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Small Mammals in Successional Prairie Woodlands of the Northern Great Plains

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Abstract

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Prairie woodlands comprise about 1 percent of the landscape in the northern Great Plains. However, prairie woodlands provide habitat for far more than 1 percent of the wildlife species that occur in the prairie region. With increasing pressures on natural resources, managers need methods for managing wildlife habitat and biodiversity that are based on ecological processes. We studied the small mammals and vegetation in seral stages of four woodland types in central South Dakota. None of the species was restricted to a single seral stage, but abundance of some small mammals varied depending on seral stages of woodland types. To ensure the biodiversity of the prairie, managers should retain all seral stages of all prairie woodlands.

Keywords: small mammals, succession, prairie woodlands, green ash, cottonwood, bur oak, eastern red cedar.

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Mark A. Rumble
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Introduction

Prairie woodlands are an important vegetation community in the northern Great Plains. They occupy about 1 percent of the land area and are restricted to areas of increased soil moisture (Girard and others 1989). The abundance of many birds and mammals would be lower, and some would not exist in the northern Great Plains, without woodlands (for example, Faanes 1984; Kaufman and Fleharty 1974; Knopf 1984; Rumble 1989; Rumble and others 1998; Sieg 1988). Prairie woodlands are used by livestock for forage and shade (Bjugstad and Girard 1984; Severson and Boldt 1978) and provide economic benefits to prairie regions (Bjugstad and Sorg 1985). However, in the northern Great Plains, prairie woodlands are declining due to excessive livestock grazing, insects and disease, changes in climate, construction of livestock ponds, or just old age (Boldt and others 1978; Severson and Boldt 1978).

Fine filter approaches are necessary to conserve some rare species, but are not efficient for conserving biodiversity (Hunter 1991). Coarse filter strategy based on communities will ensure biodiversity for the vast majority of species (Hunter 1991). If lands are to be managed as ecosystems, greater understanding of relations between animal populations and ecological processes in the plant communities is needed.

The relations between small mammals and successional processes in prairie woodlands are not understood. Species diversity and community coefficients for small mammals in riparian woodlands of the prairie can be similar to those in surrounding grasslands (Olson and Knopf 1988). Some small mammals are associated with woodland vegetation in the prairies (for example, Kaufman and Flerhaty 1974; Kaufman and others 1993; Rumble 1989). In western South Dakota, species richness and abundance of small mammals are greater in prairie woodlands than the surrounding grasslands (MacCracken and others 1985a,b; Sieg 1988). Hodorff and others (1988) associated small mammals with the ecological status of prairie woodlands described by the extent of canopy closure. Otherwise, we are unaware of any study associating small mammals with the ecological conditions resulting from succession in prairie woodlands on the Great Plains. Our study investigated the relations of small mammals to seral stages in four woodland types in the northern Great Plains.

Study Area and Methods

Woodland Description

Prior to initiating our study, quantitative classification methods (Uresk 1990) for seral stages of green ash (*Fraxinus pennsylvanica*), cottonwood (*Populus deltoides*), bur oak (*Quercus macrocarpa*), and eastern red cedar (*Juniperus virginiana*) woodlands were developed (unpublished report, Rocky Mountain Research Station, Rapid City, SD). We selected 40 green ash woodlands, 38 cottonwood riparian woodlands, 33 bur oak woodlands, and 25 eastern red cedar woodlands near the Missouri River between Mobridge and Fort Thompson, South Dakota. Our intent in the selection of woodlands was to ensure that the array of seral stages in each woodland type were represented in our sampling. At the time we selected each woodland, we collected the vegetation measurements necessary to classify the seral stage using the quantitative procedures (cited above). These measurements are described below.

Initial site selection was designed to include 10 sites in each seral stage of each woodland type. However, refinements to the classification coefficients after our sites were selected, coupled with uncommon occurrence of some seral stages, resulted in an unbalanced design. Four seral stages were described for green ash, cottonwood, and bur oak woodland types. In green ash woodlands we included 6, 7, 14, and 13 sites in late, late intermediate, early intermediate, and early seral stages, respectively. In cottonwood riparian woodlands, we selected 6, 18, 4, and 9 sites in late, late intermediate, early intermediate, and early seral stages, respectively. In bur oak woodlands, we selected 2, 11, 8, and 12 sites in late, late intermediate, early intermediate, and early seral stages, respectively. In eastern red cedar woodlands only three seral stages were described, and we selected 5, 6, and 14 sites classified as late, intermediate, and early seral stages, respectively.

Green ash woodlands occur in upland drainages and patches where topography or aspect create areas of increased soil moisture (Girard and others 1989; Hansen and others 1984). Green ash often occurs with box elder (*Acer negundo*) and American elm (*Ulmus americana*) as subdominants (Hansen and Hoffman 1988). Common shrubs in the understory of green ash woodlands include common chokecherry (*Prunus virginiana*), Saskatoon serviceberry (*Amelanchier alnifolia*), American plum (*P. americana*), and western snowberry (*Symphoricarpos occidentalis*).

Cottonwood riparian woodlands occur on the floodplains along the Missouri River and its tributaries. Willow (*Salix* spp.) often occurs with cottonwood on early seral sites and green ash is common on late seral sites. Hydrologic and ecological relationships of cottonwood woodlands are described by Johnson and others (1976) and Johnson (1992). Common understory plants include Wood's rose (*Rosa woodsii*), western snowberry, Kentucky bluegrass (*Poa pratensis*), and smooth brome (*Bromus inermis*) (Hansen and others 1984; Hansen and others 1995). However, shrubs in late seral cottonwood can be eliminated by livestock grazing and are replaced with prairie grasses or sagebrush (Hansen and others 1995).

Bur oak in central South Dakota is near the western limit of its range (Johnson 1990). Bur oak woodlands are widely scattered and are not as common as green ash, but they frequently include green ash within stands (Girard and others 1989). Understory shrubs and herbaceous vegetation that occur in green ash woodlands also occur in bur oak woodlands (Girard and others 1989).

Eastern red cedar woodlands exist in scattered stands in the Missouri River basin. Because of its growth form and occurrence in highly eroded and rugged terrain, eastern red cedar woodlands along the Missouri River have been mistaken for Rocky Mountain juniper (*J. scopulorum*). Eastern red cedar hybridizes with Rocky Mountain juniper in this region, and little-seed ricegrass (*Oryzopsis micrantha*) is the dominant understory grass beneath mature stands of both (Girard and others 1989; Hansen and others 1984).

Vegetation Measurements

At the time we selected sites, we established a macroplot (Daubenmire 1952) of 20 x 40 m within the woodland. In a few narrow woodlands, our macroplots were 15 x 40 m or 10 x 40 m to ensure that they were within the woodland. In all woodlands, we recorded the diameter-at-breast height (d.b.h.) of all trees (>2.5 cm d.b.h.) within the macroplot boundaries. In green ash and bur oak woodlands, we estimated percent canopy cover of chokecherry and western snowberry in thirty 0.1-m^2 quadrats (Daubenmire 1959) at 1-m intervals along two transects. In cottonwood riparian woodlands we estimated percent canopy cover (Daubenmire 1959) of western snowberry in 30 quadrats at 1-m intervals along two transects and counted the number of seedlings (<2.5 cm d.b.h.) in two 30- x 1-m belt transects. In eastern red cedar woodlands, we estimated percent canopy cover of little-seed ricegrass (Daubenmire 1959) in 30 quadrats at 1-m intervals along two transects and counted the number of cottonwood seedlings in two 30- x 1-m belt transects. These vegetation measurements were summarized and applied to classification functions to determine the seral stages of woodland in the field.

During the course of our study, we collected additional measurements to characterize the vegetation at each site one time. We estimated percent canopy cover (Daubenmire 1959) of all understory (<1 m tall) vegetation, grasses, forbs, shrubs, and shrub species at 1-m intervals along the two 30-m transects. We recorded the density of vegetation in the intervals 0–0.5 m and >0.5–1.0 m (foliage-height density) as number of contacts on a vertical pole (Noon 1981) at 2-m intervals along the 30-m transects. At the beginning, mid-point, and end of each transect, we recorded overstory cover using a spherical densiometer (Griffing 1985). We estimated the density of shrubs and seedlings not already counted in two 30- x 1-m belt transects.

Small Mammal Trapping

During each year from 1990 to 1992 and between the last week of July and the third week of August, we trapped small mammals four consecutive nights at each site. Small mammal trapping consisted of two trap lines 10 m apart of ten 7.6- x 8.9- x 22.9-cm collapsible Sherman live traps spaced at 5-m intervals. We baited the traps with a commercial bird seed mix in combination with a mixture of peanut butter and rolled oats. Because some woodlands were within 400 m of another, we toe-clipped each animal caught for unique identification. All individuals were released at the capture site.

Data Analyses

We calculated the average for each vegetation measurement for each site. Minor variables, those that occurred on <5 percent of the sites or averaged <1 percent understory canopy cover, were omitted from analyses (Uresk 1990). We calculated measures of vegetation heterogeneity from the coefficients of variation for overstory canopy cover and intervals of foliage-height density (Rotenberry and Wiens 1980).

We estimated small mammal abundance as the average unique captures per night for each site. Small mammal species richness was tallied as the number of species captured on each site during our study. We tested these data for normality and homogeneity of variances using the Kolomogrov-Smirnov Lilliefors test and Levene's test, respectively. These tests were significant for most variables. Therefore, we used a multiresponse permutation procedure (MRPP) (Mielke 1984) to test hypotheses that small mammal abundance did not differ among years. We then used the MRPP test to test hypotheses that small abundance and species richness did not differ among seral stages of woodland types. Statistical tests were considered significant at $\alpha \leq 0.05$; marginal significance was determined at $\alpha \leq 0.10$. Multiple comparison tests were formulated by pair-wise comparisons of seral stages and included a Bonferroni adjustment to the significance levels to maintain Type I error rates. We followed Higgins and others (2000) for scientific names of small mammals and Great Plains Flora Association (1986) for plant names.

Data on small mammal abundance in eastern red cedar were previously summarized in Rumble and Gobeille (1995). These data are included here to present an ecologically based understanding of small mammal relations to succession in prairie woodlands. At the time Rumble and Gobeille (1995) was published, eastern red cedar along the Missouri River was erroneously identified as Rocky Mountain juniper.

Results

Vegetation

In green ash woodlands, percent canopy cover of grasses declined and percent canopy cover of forbs and shrubs increased from early to late seral stages (table 1). Among the shrubs, percent cover of chokecherry and the density of chokecherry >1 m tall but <2.5 cm d.b.h. increased from early to late seral stages, but western snowberry was less abundant in late seral stages than in earlier seral stages. Diameter-at-breast height and basal area of green ash, and percent overstory canopy cover, increased from early to late seral stages.

In cottonwood woodlands the seral stages could be briefly summarized chronologically from many seedlings in the early seral stage to a few large d.b.h. trees in the late seral stage. Cottonwood woodlands frequently included other species of trees as indicated by the difference between cottonwood tree density and total tree density. Willows were common in early to late intermediate seral cottonwood, and some willows were tallied as trees (>2.5 cm d.b.h.). There was little evidence of the widespread flooding that occurred historically and maintained cottonwood woodlands across the flood plains. Early and early intermediate seral stages of cottonwood woodlands occurred in narrow bands (sometimes <10 m wide) along the Missouri River and its tributaries. Western snowberry was the most common shrub in the late seral stage of cottonwood.

Vegetation characteristics in the seral stages of bur oak were similar to those in green ash woodlands. Percent cover of grasses declined from early to late seral stages, while forbs and shrubs increased. Chokecherry cover in the understory and density of chokecherry trees (>2.5 cm d.b.h.) increased from early to late seral stages. Green ash trees were common as subdominants in bur oak woodlands. The basal area, d.b.h., and overstory canopy cover of bur oak and green ash increased from early to late seral stages of bur oak.

Three seral stages occurred in eastern red cedar woodlands. In eastern red cedar, similar to cottonwood, the seral stages were identified by many seedlings in the early seral stage, maturing to fewer larger trees in the late seral stage. The most notable understory characteristic was the increased cover of littleseed ricegrass in the understory as succession progressed from early to late seral stages.

Small Mammals

We captured nine species of small mammals, eight of which were sufficiently abundant to perform statistical analyses; only one thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) was captured. Although total small mammal abundance in 1992 was 40 percent lower than 1990 or 1991, it was not significantly less. Therefore, all subsequent analyses are based on data across years for each site. White-footed mice (*Peromyscus leucopus*) and deer mice (*P. maniculatus*) were the most common small mammals in prairie woodlands.

Green Ash—We found no differences in total small mammal abundance or species richness among seral stages of green ash woodlands (table 2). Abundance of meadow voles (*Microtus pennsylvanicus*) differed among seral stages of green ash ($P \leq 0.04$) in the overall MRPP test; but no significant differences were apparent among seral stages in the Bonferroni corrected multiple comparisons. Significant differences in the MRPP test were most likely from greater abundance of meadow voles in early seral green ash than late intermediate ($P = 0.12$) seral green ash; all other multiple comparisons were not different ($P \geq 0.99$).

Cottonwood—Early seral cottonwood had more ($P = 0.04$) small mammals than late seral stages of cottonwood (table 3). Richness of small mammals in the early and early intermediate seral stages was

Table 1—Vegetative characteristics of seral stages in four prairie woodland types of the northern Great Plains, South Dakota, 1990–1992.

Woodland type vegetation characteristic (units)	Early $\bar{x}$	± SE	Early intermediate $\bar{x}$	± SE	Late intermediate $\bar{x}$	± SE	Late $\bar{x}$	± SE
Green ash								
Percent grass cover	24.7	1.3	15.6	0.8	19.3	2.1	11.2	1.8
Percent forb cover	8.2	.4	11.0	.5	12.5	2.4	11.8	2.1
Percent shrub cover	22.0	1.4	22.4	.8	27.1	2.3	26.5	2.4
Percent chokecherry/plum cover	2.7	.2	8.7	.5	21.2	1.7	16.5	1.3
Percent western snowberry cover	13.3	1.5	7.6	.5	1.6	.3	3.9	.8
Density chokecherry/plum 1–2 m tall (no./ha)	135.0	17.0	370.0	45.0	571.0	77.0	967.0	84.0
Basal area green ash (m^2/ha)	4.2	.2	10.2	.2	10.9	1.1	19.8	1.0
Average d.b.h. green ash (cm)	8.8	.4	9.6	.2	13.4	1.0	18.5	.5
Percent overstory canopy cover	38.3	1.9	63.2	1.1	69.1	3.2	77.1	1.2
Vegetation density <0.5 m (no.)	4.1	.2	2.8	.1	4.3	.5	1.6	.2
Vegetation density 0.51–1.0 m (no.)	2.0	.1	1.9	.1	3.4	.5	1.8	.1
Heterogeneity of vegetation <0.5 m (SE)	1.0	<0.1	1.2	<0.1	1.1	.1	1.6	.1
Heterogeneity of vegetation 0.51–1.0 m (SE)	1.6	.1	1.7	.1	1.5	.1	1.5	<0.1
Heterogeneity of overstory cover (SE)	.8	.1	.4	<0.1	.4	.1	.3	<0.1
Cottonwood								
Percent grass cover	12.1	1.4	8.9	.8	11.0	.5	16.8	1.8
Percent forb cover	14.0	.6	11.6	1.5	13.4	.7	8.7	1.1
Percent shrub cover	12.8	1.5	10.2	2.6	12.5	1.0	17.6	2.1
Percent western snowberry cover	.4	.1	.3	.1	6.9	.9	5.0	.5
Density cottonwood seedlings (no./ha)	52,449.0	4,299.0	1,043.0	215.0	124.0	10.0	2.0	2.0
Density of willow seedlings (no./ha)	61.0	11.0	56.0	18.0	46.0	8.0	8.0	3.0
Density of cottonwood trees	30.0	4.0	2,472.0	96.0	950.0	30 .0	117. 0	9.0
Total tree density (no./ha)	91.0	12.0	2,726.0	1,12.0	1,144.0	32.0	196.0	22.0
Basal area of cottonwood (m^2/ha)	.0	.0	11.4	1.7	17.5	.5	40.2	2.2
Average d.b.h. cottonwood (cm)	1.3	.3	7.6	.5	17.0	.6	67.3	2.1
Percent overstory canopy cover	13.0	1.9	59.2	2.6	58.7	.9	48.5	3.6
Vegetation density <0.5 m (no.)	1.5	.1	1.5	.2	1.6	<0.1	2.3	.1
Vegetation density >0.5–1 m (no.)	2.3	.2	1.2	.2	2.0	.1	1.7	.1
Heterogeneity of vegetation <0.5 m (SE)	1.4	.1	1.3	.1	1.4	.1	.9	<0.1
Heterogeneity of vegetation >0.5–1 m tall (SE)	1.7	.1	1.6	.1	1.4	<0.1	1.4	<0.1
Heterogeneity of overstory cover (SE)	.7	.1	.4	.1	.4	<0.1	.5	.1
Bur oak								
Percent grass cover	31.3	.8	11.2	.8	14.1	.8	1.4	.8
Percent forb cover	7.0	.3	7.1	.6	14.0	.9	26.2	7.7
Percent shrub cover	13.3	.9	20.7	.9	18.3	1.9	22.1	1.5
Percent chokecherry/plum cover	1.5	.2	1.7	.6	4.4	.2	14.1	.1
Percent western snowberry cover	4.3	.4	10.5	.5	7.4	1.3	4.2	.6
Density chokecherry/plum 1–2 m tall (no./ha)	5.0	1.0	14.0	6.0	33.0	3.0	394.0	22. 0
Basal area green ash (m^2/ha)	1.2	.2	3.6	.2	1.5	.5	2.7	.8
Basal area bur oak (m^2/ha)	4.9	.4	16.5	.5	25.0	.7	26.1	1.3
Average d.b.h. bur oak (cm)	7.0	.4	18.1	.4	16.6	1.4	14.0	2.7
Percent overstory canopy cover	26.2	2.4	70.6	1.3	65.5	2.7	83.3	.7
Density vegetation <0.5 m (no.)	5.9	.4	3.0	.1	3.6	.2	.7	<0.1
Density of vegetation >0.5–1 m (no.)	1.2	.1	1.4	.1	1.9	.2	1.6	.4
Heterogeneity of vegetation <0.5 m (SE)	.8	<0.1	1.1	<0.1	1.0	.1	1. 8	.2
Heterogeneity of vegetation >0.5–1 m (SE)	2.3	.1	2.0	.1	1.5	.1	1.5	<0.1
Heterogeneity of overstory cover (SE)	1.2	.1	.4	<0.1	.4	.1	.1	<0.1

(con.)

Table 1—Con.

Woodland type vegetation characteristic (units)	Early		Intermediate		Late	
	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE
Eastern red cedar[a]						
Percent grass cover	41.8	0.8	17.8	1.2	33.6	3.0
Percent forb cover	5.2	.3	6.4	.6	3.4	.6
Percent shrub cover	12.5	.8	30.3	3.0	4.8	.8
Percent little-seed ricegrass cover	3.3	.2	2.9	.6	19.1	1.8
Percent western snowberry cover	4.8	.3	4.1	.7	2.2	.5
Density of eastern red cedar seedlings (no./ha)	327.0	20.0	2,089.0	169.0	528.0	114.0
Basal area eastern red cedar (m^2/ha)	3.8	.3	8.4	.7	17.9	.6
Average d.b.h. eastern red cedar (cm)	9.2	.3	7.6	.4	12.7	.5
Percent overstory canopy cover	19.9	1.4	50.1	3.9	54.0	3.1
Vegetation density <0.5 m (no.)	4.0	.2	4.7	.7	5.2	.2
Vegetation density >0.5–1 m (no.)	2.5	.1	5.3	.9	1.1	.1
Heterogeneity of vegetation <0.5 m (SE)	.9	<0.1	1.3	.1	1.0	<0.1
Heterogeneity of vegetation >0.5–1 m (SE)	1.8	.1	1.4	.1	2.5	.1
Heterogeneity of overstory cover (SE)	1.2	.1	.6	<0.1	.7	.1

[a]Eastern red cedar had three seral stages: early, intermediate, and late.

Table 2—Average ($\bar{x}$ ± SE) abundance of small mammals among seral stages of green ash woodlands along the Missouri River, South Dakota, 1990–1992.[a]

Species	Early		Early intermediate		Late intermediate		Late	
	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE
White-footed mouse	1.46	0.19	1.19	0.13	1.14	0.13	1.53	0.32
Deer mouse	.74	.18	.83	.16	1.14	.35	.46	.07
Meadow vole	.06	.02	.01	.01	.02	.01	.00	
Prairie vole	.11	.04	.08	.07	.14	.12	.00	
Northern pocket gopher	.00		.01	.01	.00		.00	
Hispid pocket mouse	.01	.01	.03	.01	.03	.02	.00	
House mouse	.01	.01	.02	.01	.00		.03	.03
Total small mammals	2.39	.17	2.15	.23	2.47	.44	2.02	.33
Species richness	2.08	.15	1.91	.12	2.12	.14	2.00	.09

[a]Abundance is estimated as average number of unique individuals captured per day over a 4-day trap session.

Table 3—Average ($\bar{x}$ ± SE) abundance of small mammals among seral stages of cottonwood riparian woodlands along the Missouri River, South Dakota, 1990–1992.[a,b]

Species	Early		Early intermediate		Late intermediate		Late	
	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE
White-footed mouse	0.41	0.17A	1.19	0.48AB	1.24	0.18B	0.82	0.24AB
Deer mouse	1.70	.36A	.73	.26ABC	.86	.11B	.25	.07C
Meadow vole	.05	.04	.00		.03	.02	.00	
Prairie vole	.02	.02	.00		<.01	<.01	.00	
Northern pocket gopher	.03	.03	.00		.01	.01	.00	
Hispid pocket mouse	.31	.13	.23	.14	.06	.03	.08	.05
House mouse	.01	.01	.06	.06	.02	.01	.00	
Total small mammals	2.51	.29A	2.25	.47AB	2.23	.23AB	1.15	.25B
Species richness	2.42	.18A	2.33	.14A	2.15	.13AB	1.72	.06B

[a]Abundance is estimated as average number of unique individuals captured per day over a 4-day trap session.
[b]Averages followed by different letters differed ($\alpha \leq 0.05$) among seral stages of cottonwood riparian woodlands, MRPP test.

greater than in the late seral stage ($P \leq 0.05$) of cottonwood. Abundance of white-footed mice was greater ($P = 0.04$) in late intermediate seral cottonwood than early seral cottonwood. Deer mice were marginally more ($P = 0.08$) abundant in early seral stages of cottonwood than late intermediate seral stages of cottonwood and more abundant ($P \leq 0.01$) than in late seral cottonwood; abundance of deer mice in late intermediate seral stages of cottonwood was greater ($P = 0.03$) than in late seral cottonwood. Voles and pocket gophers (*Geomys bursarius*) were uncommon in cottonwood. Although not significant, the abundance of hispid pocket mice was greater in the early and early intermediate seral stages of cottonwood.

Bur Oak—White-footed mice were the only species that differed in abundance among seral stages of bur oak woodlands (table 4). More ($P = 0.02$) white-footed mice occurred in late intermediate and early intermediate ($P \leq 0.01$) seral bur oak than early seral bur oak. Other than white-footed mice and deer mice, small mammals were uncommon in bur oak woodlands.

Eastern Red Cedar—Intermediate seral eastern red cedar woodlands had more ($P \leq 0.03$) small mammals than the early or late seral eastern red cedar woodlands (table 5). Richness of small mammal species in intermediate seral sites of eastern red cedar was marginally greater ($P = 0.06$) than the late seral sites but not different from early seral sites ($P = 0.11$). White-footed mice were more abundant in intermediate seral eastern red cedar woodlands than early seral cedar woodlands. Deer mice were marginally more abundant ($P = 0.09$) in intermediate seral stages than late seral stages and more abundant ($P = 0.02$) than in early seral stages of eastern red cedar. Meadow voles were marginally more abundant ($P = 0.06$) in early seral cedar than intermediate seral cedar or late ($P = 0.04$) seral cedar woodlands.

Discussion

Although abundance of small mammals fluctuated greatly, statistically significant annual differences were not evident. Nonetheless, land managers cannot alter seral stages of woodlands within short time periods to respond to annual fluctuation in abundance. Thus, the annual variation in small mammal populations is largely academic from an ecosystem management perspective across landscapes.

This study and others (Hodorff and others 1988; MacCracken and others 1985b; Rumble 1989; Sieg 1988) suggest that small mammal species richness averages from six to nine species in shrub and woodland habitats in the northern Great Plains. We averaged approximately two species per site across woodland types in our study. The low richness of small mammals among woodland types reflects the relatively few species of rodents that occur in Great Plains woodlands. We did not capture any shrews, but our trapping techniques were not designed to optimize their capture.

Deer mice and white-footed mice were the most abundant among the species of small mammals. While deer mice were most abundant in eastern red cedar, white-footed mice were most abundant in green ash. These species frequently partition habitats at the macrohabitat scale (woodland types) but use similar microhabitats (Ribble and Samson 1987). We found some indication of competitive exclusion between deer mice and white-footed mice. Rank correlation of abundance of these species at sites was significant and negative ($r = -0.2$, $P = 0.05$). In cottonwood, eastern red cedar, and bur oak woodlands, white-footed mice were most abundant in the mid-seral stages. Deer mice tended to decline from early to late seral stages in all woodland types. To tease out microhabitat selection of these species, we conducted canonical correlation

Table 4—Average ($\bar{x} \pm$ SE) abundance of small mammals among seral stages of bur oak woodlands along the Missouri River, South Dakota, 1990–1992.[a,b]

Species	Early		Early intermediate		Late intermediate		Late	
	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE
White-footed mouse	0.38	0.09A	1.28	0.32B	1.04	0.20B	0.83	0.25AB
Deer mouse	.87	.19	.52	.14	.51	.13	.38	.21
Meadow vole	.06	.02	.01	.01	.04	.03	.00	
Prairie vole	.00		.00		.01	.01	.00	
Northern pocket gopher	.04	.02	.03	.03	.00		.00	
Hispid pocket mouse	.06	.03	.00		.03	.02	.04	.04
House mouse	.01	.01	.03	.01	.02	.02	.00	
Total small mammals	1.41	.23	1.86	.29	1.64	.25	1.25	.01
Species richness	2.00	.23	1.69	.10	1.79	.19	1.5	.17

[a]Abundance is estimated as average number of unique individuals captured per day over a 4-day trap session.
[b]Averages followed by different letters differed ($\alpha \leq 0.05$) among seral stages of bur oak woodlands, MRPP test.

Table 5—Average ($\bar{x}$ ± SE) abundance of small mammals among seral stages of eastern red cedar woodlands along the Missouri River, South Dakota, 1990–1992.[a,b]

Species	Early		Intermediate		Late	
	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE
White-footed mouse	0.38	0.09A	1.14	0.25B	0.81	0.19AB
Deer mouse	1.32	.36A	2.59	.19B	1.10	.46A
Meadow vole	.30	.07A	.04	.03AB	.04	.03B
Prairie vole	.02	.02	.16	.09	.08	.05
Hispid pocket mouse	.03	.02	.00		.00	
House mouse	.02	.01	.05	.03	.03	.03
Total small mammals	2.07	.36A	3.99	.11B	2.06	.42A
Species richness	2.08	.14AB	2.57	.11B	2.11	.11A

[a]Abundance is estimated as average number of unique individuals captured per day over a 4-day trap session.
[b]Averages followed by different letters differed ($\alpha \leq 0.05$) among seral stages of eastern red cedar woodlands, MRPP test.

analyses (M. Rumble, Rocky Mountain Research Station, unpublished data) that suggested that while both species occurred together, white-footed mice dominated in woodlands with greater overstory canopy. White-footed mice preferred woodlands with greater canopy cover (Kaufman and others 1983), but Hodorff and others (1988) found both white-footed mice and deer mice to be more abundant in closed canopied green ash in northwestern South Dakota. Deer mice are ubiquitous in their habitats in South Dakota (Higgins and others 2000).

Meadow voles were the third most abundant rodent species captured. They were abundant in eastern red cedar woodlands but were otherwise uncommon. Meadow voles are most often associated with areas of high vegetative cover (Huntly and Inouye 1987), and they also occur in shrublands (Snyder and Best 1988). Meadow voles usually occur in moist meadows, but also inhabit upland grasslands in western South Dakota if sufficient vegetation is present (Jones and others 1983; Sieg 1988). Early seral sites in the woodlands we studied had high cover by grass in the early seral stages that suited conditions for meadow voles.

Prairie voles were common in eastern red cedar woodlands. Upland habitats with sufficient herbaceous cover appear to be the best habitats for this species (Moulton and others 1981). Prairie voles appear to partition habitats with meadow voles to prevent competition where their distribution overlaps (Jones and others 1983). Rank correlation indicated significant negative correlations between the abundance of meadow voles and prairie voles (r = –0.3, $P \leq 0.01$). In eastern red cedar, prairie voles were most abundant in intermediate and late seral stages, but in the deciduous woodlands no patterns could be summarized. Prairie voles were rare in cottonwood and bur oak woodlands.

Hispid pocket mice were most abundant in cottonwood riparian woodlands and they occurred primarily in early and early intermediate seral stages. Hispid pocket mice are associated with upland habitats with bare ground or shortgrass prairie in loamy soils (Jones and others 1983; Moulton and others 1981). Recently deposited sandy soil typical of early and early intermediate seral cottonwood with little understory was most similar to the habitat conditions described for hispid pocket mice.

Management Implications

Prairie woodlands in the northern Great Plains are jeopardized by degeneration and lack of regeneration (Boldt and others 1978). Many formerly high seral stages of green ash and bur oak woodlands have retrogressed to low or low intermediate seral stages due to excessive livestock grazing, disease, or lack of fire (Boldt and others 1978; Sieg 1997; Uresk and Boldt 1986). Many cottonwood riparian woodlands are old (D. Uresk, Rocky Mountain Research Station, Rapid City, SD, personal communication). The late seral cottonwood stands occur across flood plains, but early seral cottonwoods occur in extremely narrow bands along the banks of rivers. Eastern red cedar woodlands, in contrast, are expanding due to lack of fire (Bragg and Hulbert 1976). Although early seral green ash provided habitat for voles and could possibly function as refugia during periods of drought affecting surrounding grasslands, early seral green ash and bur oak resulting from retrogression are not sustainable. A coarse filter approach to landscape management should ensure the array of seral stages in each woodland type.

Woodlands are essential habitat for white-footed mice in the prairie. Late seral green ash and bur oak of sufficient size to establish plots for estimating wildlife abundance were scarce. Early and early intermediate seral cottonwood provided habitat for hispid pocket mice. It is unlikely that the small mammals discussed will become rare in the foreseeable future; however, adopting a coarse filter ecological approach to managing habitat will prevent common species from becoming rare.

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