Influence of Woody Vegetation on Small Mammals in Tallgrass Prairie

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ABSTRACT.—We examined response of small mammals to woody invasion of tallgrass prairie in northeastern Kansas by sampling sites that ranged from 0 to 100% in woody cover (i.e., frequently burned prairie to unburned closed-canopy gallery forest; woody coverage mapped from satellite imagery). Abundance and biomass of small mammals initially increased with increasing woody vegetation, but then decreased to their lowest level at 100% woody cover. Richness was greatest (an average of seven species) where woody cover was $\leq 17\%$ and decreased to one species where woody cover was 100%. Abundance of white-footed mice (Peromyscus leucopus) increased as woody cover increased from 0 to 62% cover, but decreased in forested sites (100% cover). Abundance of western harvest mice (Reithrodontomys megalotis) decreased as woody cover increased; they were not recorded in forested sites. Deer mice (P. maniculatus) were present in sites with no to low levels of woody vegetation, but were absent in sites with moderate to high levels of woody cover. The 11 species captured were recorded in sites that had little woody vegetation ($\leq 17\%$ cover), whereas only seven species were captured at sites where considerable woody vegetation (≥28% cover) occurred. Even white-footed mice and eastern woodrats, which are considered woodland forms, decreased in abundance or were absent from forested sites. Overall, the results demonstrate that even relatively small amounts of woody vegetation in prairie landscapes can alter abundance, biomass and species richness and composition of small mammal communities.

INTRODUCTION

Tallgrass prairie once covered most of central North America from Canada south to Texas; however, since European settlement, the area occupied by tallgrass prairie has declined (>82%; Samson and Knopf, 1994). The conservation value of the remaining native tallgrass prairie is obvious, but much of the remaining prairie is in danger of being degraded further by human activities. For example, fire suppression and grazing have been linked to expansion of woody vegetation into prairies (Bragg and Hulbert, 1976; Briggs *et al.*, 2002a, b; Knight *et al.*, 1994). Without fire or other management, tallgrass prairie undergoes successional changes that result in an increase in cover of woody vegetation through time and ultimately coniferous or deciduous forests develop (Bragg and Hulbert, 1976; Briggs *et al.*, 2002a; Knight *et al.*, 1994). If fire is suppressed, native tallgrass prairie can be converted to closed-canopy red cedar forest (*Juniperus virginiana*) in as little as 40 y in eastern Kansas (Briggs *et al.*, 2002a). Furthermore, the area of gallery forests expanded more than 50% in tallgrass prairie in northeastern Kansas during 1939–1985 (Knight *et al.*, 1994).

Invasion of woody vegetation, which changes habitat structure, leads to changes in distribution, abundance and occurrence of small mammals in prairie (Horncastle *et al.*, 2005; M'Closkey and Lajoie, 1975; McMillan and Kaufman, 1994; Sietman *et al.*, 1994; Swihart and Slade, 1990). In Oklahoma, invasion by red cedar drastically changed composition of the small mammal community (Horncastle *et al.*, 2005). For example, white-footed mice (*Peromyscus leucopus*) and eastern woodrats (*Neotoma floridana*) responded positively to red cedar invasion, whereas western harvest mice (*Reithrodontomys megalotis*) and

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hispid cotton rats (*Sigmodon hispidus*) responded negatively. The end result was that a change in overstory cover of red cedar from 0 to 40% reduced a species-rich grassland small mammal community into a depauperate one dominated by a single species, the white-footed mouse.

We used Sherman live traps and pitfall traps to sample small mammals on Konza Prairie Biological Station in northeastern Kansas. Woody vegetation in our sampling sites varied from complete absence to closed-canopy forest. We hypothesized that increased woody cover would lead to compositional changes in the small mammal community. We predicted that increased woody cover would increase the abundance of woodland species (*e.g.*, whitefooted mice and eastern woodrats) and reduce the abundance or result in the absence of grassland species [*e.g.*, deer mice (*Peromyscus maniculatus*), western harvest mice and prairie voles (*Microtus ochrogaster*)]. Furthermore, we expected species richness to peak at an intermediate level of woody vegetation owing to the presence of both woodland and grassland species.

METHODS

Study site and sampling locations.—We sampled small mammals from Sep. 1999 through Nov. 2000 on Konza Prairie Biological Station, a 3487-ha tallgrass prairie located in Riley and Geary counties in the Flint Hills of northeastern Kansas ($39^{\circ}05'$ N, $96^{\circ}35'$ W; Marzolf, 1988). Konza Prairie is divided into >50 units that have experimental treatment regimes that consist of a combination of controlled burning (fire return frequencies range from 1 to 20 y) and grazing (grazed by bison or cattle or ungrazed). More than 90% of Konza Prairie is native tallgrass prairie and is dominated by C₄ grasses, such as big bluestem (*Andropogon* gerardii), indian grass (*Sorghastrum nutans*) and switch grass (*Panicum virgatum*; Freeman, 1998). Woody vegetation on the study area, composed almost exclusively of deciduous species, included bur oak (*Quercus macrocarpa*), American elm (*Ulmus americana*), hackberry (*Celtis occidentalis*), honey locust (*Gleditsia triacanthos*), rough-leaved dogwood (*Cornus drummondii*) and smooth sumac (*Rhus glabra*).

Sampling locations, which ranged from grass-dominated sites to closed-canopy forest, were selected to provide a wide range of variation in woody vegetation that could represent grasslands in various stages of woody invasion. We sampled small mammals in three ungrazed prairie treatments: K20A, which was last burned in spring 1991 during a wildfire; K04A, which was last burned in spring 1997; and K02A, which was burned in spring 1998 and again in spring 2000 (Fig. 1). We also sampled in ungrazed forest (AL), which was dominated by bur oak and other deciduous trees, that had not been burned in >20 y. This site was chosen as an end point in the succession of grassland to forest.

Vegetation analysis.—The location of each of 82 sampling stations that we used was determined by using a global positioning system (GPS) and was incorporated into a geographic information system (GIS). Post-processing improved accuracy of the GPS locations. The distribution of woody vegetation was derived in GIS from high-resolution satellite imagery from the IKONOS earth imaging satellite. Satellite images, captured during the period of study, reflected the distribution of woody vegetation within 40 m of each sampling station. Grassland stations were grouped into eight cover categories, each containing nine stations, based on the proportion of woody cover. The first category contained the nine stations with the least woody vegetation, the second category, the nine stations with the 10th to 18th least woody cover, and so forth (Table 1). The 10 sampling stations in the ninth category were located in closed-canopy forest and had 100% woody cover.

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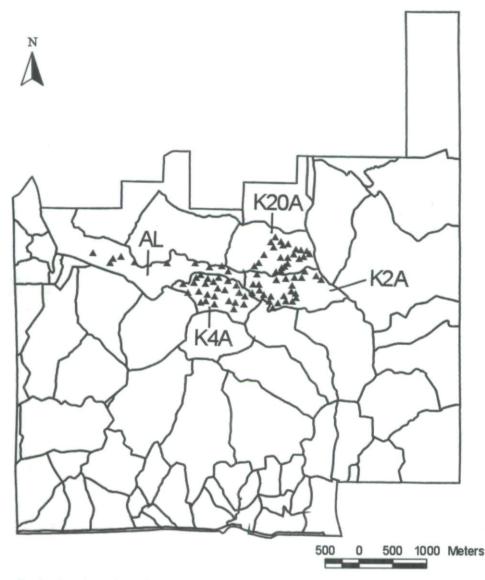


FIG. 1.—Locations of sampling stations (triangles) on Konza Prairie Biological Station, Kansas. The number in the four-digit code indicates fire return frequency in grassland sites (*e.g.*, K04A has fire return frequency of 4 y). All unburned forest sites were located in unit AL

Trapping.—We sampled small mammals every 1–1.5 mo at each of the 82 sampling stations (K02A: 24 stations, K04A: 25 stations, K20A: 23 stations and AL: 10 stations; Fig. 1). In AL, 10 stations were placed in closed-canopy forest where little or no grass understory occurred. Adjacent sampling stations were at least 50 m apart. At each station, we used a trap array that consisted of three pitfall traps and two live traps (Fig. 2). We added pitfalls to the sampling stations because shrews are more likely to be captured in these than in live

Category	% Cover ±1 sp	Range
1	0.0 ± 0.0	0.0-0.0
2	0.0 ± 0.4	0.0-1.3
3	3.8 ± 1.3	1.4-5.4
4	8.1 ± 1.8	5.5-10.7
5	17.4 ± 2.7	13.9-23.1
6	27.8 ± 2.7	23.5-31.4
7	42.0 ± 5.5	34.5-49.5
8	62.4 ± 6.8	54.6-74.5
9	100.0 ± 0.0	100.0-100.0

TABLE 1.—Mean cover of woody vegetation $(\pm 1 \text{ sd})$ within 40 m of a sampling site and the range of cover values observed within each cover category on Konza Prairie Biological Station, Kansas

traps (Briese and Smith, 1974; Williams and Braun, 1983). Three pitfall traps were arranged in an L-shaped array, which had a 2-m long drift fence of aluminum (25 cm tall) between the center pitfall and each of the other two pitfalls; drift fences were buried a few cm into the ground. Pitfall traps, constructed of PVC pipe and caps, were 15 cm in diameter and 25 cm deep. Each pitfall trap had a cover board that closed pitfall traps when not in use and prevented them from filling with water during precipitation events. Cover boards also provided shade for captured animals. At each sampling station, we placed each of two large Sherman live traps ($7.6 \times 8.9 \times 22.9$ cm; H. B. Sherman Traps, Inc., Tallahassee, Florida)

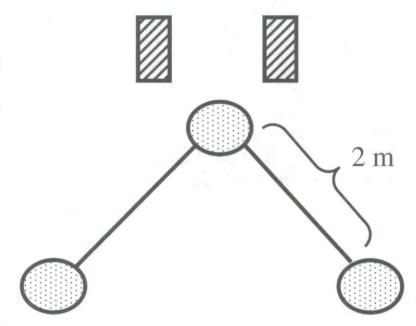


FIG. 2.—Diagram of sampling array that shows the placement of Sherman live traps (hatched boxes) and pitfall traps (stippled circles) used to sample small mammals on Konza Prairie Biological Station, Kansas. Drift fences (solid line) were placed between the central pitfall trap and each of the outer pitfall traps

To identify previously captured individuals, we marked rodents by ear tagging (monel #1005-1 tag; National Band and Tag Co., Newport, Kentucky) and by clipping a patch of fur. We only marked shrews by clipping a patch of fur. We recorded sex and mass (nearest 0.5 g) of captured individuals, but measured length of the hind foot and tail only for *Peromyscus* to aid in their identification. Only the mass of individuals at first capture was used. For four individuals not weighed at first capture, we estimated mass as the average mass of all weighed individuals of the same species. All procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (Protocol No. 1661) and conformed to the "Guidelines for capture, handling and care of mammals" as approved by the American Society of Mammalogists (Animal Care and Use Committee, 1998).

Statistics.—The relationship between abundance, richness and biomass of small mammals captured and proportion of woody vegetation within the nine cover categories was examined by using simple regression (SigmaPlot 8.0; Systat Software Inc., Richmond California).

RESULTS

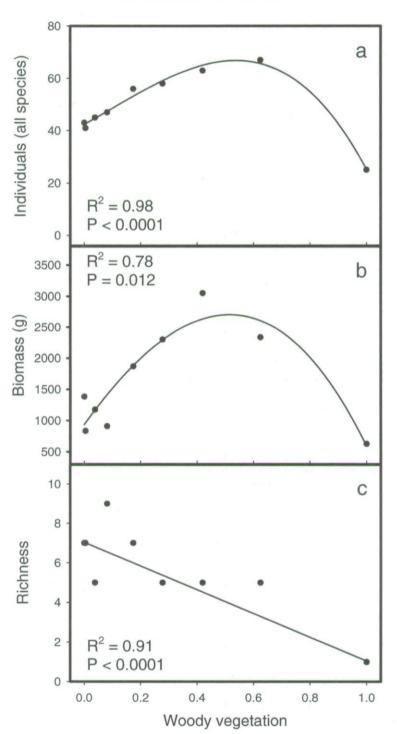
We captured 445 individuals of 11 species during the 15-mo study. The white-footed mouse (225 individuals) was the most abundant species followed by the western harvest mouse (82), hispid cotton rat (45), deer mouse (39), Elliot's short-tailed shrew (*Blarina hylophaga*; 20), and eastern woodrat (17). Species with fewer than 10 individuals captured included the prairie vole (9), least shrew (*Cryptotis parva*; 3), hispid pocket mouse (*Chaetodipus hispidus*; 2), southern bog lemming (*Synaptomys cooperi*; 2), and thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*; 1).

The white-footed mouse accounted for 39% (5525 g) of the total biomass (14,061 g) of small mammals captured, followed by the hispid cotton rat (26%; 3630 g) and eastern woodrat (20%; 2770 g). The western harvest mouse was the second most abundant species, but accounted for only 5% (750 g) of the total biomass. The seven remaining species accounted for only 10% (1386 g) of the total biomass of small mammals.

Small mammal community response.—Numbers of small mammals initially increased with increasing woody cover, but then decreased for forest stations $[y = 42.35 + 59.57x + 32.73x^2 + (-109.49)x^3]$, where y = number of small mammals and x = proportion of woody vegetation; $R^2 = 0.98$, df = 8, P < 0.0001; Fig. 3a]. Total biomass of small mammals also initially increased with increasing woody cover, but decreased as woody vegetation exceeded 42% to a low in the forest stations $[y = 935.56 + 6259.12x + (-4294.18)x^2 + (-2308.87)x^3]$, where y = biomass of small mammals and x = proportion of woody vegetation; $R^2 = 0.78$, df = 8, P = 0.012; Fig. 3b]. Species richness ranged from one to nine for the 10 cover categories and was related negatively in a linear fashion to woody cover [y = 7.03 + (15.99)x], where y = richness of small mammals and x = proportion of woody vegetation; $R^2 = 0.91$, df = 8, P < 0.0001; Fig. 3c]. For example, species richness averaged seven species per cover category for woody cover $\leq 17\%$, but only four species per cover categories for woody cover $\geq 28\%$. The white-footed mouse was the only species captured in stations with 100% woody cover.

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Species responses.—Only two species (the white-footed mouse and eastern woodrat) showed a somewhat positive response to increasing woody cover. White-footed mice, which were captured in every cover category, were most abundant where woody cover was between 42 and 62% (Fig. 4a). Their abundance initially increased with increasing woody cover, but then decreased in closed-canopy forest [$y = 7.77 + 100.39x + 10.39x^2 + (-93.21)x^3$, where y = number of white-footed mice and x = proportion of woody vegetation; $R^2 = 0.88$, df = 8, P = 0.003]. Eastern woodrats were present at stations that occurred in the intermediate woody cover categories, but were absent from sites where woody cover was $\leq 8\%$ and where closed-canopy woodlands occurred (Fig 4b).

Three prairie species (the western harvest mouse, deer mouse and Elliot's short-tailed shrew) tended to show a negative response to increasing proportions of woody cover. Western harvest mice were most abundant in grassland sites that had little woody vegetation and decreased non-significantly to zero, as the cover of woody vegetation increased ($R^2 =$ 0.49, df = 8, P = 0.2; Fig. 4c). Because cover category one was composed of only stations that burned in 1998 and 2000, and because western harvest mice respond negatively to recently burned grasslands (Kaufman et al. 1990), we removed data for cover category one from the analysis and, subsequently, found a strong negative relationship between abundance of harvest mice and proportion of woody cover [y = 16.66 + (-21.12)x], where y = number of western harvest mice and x = proportion of woody vegetation, $R^2 = 0.78$, df = 7, P = 0.009]. The greatest abundance of deer mice occurred in cover category one, those stations burned in 1998 and 2000 (Fig. 4d). Deer mice also were present in the four cover categories that had <20% woody cover, but were absent from sites with moderate to high levels of woody cover. Elliot's short-tailed shrews were absent from only two cover categories (4% and 100%; Fig. 4e). However, abundance of shrews averaged 2.6 individuals where woody cover was $\leq 28\%$, but only 1.3 individuals for the three cover categories where woody vegetation was $\geq 42\%$.

Hispid cotton rats were variably present in the eight lowest cover categories, but always absent in the forest stations (Fig. 4f). Abundance of cotton rats tended to be higher in sites, which had moderate woody invasion (three sites that ranged from 28 to 62% woody cover). Although all cotton rats were captured in non-forest sites, they were present at only 24% of the sampling stations. Furthermore, we found that 64% of the 45 cotton rats were captured at only six stations.

The remaining five species were uncommon and contributed only 4% of all individuals captured. Prairie voles were present in only four cover categories and these had woody cover of $\leq 17\%$. Similarly, least shrews, hispid pocket mice and the thirteen-lined ground squirrel were only present in sites with limited woody invasion (categories with $\leq 8\%$ woody cover). The two southern bog lemmings were captured in cover categories with 8 and 62% woody cover.

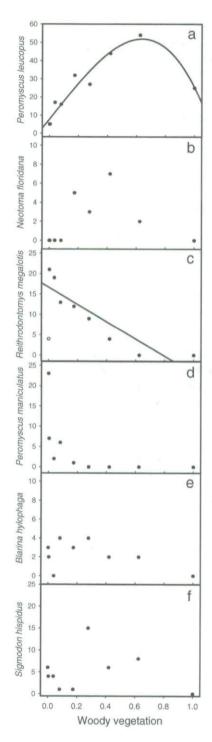
DISCUSSION

Because the tallgrass prairie is one of the most endangered ecosystems in North America (Samson and Knopf, 1994), woody invasion that leads to either deciduous or coniferous forest is of great concern, as it impacts not only plant communities, but also animal

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FIG. 3.—Relationships between the proportion of cover of woody vegetation within 40 m of a sampling station and: a) number of small mammals, b) biomass of small mammals and c) species richness of small mammals captured on Konza Prairie Biological Station, Kansas

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communities. As expected, our results demonstrate that invasion of native tallgrass prairie by woody vegetation, even the early stages of invasion, leads to changes in species richness and composition of the small mammal community. That is, species richness (an average of seven small mammal species) was greatest when woody cover was $\leq 17\%$, but this species-rich community decreased to only one species, the white-footed mouse, in closed-canopy deciduous forest sites. Likewise, where prairie was invaded by eastern red cedar in Oklahoma, a species-rich small mammal community was reduced to one dominated by white-footed mice (Horncastle *et al.*, 2005).

All 11 species captured on Konza Prairie were recorded in prairie sites, which had little woody cover ($\leq 17\%$), whereas only seven of the 11 species were documented at the remaining sites, which had moderate to high levels of woody cover ($\geq 28\%$). We predicted wrongly that the greatest number of species would be found at sites that had intermediate levels of woody vegetation, as we found the highest species richness in sites that had the lowest proportion of woody vegetation. This pattern results from the fact that only a small amount of woody cover is required for woodland forms, such as the white-footed mouse and eastern woodrat, to invade tallgrass prairie, whereas grassland species, such as the western harvest mouse and deer mouse, are influenced strongly and negatively by early stages of woody invasion. Accompanying these changes in species richness, both biomass and abundance of small mammals initially increased with increasing woody cover, but then decreased and were lowest in forested sites. It should be noted that much of the initial increase in abundance and biomass was due to the positive response of white-footed mice to increasing proportions of woody cover.

Positive response to woody invasion.—White-footed mice, the most abundant species captured, initially exhibited a strong positive response to increasing proportions of woody cover, but decreased in abundance in closed-canopy deciduous gallery forest. We predicted that the white-footed mouse would increase with the initial increase in woody cover, as we found. However, we did not foresee the decreased abundance of white-footed mice in closed-canopy forests, as compared to less woody grasslands. A positive association between the white-footed mouse and woody vegetation is well documented (Beckwith, 1954; Clark *et al.*, 1987; Kaufman *et al.*, 2000; Sietman *et al.*, 1994; Swihart and Slade, 1990), and earlier studies on Konza Prairie demonstrated that white-footed mice prefer areas that contain both trees and shrubs, as compared to those with only trees (Kaufman *et al.*, 1983b; McMillan and Kaufman, 1994).

The positive response of the white-footed mouse appears to be influenced by the complexity of the woody vegetation, and not simply by the presence of woody cover. In Ontario, Canada, greater numbers of white-footed mice occurred in brushy areas, as compared to deciduous forests; this result was attributed to the greater vertical complexity of vegetation in brushy areas (M'Closkey and Lajoie, 1975). Furthermore, patch size might influence the abundance of white-footed mice, as higher densities were found in small wooded patches than in large wooded patches in Ohio (Anderson *et al.*, 2003). Most captures of these white-footed mice occurred along the edge of wooded patches where

FIG. 4.—Relationships between proportion of woody vegetation within 40 m of a sampling station and number of: a) *Peromyscus leucopus*, b) *Neotoma floridana*, c) *Reithrodontomys megalotis*, d) *P. maniculatus*, e) *Blarina hylophaga* and f) *Sigmodon hispidus* captured on Konza Prairie Biological Station, Kansas. The significant decrease in abundance of western harvest mice was found when recently burned sites (open circle) were excluded in the regression analysis

structural complexity of vegetation again was greatest. Thus, it seems likely that a decrease in abundance of the white-footed mouse in gallery forest relative to other woody habitats we sampled resulted from a lack of complexity of understory woody vegetation in our forested areas, which were dominated by trees and contained few shrubs. Alternatively, the decreased abundance of white-footed mice in forested stations might have occurred because of the larger patch size of gallery forest in the prairie landscape, as compared to shrub islands that occurred at stations with lower proportions of woody cover.

Eastern woodrats were absent where woody cover was $\leq 8\%$ and where closed-canopy forested sites occurred, but they were captured in all other cover categories. Similar to whitefooted mice, woodrats might prefer woodlands that have a complex vertical structure, but lack a closed canopy. Previously, eastern woodrats were noted to occur more commonly in narrow woodlands associated with limestone outcrops than in gallery forest on Konza Prairie (Beckmann *et al.*, 2002; Kaufman *et al.*, 1993); an association likely driven by greater availability of food and nest sites along wooded limestone outcrops than in gallery forests. Even within forested habitats on Konza Prairie, woodrats selected woodlands that had large shrubs over more open woodlands (McMillan and Kaufman, 1994). Consistent with these responses, we captured woodrats in all woody cover categories that had an abundance of shrubs, but found them absent in closed-canopy woodlands where large shrubs were absent. In mixed grass prairie in northcentral Kansas, eastern woodrats also were more common along edges of woodlands than in the interior of these woodlands (*e.g.*, shelterbelts and gallery forest; Beckmann *et al.*, 2001).

Negative response to woody invasion .- Western harvest mice were most abundant in areas where woody vegetation was absent or nearly so; their abundance decreased as proportions of woody vegetation increased, as we predicted. Abundance of this species in cover categories one and two, those with the lowest woody cover, varied greatly; this difference likely occurred because of the difference in fire history of stations in these two cover categories. In cover category one, all nine sampling stations were burned in 1998 and again in 2000; we captured only four harvest mice at these stations. In contrast, seven of the nine sampling stations in cover category two were left unburned in 1998 and 2000; subsequently, we captured 20 harvest mice at these stations. This difference in abundance between these two cover categories was consistent with the negative response of the western harvest mouse to fire previously found for tallgrass prairie (Clark and Kaufman, 1990; Kaufman et al., 1990). Furthermore, the negative impact of woody invasion on western harvest mice that we observed agrees with previous observations made in wooded habitats on Konza Prairie. That is, western harvest mice comprise <1% of all small mammals in wooded habitats on Konza Prairie (Kaufman et al., 1993); they also are more abundant in open, grassy areas associated with edges of woody habitats than in the wooded habitat itself (McMillan and Kaufman, 1994).

Deer mice were most abundant in sites lacking woody vegetation and were absent from sites that had $\geq 28\%$ woody cover. However, abundance varied greatly between cover categories one and two, those with the lowest proportions of woody cover. All sites in cover category one were burned in 1998 and again in 2000; we captured 23 deer mice at these nine stations. Only two of the nine category two sites were burned in 1998 and 2000 and six of the seven deer mice were captured at these two burned sites. Consistent with our observed patterns, the deer mouse is known to exhibit a strong positive response to fire (Clark and Kaufman, 1990; Clark *et al.*, 1989; Kaufman *et al.*, 1983a, 1988a, b, 1990), and have a strong preference for bare soil and sparse plant litter (Clark *et al.*, 1989; Kaufman *et al.*, 1980; Kaufman, 1990a, b; Kaufman *et al.*, 1988b). Absence of deer mice from sites with moderate

to high levels of woody cover agrees with the documented avoidance of woody vegetation (*e.g.*, mixed grass prairies and croplands in northcentral Kansas: Kaufman and Kaufman, 1990b; Kaufman *et al.*, 2000; tallgrass prairie in southeastern Oklahoma; Clark *et al.*, 1998).

Elliot's short-tailed shrews were captured in seven of eight cover categories that had grassy vegetation, but were absent from sites in closed-canopy woodlands. Short-tailed shrews have been captured in woodland habitats on Konza Prairie in the past (Kaufman *et al.*, 1993). However, these shrews also are a relatively common species in unburned tallgrass prairie where a dead plant litter layer has developed (Clark *et al.*, 1995; Kaufman *et al.*, 1989; Matlack *et al.*, 2002). Although Elliot's short-tailed shrews were relatively uncommon in our sampling, they were twice as abundant at stations that had $\leq 28\%$ woody cover than at stations that had $\geq 42\%$ woody cover, so this result was not unexpected.

Intermediate response to woody invasion.—Hispid cotton rats, which were captured in all cover categories except closed-canopy woodlands, did not exhibit a clear response to changes in woody vegetation. However, cotton rats use a variety of habitats, including grasslands and woodlands, in eastern Kansas (Swihart and Slade, 1990). On Konza Prairie, cotton rats make greater use of grassland habitats, especially those that have tall herbaceous plants (Brillhart et al., 1995), but they are captured in woodland habitats as well (McMillan and Kaufman, 1994). This use of both grassland and shrubby grassland also occurs in mixed grass prairie in Kansas (Kaufman et al., 2000; Kaufman and Kaufman, 2006).

Implications of small mammal responses to woody invasion.-Less than 18% of the historic extent of native tallgrass prairie in North America remains and this large reduction has been due primarily to human activities (Samson and Knopf, 1994). Along with changes in plant communities, small mammal populations and communities have been altered by the production of food on croplands, ranching practices on rangelands and development of urban areas that have fragmented the prairie landscape (Kaufman and Kaufman, 1997). The quality of the remaining prairie is being degraded further by woody invasion owing to fire suppression, and these subsequent changes are altering the structure and function of much of the remaining prairie (Briggs et al., 2002a). The rate at which prairie can be invaded by woody vegetation is alarming (Briggs et al., 2002a; Knight et al., 1994). Our results demonstrate that invasion by even relatively small amounts of woody vegetation can alter abundance, biomass and species richness and composition of small mammals communities in tallgrass prairie. Therefore, conservation and management efforts should be focused on conserving prairie ecosystems, including the prairie small mammal community, at a high quality level by methods (e.g., frequent prescribed fires or mowing) that eliminate woody vegetation or prevent woody invasion.

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