% cover; -- = data not collected. Superscripts following SE indicate significant differences at $P \leq 0.05$ among the distances according to the Student-Newman-Keuls Multiple Comparison Test. ANOVA *P*-Values indicate results from single factor ANOVA tests among distances.

Species or Community Parameter	Year/Season	Distance from Road (5 = closest to the road) 1	2	3	4	5	ANOVA P-Values
Scutellaria parvula	1984 Fall	0	0	0	0	0	1.0000
Skull cap	2000 Fall	0	0	tr	tr	0	0.4635
Senecio plattensis	1984 Fall	0	tr	0	0	0	0.4097
Prairie Ragwort	2000 Fall	0	0	0	0	0	1.0000
Solidago missouriensis	1984 Fall	0	1±0.5	0	1±0.7	tr	0.2818
Prairie goldenrod	2000 Fall	15±4.6^{A}	1±0.5^{B}	1±0.5^{B}	0^{B}	21±5.9^{A}	<.0001
Sorghastrum nutans	1984 Fall	22±5.0	15±4.7	11±3.5	10±2.8	15±3.7	0.2201
Indian grass	2000 Fall	4±2.1	1±0.5	1±0.5	4±1.8	3±2.2	0.3621
Sporobolus asper	1984 Fall	0	0	1±1.3	0	1±0.5	0.5096
Rough dropseed	2000 Fall	0	0	0	0	0	1.000
Stipa spartea	1984 Fall	41±4.9^{A}	43±5.9^{A}	14±3.9^{B}	15±4.6^{B}	4±2.4^{C}	<.0001
Porcupine grass	2000 Fall	0	0	0	0	0	1.0000
	Spring	0	tr	0	0	0	0.4097
	Combo	0	tr	0	0	0	0.4097
Toxicodendron rydbergii	1984 Fall	5±3.5	0	0	0	tr	0.0971
Poison ivy	2000 Fall	--	--	--	--	--	--
	Spring	17±5.6^{A}	0^{B}	0^{B}	0^{B}	0^{B}	<.0001
	Combo	17±5.6^{A}	0^{B}	0^{B}	0^{B}	0^{B}	<.0001

Table 1. Mean canopy cover (%) ± Standard Error (SE) of community parameters and individual species for Fall 1984 and Fall 2000. For those species where spring canopy cover was greater than fall cover, combined data (= *Combo*) are also listed. See text for details on these calculations. ** = introduced or non-native species; tr = ≤ 0.5% cover; -- = data not collected. Superscripts following SE indicate significant differences at $P \leq 0.05$ among the distances according to the Student-Newman-Keuls Multiple Comparison Test. ANOVA *P*-Values indicate results from single factor ANOVA tests among distances.

Species or Community Parameter	Year/Season	Distance from Road (5 = closest to the road) 1	2	3	4	5	ANOVA P-Values
Trifolium pratense	1984 Fall	3±1.1	8±2.8	6±1.9	18±4.3	13±3.8	0.0077
**Red clover	2000 Fall	0	0	0	0	0	1.0000
Viola pedatifida	1984 Fall	tr	2±0.8	1±0.7	2±0.8	4±1.8	0.1485
Prairie violet	2000 Fall	tr	tr	tr	tr	0	0.5134
Vitis ripara	1984 Fall	0	0	0	0	0	1.0000
Riverbank grape	2000 Fall	0	0	0	1±1.3	0	0.4097

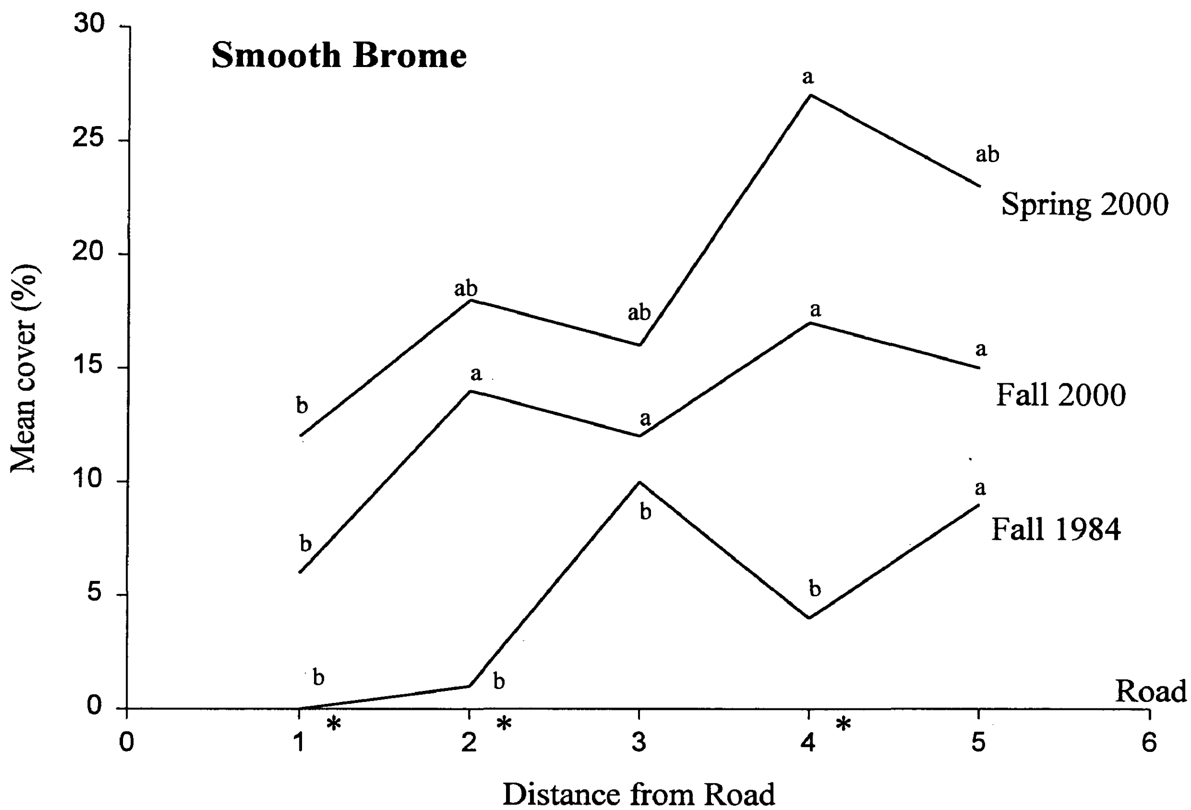

Fig. 1. Mean canopy cover of smooth brome for 1984 and 2000, by distance from the road; a, b = significant differences among distances for the year and season shown; different alphabetic letters differ significantly ($P \leq 0.05$); * = significant difference between Fall 1984 and Fall 2000 based on 2-Factor *t*-Test ($P \leq 0.05$).

suggested by Blankespoor and May (1996). Whatever the cause, further significant increases at Distance 3 during the 16 years of the study were unlikely, as was the case at Distance 5. In combination, these and other results provide one example of a hypothetical background of the dynamics at each of the five distances evaluated for this study. This background is particularly relevant to further discussion of the results of this study. Distances 1-5 are listed below in order of inferred time of smooth brome establishment.

1. *Distance 1* was recently invaded (within the last 16 years) and thus the community composition is likely to be in a state of transition. Any effect of smooth brome on community composition has not yet been fully expressed.
2. *Distance 2* supported some smooth brome in 1984. Any effect of encroachment should be more fully expressed here than in Distance 1.
3. *Distance 4* is intermediate between Distance 2 and Distances 3 and 5 with respect to the time since initially invaded.
4. *Distances 3 and 5* both had substantial smooth brome cover in 1984, which did not increase significantly by 2000. This suggests that any effect of smooth brome on tallgrass prairie was already expressed in these locations in 1984 so that further change was less likely. The difference between the two is that Distance 5, being closest to the source of smooth brome, is assumed to reflect the effect of smooth brome over the longest period of time. Distance 5, for example, may reflect factors such as long-lived species or species more competitive with smooth brome for which

any decline would be effected through lower reproductive success expressed over time. In contrast, short-term (i.e. years-long) responses, such as an initial rapid decline in those species most susceptible to invasion, would be better shown in Distance 3 than in Distance 5.

Effect of Smooth Brome

Smooth brome was hypothesized to affect the diversity and composition of tallgrasss prairie adversely. This hypothesis was less clearly substantiated for diversity than it was for individual prairie species.

Species Diversity: In all instances, *Species Richness* and species diversity (*H'*) were higher in 1984 than in 2000, although this difference was significant at $P \leq 0.05$ only for Distance 2 (Table 2, Fig. 2). As previously explained, this is the distance hypothesized to be most likely to reflect effects of smooth brome during the time period of the study. On the other hand, the same comparison for Distance 1 was significant, but only at $P \leq 0.10$. Also previously discussed, this distance was only recently invaded and may not have been affected for a sufficiently long time for substantive community composition change. The lack of significant differences for Distances 3 and 4 would be consistent with the assumption that both may reflect only an intermediate-time effect. Distance 5, which was significant, but only at $P \leq 0.10$, may reflect the longer-term impact of smooth brome on community composition. Taken together, these results suggest that changes in prairie species diversity in response to smooth brome encroachment occur more slowly than anticipated. There may be, however, an initial, comparatively rapid loss of diversity

Table 2. Species diversity by distance for 1984 and 2000; H' = Shannon-Wiener Index; *S* = Species Richness; *P*-Value indicates level of significance of H' value between years; ns = not significant.

	Species Richness		H'		
Distance	1984	2000	1984	2000	*P*-Value
1	33	25	1.01	0.93	$.10 < P < .05$
2	34	24	1.06	0.85	$P < .05$
3	28	29	1.03	0.97	ns
4	30	26	1.12	1.10	ns
5	32	20	0.98	0.89	$.10 < P < .05$

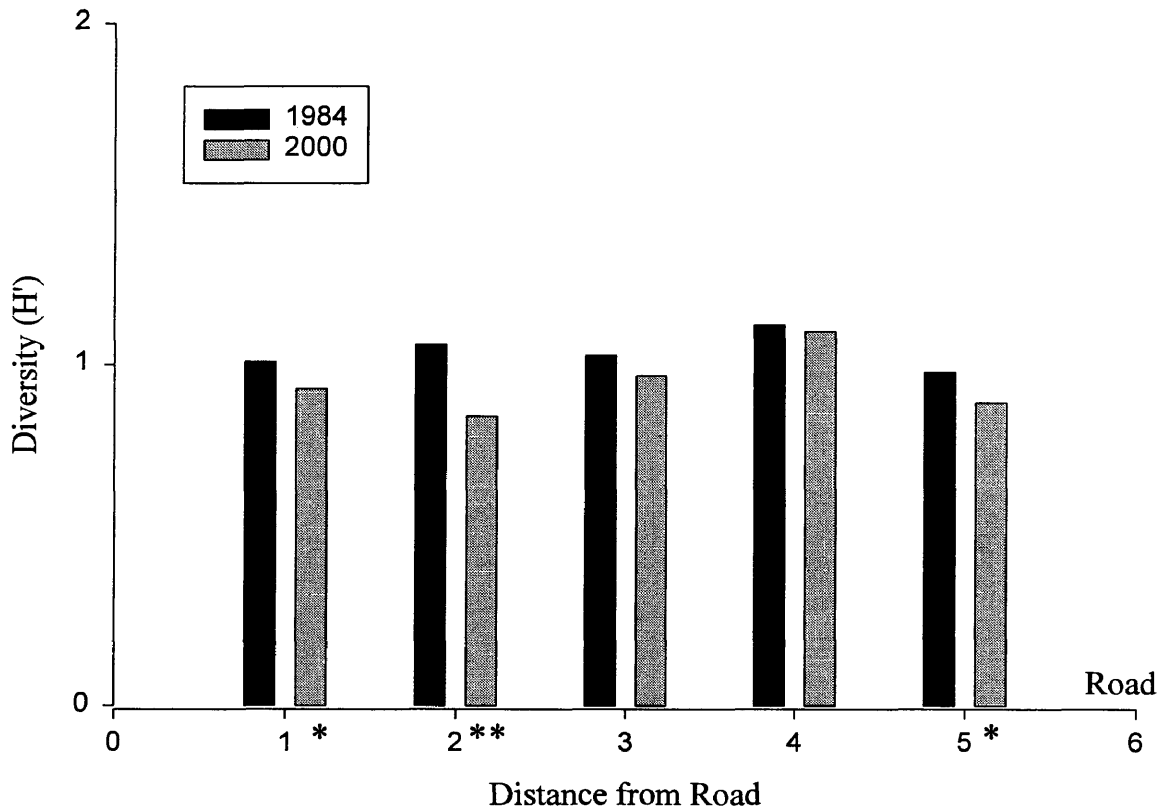

Fig. 2. Species diversity (H') for 1984 and 2000 by distance from the road.
* = significant difference at $0.10 \leq P \leq 0.05$; ** = $P \leq 0.05$

reflecting the decline of those species most susceptible to encroachment. An assessment of individual species responses is essential to further understand the effect of smooth brome on tallgrass prairie.

Individual Species: Twenty-three species, 17 native and 6 non-native, showed a significant change in cover between 1984 and 2000 for at least 2 of the 5 distances evaluated (Table 3). An assessment of these species suggests three general categories: those that decline, those that increase, and those that appear unaffected.

Species Declining.—Of the 17 native species with some significant effects, the majority (thirteen) declined, including two annual forbs (compact stiffstem flax [*Linum rigidum*] and black-eyed susan [*Rudbeckia hirta*]), two perennial forbs (prairie phlox [*Phlox pilosa*] and prairie violet [*Viola pedatifida*]), four perennial, cool-season graminoids (sedge [*Carex*], Scribner dichanthelium [*Dichanthelium oligosanthes* var *scribnarium*], porcupine grass [*Stipa spartea*], and Canada wild rye [*Elymus canadensis*]), three warm-season grasses (big bluestem [*Andropogon gerardii*], sideoats grama [*Bouteloua curtipendula*], and Indian grass [*Sorghastrum nutans*]), one woody plant (prairie wild rose [*Rosa arkansana*]) and horsetail (*Equisetum laevagaetum*) (Table 3). Of these thirteen species, the fewest number of significant declines (6 species) occurred in each of Distances 1 (most distant from the road) and 5 (closest to the road). These results are consistent with my hypotheses relating distance from the source of smooth brome establishment (e.g. the road) and the expected community response. Specifically, recent smooth brome encroachment in areas most distant from the road was

Table 3. *P*-values from Two-factor *t*-Test comparing canopy cover between 1984 and 2000 for each species and distance. * = $P \leq 0.05$ between 1984 and 2000 at that distance; ** = species significant between years at 2 or more distances; --- = canopy cover equaled zero for both 1984 and 2000 (*P*-Values were not calculated); similarly, for Distance 5 *Total Cover*, was 100% cover for both years so a *P*-value was not calculated.

Species or Community Parameter	Distance from Road (5 = closest to road)				
	1	2	3	4	5
Total Cover	0.1911	0.3215	0.5614	0.3215	---
Green Biomass	0.1625	0.5265	0.4969	0.5616	0.0123*
**Litter	<.0001*	<.0001*	0.5027	<.0001*	<.0001*
**Soil	<.0001*	0.0004*	0.9650	0.0018*	<.0001*
Grass	0.4367	0.4367	0.2843	0.7232	0.8531
**Forb	<.0001*	0.7225	<.0001*	0.0033*	<.0001*
**Woody	0.0035*	0.0025*	0.0030*	<.0001*	0.0003*
Achillea millefolium Yarrow	0.1942	0.0779	0.3215	0.0839	0.3215
Amorpha canescens Lead plant	0.2071	0.1225	0.1031	0.0395*	0.4090
Andropogon gerardii **Big bluestem	0.09051	0.2956	<.0001*	0.5292	0.0440*
Andropogon scopaius Little bluestem	0.3215	0.1134	---	---	---

Table 3. *P*-values from Two-factor *t*-Test comparing canopy cover between 1984 and 2000 for each species and distance. * = $P \leq 0.05$ between 1984 and 2000 at that distance; ** = species significant between years at 2 or more distances; --- = canopy cover equaled zero for both 1984 and 2000 (*P*-Values were not calculated); similarly, for Distance 5 *Total Cover*, was 100% cover for both years so a *P*-value was not calculated.

Species or Community Parameter	Distance from Road (5 = closest to road)				
	1	2	3	4	5
Anemone cylindrica Candle anemone	0.3215	0.3215	0.3215	---	---
Asclepias syriaca Common milkweed	0.1249	0.0646	0.2438	0.3215	---
Aster ericoides White aster	0.0628	---	0.3215	0.6342	0.4293
Aster laevis Smooth blue aster	---	---	---	0.0612	---
Aster sericeus Silky Aster	---	---	---	0.3215	---
Bouteloua curtipendula **Sideoats grama	0.0281*	0.0406*	0.3215	0.1249	0.1942
Bromus inermis **Smooth brome	0.0027*	<.0001*	0.6244	0.0028*	0.1875
Bromus japonicus Japanese brome	0.0070*	---	---	---	---
Carduus nutans Musk thistle	---	---	0.3215	---	---

Table 3. *P*-values from Two-factor *t*-Test comparing canopy cover between 1984 and 2000 for each species and distance. * = $P \leq 0.05$ between 1984 and 2000 at that distance; ** = species significant between years at 2 or more distances; --- = canopy cover equaled zero for both 1984 and 2000 (*P*-Values were not calculated); similarly, for Distance 5 *Total Cover*, was 100% cover for both years so a *P*-value was not calculated.

Species or Community Parameter	Distance from Road (5 = closest to road)				
	1	2	3	4	5
Carex spp **Sedge	<.0001*	<.0001*	<.0001*	<.0001*	<.0001*
Ceanothus americanus New Jersey Tea	---	0.3024	0.7477	0.9584	0.7429
Chenopodium spp. Lamb's quarters	0.3215	---	0.1555	---	---
Cirsium altissimum Tall thistle	0.3055	0.3215	---	---	---
Convolvulus arvensis **Field bindweed	0.3215	0.0122*	0.0017*	0.0478*	0.0198*
Conyza canadensis **Mare's tail	0.0093*	0.0913	---	0.0215*	0.2519
Desmanthus illinoensis Illinois tickclover	---	---	0.3215	---	---
Dichanthelium acuminatum Dichanthelium	---	0.3215	---	---	---
Dichanthelium oligosanthes **Scribner dichanthelium	0.0682	0.0350*	0.0019*	0.0070*	0.0892

Table 3. *P*-values from Two-factor *t*-Test comparing canopy cover between 1984 and 2000 for each species and distance. * = $P \leq 0.05$ between 1984 and 2000 at that distance; ** = species significant between years at 2 or more distances; --- = canopy cover equaled zero for both 1984 and 2000 (*P*-Values were not calculated); similarly, for Distance 5 *Total Cover*, was 100% cover for both years so a *P*-value was not calculated.

Species or Community Parameter	Distance from Road (5 = closest to road)				
	1	2	3	4	5
Dichanthelium wilcoxianum Wilcox dichanthelium	0.0023*	0.2519	0.1200	---	0.0749
Echinacea angustifolia Purple cone flower	---	0.3215	---	---	0.3215
Elymus canadensis **Canada Wild Rye	0.4579	0.5820	0.0023*	0.0175*	0.6449
Equisetum laevigatum **Horsetail	0.0498*	0.1392	0.0420*	0.2802	0.3215
Erigeron strigosus Daisy fleabane	0.3215	0.0779	---	0.1099	0.0779
Euphorbia corollata Flowering Spurge	0.6607	0.0515	0.7671	0.0189	0.2150
Eupatorium rugosum White snakeroot	---	---	0.3215	---	0.3055
Hedeoma hispida Rough false pennyroyal	0.3215	---	---	---	---
Helianthus annuus Common sunflower	0.3215	---	---	---	---

Table 3. *P*-values from Two-factor *t*-Test comparing canopy cover between 1984 and 2000 for each species and distance. * = $P \leq 0.05$ between 1984 and 2000 at that distance; ** = species significant between years at 2 or more distances; --- = canopy cover equaled zero for both 1984 and 2000 (*P*-Values were not calculated); similarly, for Distance 5 *Total Cover*, was 100% cover for both years so a *P*-value was not calculated.

Species or Community Parameter	Distance from Road (5 = closest to road)				
	1	2	3	4	5
Heliopsis helianthoides **False sunflower	0.6526	0.0608	0.0006*	0.4496	0.0331*
Helianthus rigidus **Stiff sunflower	<.0001*	.00118	<.0001*	0.0008*	<.0001*
Koeleria pyramidata Junegrass	---	---	---	0.1555	0.1555
Kuhnia eupatorioides False boneset	0.3215	0.1194	0.2384	0.1724	0.1555
Lactuca spp Lettuce	---	---	0.2519	---	---
Linum rigidum **Compact stiffstem flax	0.2519	0.1068	---	0.0010*	0.0029*
Lysimachia ciliata Fringed loosestrife	0.1249	---	---	---	---
Melilotus spp. Sweet clover	---	---	0.3215	---	0.3215
Oxalis dillenii **Gray-green wood sorrel	0.0504*	0.0417*	0.8901	0.1039	0.0390*

Table 3. *P*-values from Two-factor *t*-Test comparing canopy cover between 1984 and 2000 for each species and distance. * = $P \leq 0.05$ between 1984 and 2000 at that distance; ** = species significant between years at 2 or more distances; --- = canopy cover equaled zero for both 1984 and 2000 (*P*-Values were not calculated); similarly, for Distance 5 *Total Cover*, was 100% cover for both years so a *P*-value was not calculated.

Species or Community Parameter	Distance from Road (5 = closest to road)				
	1	2	3	4	5
Phlox pilosa **Prairie phlox	0.0646	0.0025*	0.0005*	<.0001*	0.0001*
Physalis heterophylla **Clammy ground cherry	0.0165*	0.6333	0.0019*	0.3246	0.0057*
Poa pratensis **Kentucky bluegrass	<.0001*	<.0001*	<.0001*	<.0001*	<.0001*
Potentilla arguta Tall cinquefoil	---	0.3215	---	---	---
Ratibida pinnata Grayhead priarie coneflower	---	0.3215	---	0.3215	---
Rhus glabra Smooth sumac	---	---	0.3215	---	---
Rosa arkansana **Prairie wild rose	0.1935	0.0495*	0.0701	0.0003	0.1688
Rudbeckia hirta **Black-eyed susan	0.0025*	0.0025*	0.1249	0.0004*	0.0325*
Scutellaria parvula Skull cap	---	---	0.3215	0.3215	---

Table 3. *P*-values from Two-factor *t*-Test comparing canopy cover between 1984 and 2000 for each species and distance. * = $P \leq 0.05$ between 1984 and 2000 at that distance; ** = species significant between years at 2 or more distances; --- = canopy cover equaled zero for both 1984 and 2000 (*P*-Values were not calculated); similarly, for Distance 5 *Total Cover*, was 100% cover for both years so a *P*-value was not calculated.

Species or Community Parameter	Distance from Road (5 = closest to road)				
	1	2	3	4	5
Senecio plattensis Prairie ragwort	---	0.3215	---	---	---
Solidago missouriensis **Prairie goldenrod	0.0015*	0.9070	0.3215	0.1555	0.0010*
Sorghastrum nutans **Indian grass	0.0013*	0.0027*	0.0048*	0.0511*	0.0071*
Sporobolus asper Rough dropseed	---	---	0.3215	---	0.3215
Stipa spartea **Porcupine grass	<.0001*	<.0001*	0.0007*	0.0019*	0.0928
Toxicodenndron rydbergii Poison ivy	0.1605	---	---	---	0.3215
Trifolium pratense **Red clover	0.0047*	0.0089*	0.0024*	0.0001*	0.0010*
Viola pedatifida **Prairie violet	0.5830	0.0403*	0.0461*	0.0163*	0.0416*
Vitis ripara Riverbank grape	---	---	---	0.3215	---

described as being less likely to reflect changes in community composition. This was the result observed for Distance 1. Similarly, the composition closest to the road was described as being unlikely to change during the time period of the study since the initial impact would already have been expressed in 1984, which was the result observed for Distance 5. The greatest number of species declining was observed for Distances 2 (9 species), 3 (10 species), and 4 (10 species). These were expected to be more responsive to smooth brome encroachment than other distances based on expected time-of-encroachment. The results support this expectation. Overall, the diversity of functional groups containing plant species that declined significantly suggests that smooth brome encroachment, or conditions that support such an invasion, affect a broad array of prairie species. This effect is likely to affect prairie diversity in the long-term, although significant differences in species diversity were shown for only a few distances in this study (Table 2).

While general trends in the loss of species provides a base for assessing community-level effects of smooth brome, several individual species showed responses that are noteworthy. The greatest significant decline in individual cover was noted for porcupine grass (−23%) (Fig. 3, Table 3). Porcupine grass, like smooth brome, is a cool-season species but, unlike smooth brome, it is not rhizomatous. Its decline may be a consequence of either poor competitiveness or the elimination of mowing, a management particularly favorable to Porcupine grass (Hover and Bragg 1981). Other species with substantial and significant declines included Indian grass (−12%) and prairie phlox (−8%) (Figs. 4 and 5). Sideoats grama, while averaging only 2% cover in 1984, was not found in 2000, a decline that coincided with an increase in litter and a decrease in bare

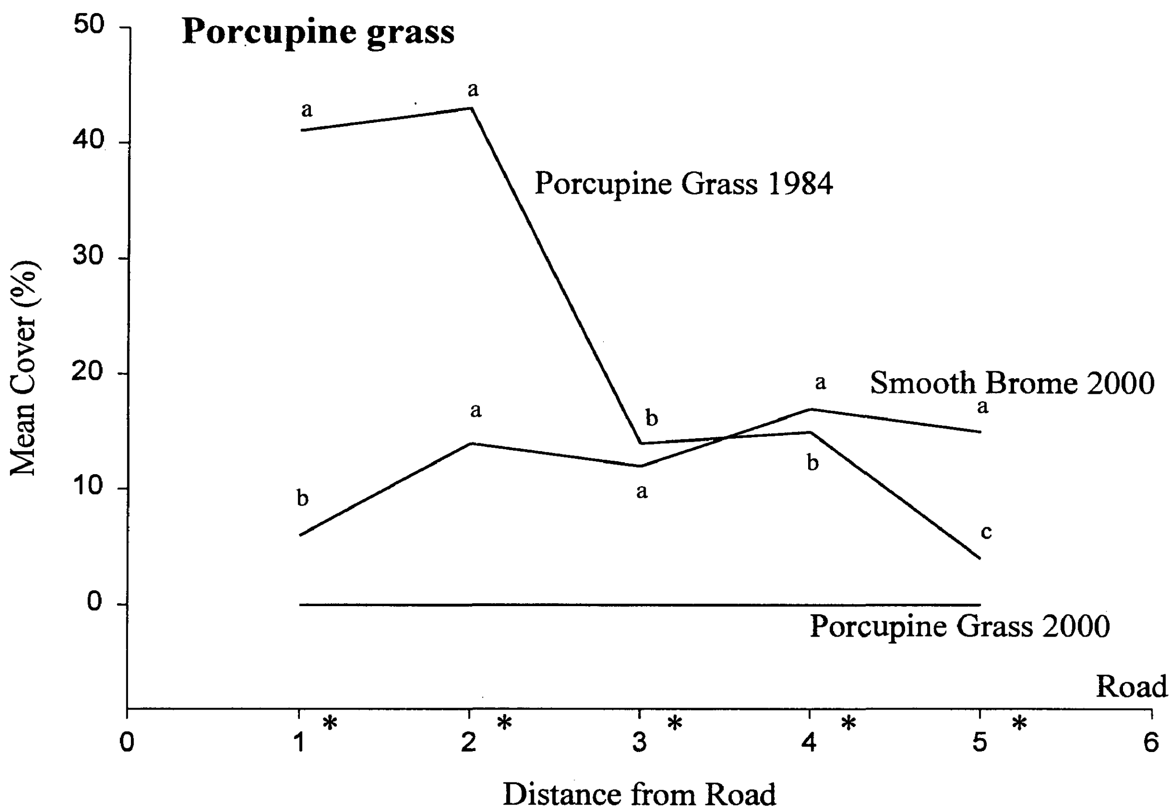

Fig. 3. Mean canopy cover of porcupine grass and smooth brome for 1984 and 2000, by distance from the road. a, b, c = significant differences among distances for the year and season shown; different alphabetic letters differ significantly ($P \leq 0.05$). Distances without letters indicate no significant differences among distances; * = significant difference between 1984 and 2000 based on 2-Factor *t*-Test ($P \leq 0.05$).

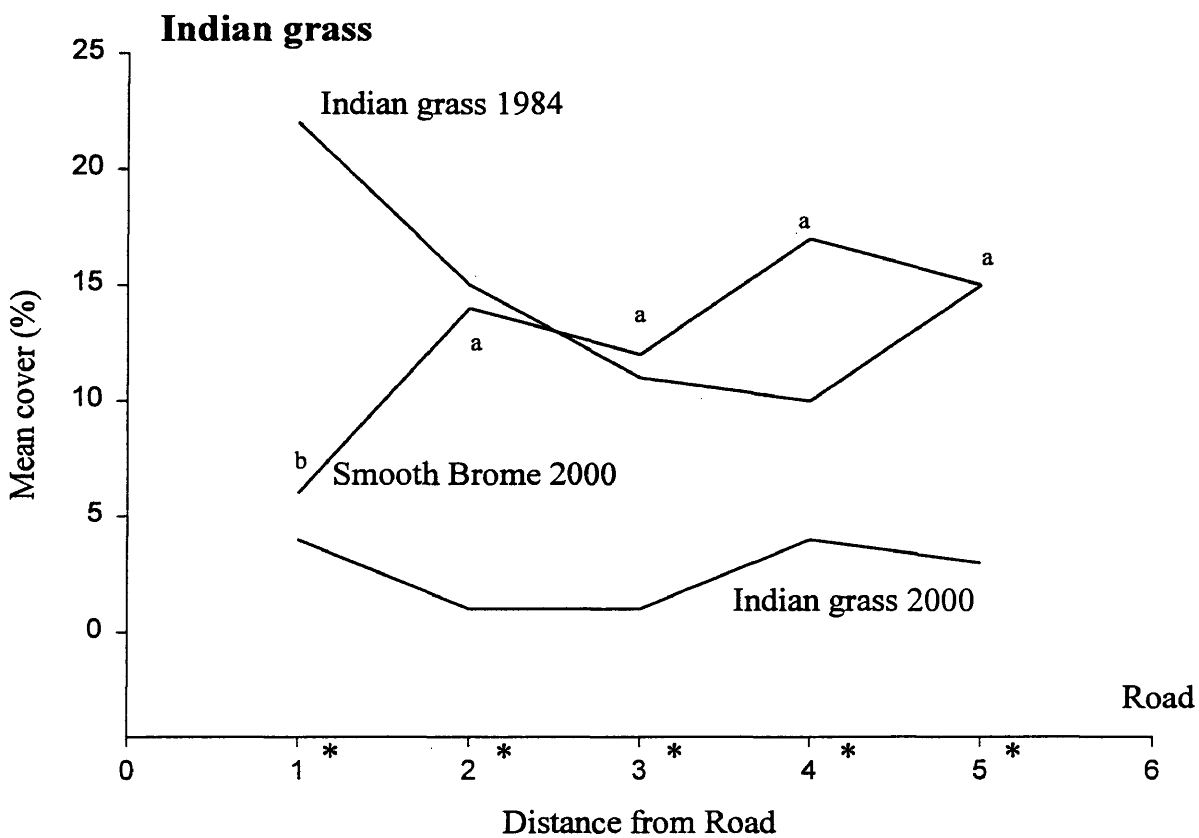

Fig. 4. Mean canopy cover of Indian grass and smooth brome for 1984 and 2000, by distance from the road. a, b, c = significant differences among distances for the year and season shown; different alphabetic letters differ significantly ($P \leq 0.05$). Distances without letters indicate no significant differences among distances; * = significant differences between 1984 and 2000 based on 2-Factor *t*-Test ($P \leq 0.05$).

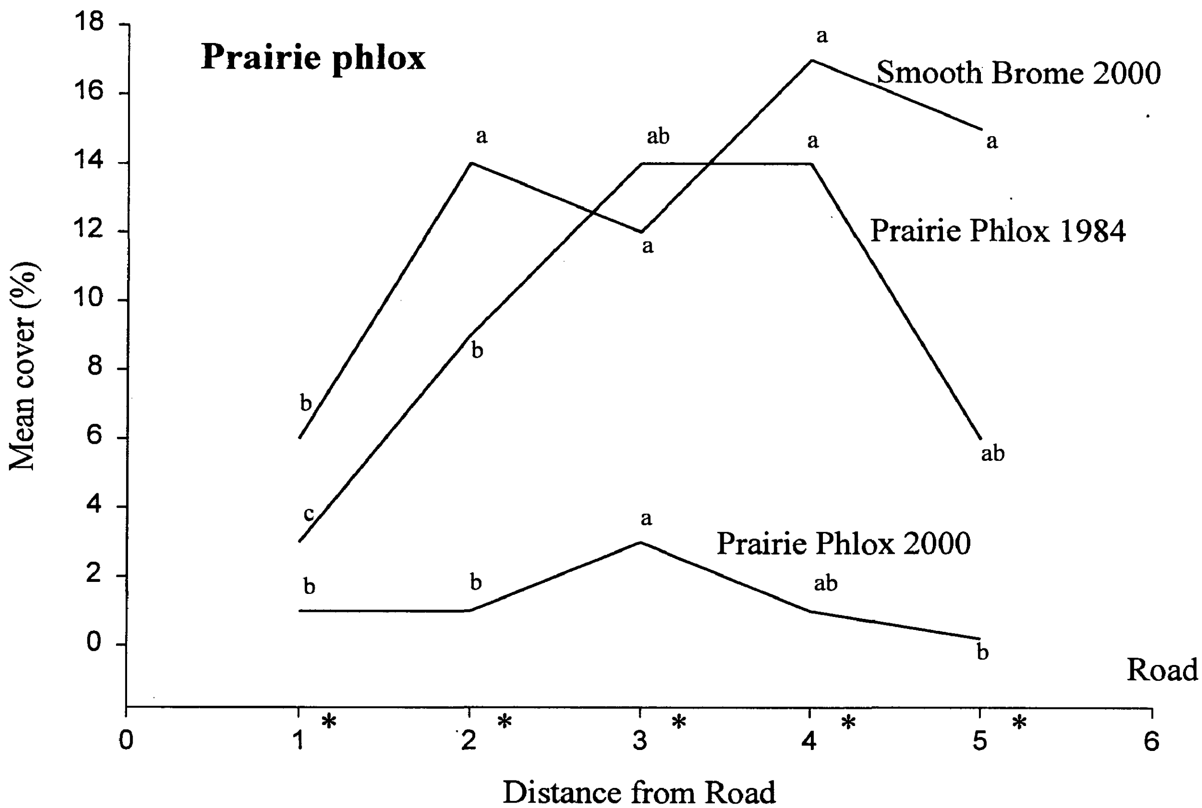

Fig. 5. Mean canopy cover of prairie phlox and smooth brome for 1984 and 2000, by distance from the road. a, b, c = significant differences among distances for the year and season shown; different alphabetic letters differ significantly ($P \leq 0.05$).
* = significant difference between 1984 and 2000 based on 2-Factor *t*-Test ($P \leq 0.05$).

soil (Tables 1 and 3). This decline suggests that short-statured species, such as sideoats grama, may be at risk with significant increases in taller grasses, such as smooth brome, or changes in accompanying microclimate. The reduction in bare soil and increase in litter may be the result of the cessation of mowing management, the increase in smooth brome, or some combination of both. More bare soil in 1984 may also account for the significantly higher amounts of compact stiffstem flax, an annual species, and black-eyed susan, a biennial species which, together, suggest that smooth brome encroachment may affect short-lived, as well as short-statured prairie species.

As previously discussed, Distance 2, and to a lesser extent Distances 3-4, are most likely to reflect any rapid response of a species to smooth brome encroachment. Thus, the significant and substantial decline at Distance 2 of porcupine grass, prairie phlox, compact stiffstem flax, and black-eyed susan (Table 3) suggests that they are among species likely to be most sensitive to smooth brome encroachment or to accompanying microclimate conditions.

The loss of individual plant species and the impact on species diversity also have implications for higher trophic levels, especially invertebrates, although little is known about the life history of many prairie invertebrates. The Regal Fritillary butterfly (*Speyeria idalia* Drury), an indicator species of tallgrass prairie, however, is an exception. Prairie violet (*Viola peditifida*), the principal host plant of its larvae (Huebschmann and Bragg 2000), is among the species that declined significantly in this study (Table 1). This result suggests that smooth brome invasion has the potential to significantly reduce Regal Fritillary populations in tallgrass prairie remnants. In the absence of life-history data, logic suggests that this possibility exists for other invertebrates as well.

Species Increasing.—Four native and two non-native species increased significantly at two or more distances between 1984 and 2000 (Tables 1 and 2). The four native species were all forbs: false sunflower (*Heliopsis helianthoides*), stiff sunflower (*Helianthus rigidus*), clammy ground cherry (*Physalis heterophylla*), and prairie goldenrod (*Solidago missouriensis*). Smooth brome (*Bromus inermis*), a non-native species, was the only graminoid to increase and field bindweed (*Convolvulus arvensis*) was the only non-native forb to do so. The increase in native forbs suggests that there is some subset of tallgrass prairie species that is able to persist in conditions that result from, or that result in, smooth brome encroachment. In this study, the subset consists of species that are strongly rhizomatous.

The significant increase in stiff sunflower, a rhizomatous forb, from its absence in 1984 to an average cover of 25% in 2000 is particularly noteworthy (Fig. 6, Table 3). The absence of this species in 1984 plots is surprising in light of its high cover in 2000 although it is consistent with findings of a 1979 survey where stiff sunflower averaged less than 0.5% cover across the site (Boettcher and Bragg 1989). The uneven distribution of this species across the road-prairie gradient in 2000 is also noteworthy but consistent with the patchy distribution expected of a rhizomatous species. A similar, uneven distribution was noted for prairie goldenrod, another of the species that increased since 1984 (Table 1). Like stiff sunflower, goldenrod is rhizomatous. While both appear to persist with smooth brome, each occupies a slightly different space along the road-prairie

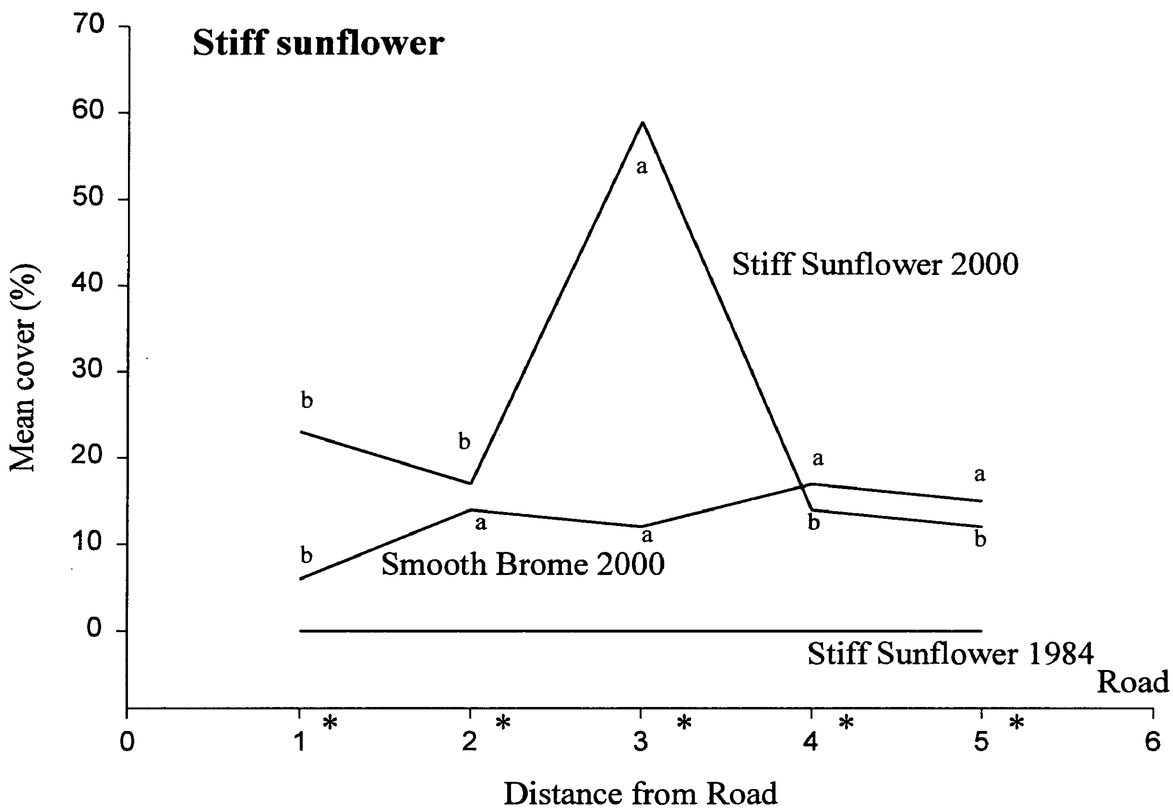

Fig. 6. Mean canopy cover of stiff sunflower and smooth brome for 1984 and 2000, by distance from the road. a, b = significant differences among distances for the year and season shown; different alphabetic letters differ significantly ($P \leq 0.05$). Distances without letters indicate no significant differences among distances; * = significant difference between 1984 and 2000 based on 2-Factor *t*-Test ($P \leq 0.05$).

gradient (Fig. 7). Whether either of these species will persist over a longer period of time is yet to be determined, but the significant decline of false sunflower in Distance 5 (Tables 1 and 3) hints at an answer. Distance 5 is considered to be the distance affected by smooth brome for the longest period of time. Thus, the significant decline of false sunflower at this distance suggests some limit to persistence, at least at the present canopy cover levels.

Neutral Responses.—In addition to species that increase and others that decrease, there are yet other species unaffected by the encroachment of smooth brome. New Jersey tea (*Ceanothus americanus*), a woody, prairie species is one such example (Table 1, Fig. 8). Given the assumption that woody species are long-lived, this lack of response is not unexpected. The absence of any significant decline in this species, however, does not necessarily indicate its long-term persistence. For example, in the absence of the establishment of new individuals, plants lost would not be replaced. Such establishment might have been reflected in an increase in cover during the 16 years of this study. The absence of any such increase could reflect a long-term decline in this species. In addition to New Jersey tea, gray-green wood sorrel (*Oxalis dillenii*), an herbaceous, non-native species, appears ambivalent to any effects of smooth brome (Table 1). While not apparently affected by smooth brome, canopy cover of this species is always at trace-levels.

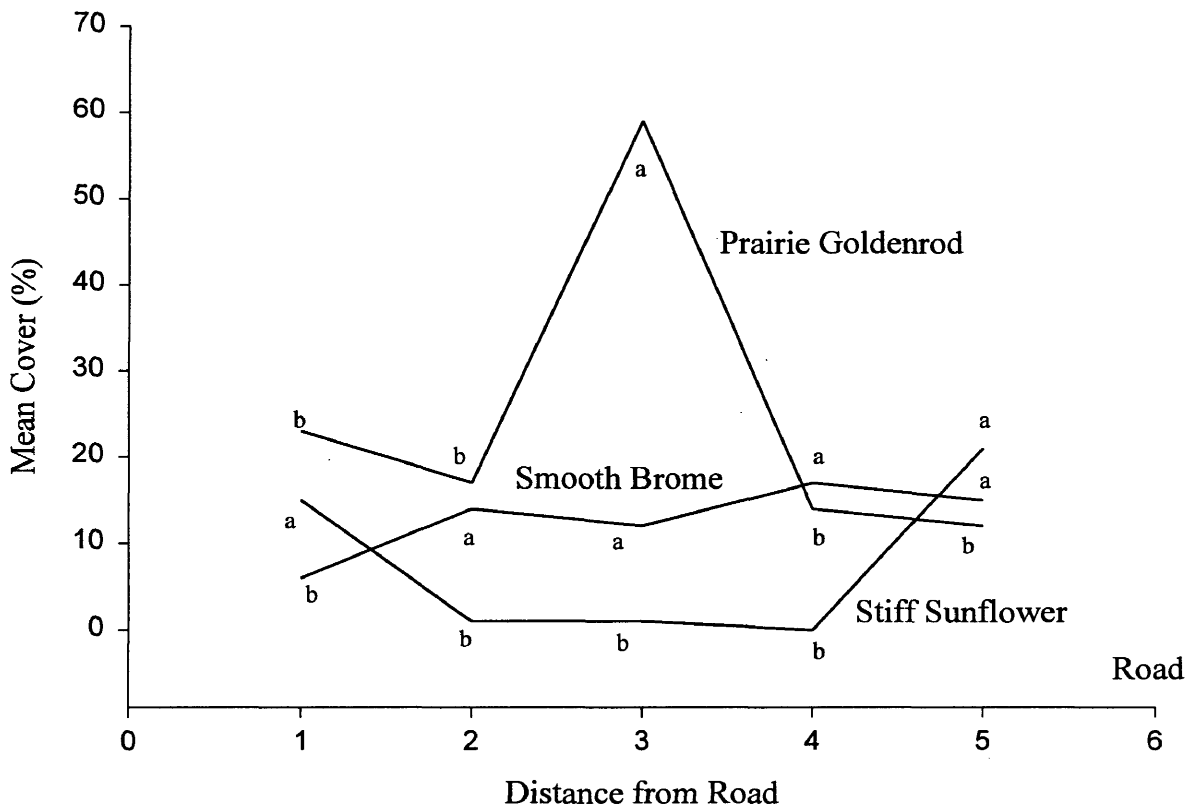

Fig. 7. Mean canopy cover of prairie goldenrod, stiff sunflower and smooth brome for 1984 and 2000, by distance from the road. a, b = significant differences distances for the year and season shown; different alphabetic letters differ significantly ($P \leq 0.05$).
* = significant difference between 1984 and 2000 based on 2-Factor *t*-Test ($P \leq 0.05$).

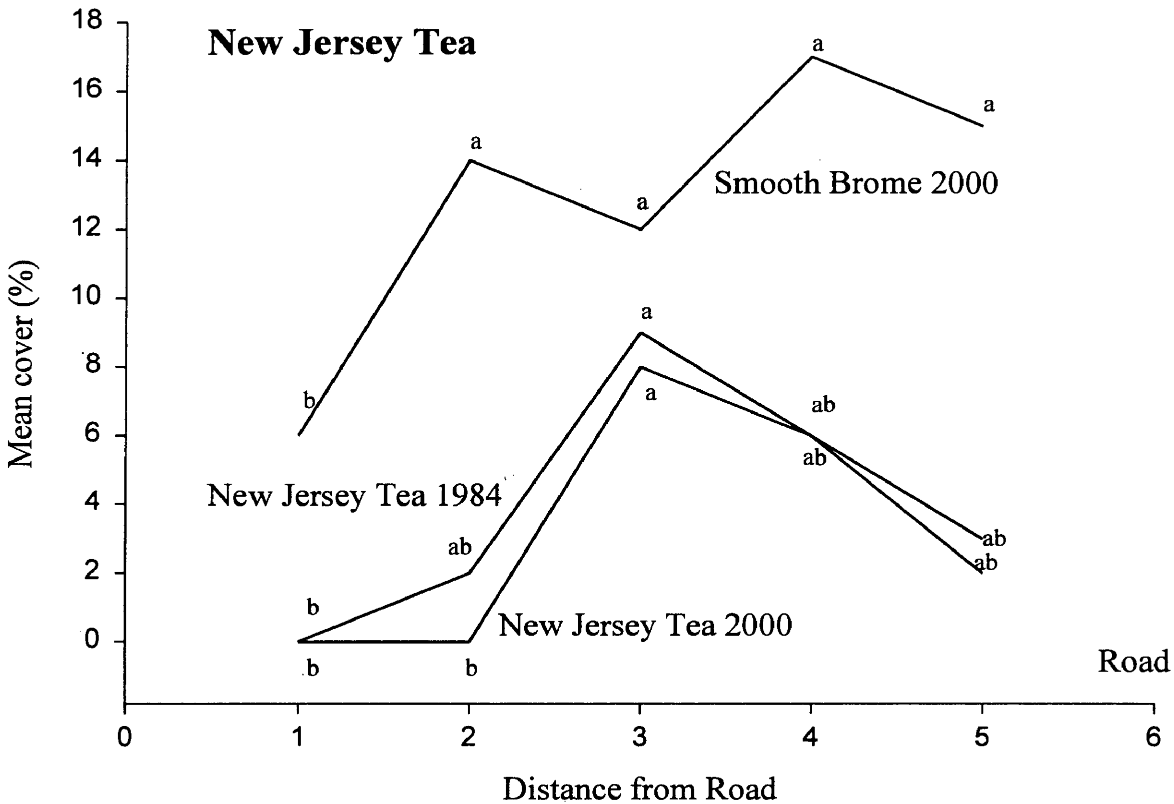

Fig. 8. Mean canopy cover of New Jersey tea and smooth brome for 1984 and 2000, by distance from the road. a, b = significant differences among distances for the year and season shown; different alphabetic letters differ significantly ($P \leq 0.05$); * = significant difference between 1984 and 2000 based on 2-Factor t-Test ($P \leq 0.05$).

Conclusion

The overall results of this study document the encroachment of smooth brome into an unmowed, tallgrass prairie managed with 3-4 year spring burns. Encroachment coincides with the significant reduction in cover or elimination of more prairie species than increase. This is reflected in a decline in species diversity, albeit not one that is significant throughout the prairie. Species lost include some from several functional plant groups, including cool- and warm-season graminoids, annual and perennial forbs and woody plants. Results also suggest that further species loss is likely in response to smooth brome increases or to changes in accompanying environmental conditions. Despite these losses, it appears that a subset of native and non-native species may persist, most of which being strongly rhizomatous. Thus, the net effect of smooth brome invasion may be a prairie in which diversity is diminished below levels normally expected with habitat fragmentation. This potential provides sufficient reason for caution when maintaining tallgrass prairie in which smooth brome is present. To preserve tallgrass prairie communities, there is a need to employ management procedures that minimize the expansion of smooth brome. Such measures would include preventing the use of smooth brome in roadside plantings, especially in areas where native prairie remains, and employing appropriately timed management, such as mowing or fire, to affect some degree of control over this invasive species.

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