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Avian Use of Successional Cottonwood (Populus deltoides) Woodlands Along the Middle Missouri River

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ABSTRACT.—Cottonwood (*Populus deltoides*) woodlands are important habitats for birds. Yet, little is known of the relations between bird habitat and succession in these woodlands. We studied the bird community in cottonwood woodlands from early to late seral stages along the Missouri River in central South Dakota from 1990 to 1992 to describe quantitative relations between avifauna and ecological patterns of succession in cottonwood woodlands along the Missouri River. The vegetation in the early seral cottonwood was characterized by a high density of seedlings and saplings that were restricted to narrow bands along the rivers. Late seral cottonwoods were characterized by a few large old trees that extended across the flood plain. Seventy-nine percent of the bird species were woodland obligates. Birds that nest in trees or cavities were the most common, while shrub and ground nesting birds were relatively uncommon. Total bird abundance, species diversity, species richness, richness of woodland obligates, abundance in the tree-nesting guild, abundance in the cavity-nesting guild and abundance in the shrub-nesting guild were greater ($P < 0.01$) in late and late intermediate seral cottonwood stands. Patterns of bird use in cottonwood seral stages by individual species were less evident. Several species were more abundant ($P < 0.08$) in late or late intermediate seral cottonwood and no species were more abundant ($P > 0.10$) in early or early intermediate seral cottonwood. Bell's vireos (*Vireo belli*), indigo buntings (*Passerina cyanea*) and brown thrashers (*Toxostoma rufum*) occurred predominantly in early or early intermediate seral stages, but no significant differences among seral stages were noted. Expanses of late seral cottonwood on flood plains will likely decline because controlled river flows reduce flooding that is necessary for cottonwood regeneration. Cottonwood regeneration was evident only in narrow bands along the river channels. Cavity nesting species will be the most negatively affected by loss of late seral cottonwood.

INTRODUCTION

Riparian woodlands and woodlands that occur in drainages of the northern Great Plains are important vegetative communities (Boldt *et al.*, 1978; Uresk and Boldt, 1986). These prairie woodlands occupy about 1% of the land area and are restricted to areas of increased moisture such as north slopes or drainages or along river systems (Girard *et al.*, 1989). Riparian habitats are important for many wildlife species (Melton *et al.*, 1983; Bjugstad and Girard, 1984), often in a disproportionate manner to the land area occupied (Thomas *et al.*, 1979). Greater vertical structure from trees results in greater species richness and density of passerine birds (Knopf, 1986; Rumble *et al.*, 1998). Whether or not plains cottonwood (*Populus deltoides*) woodlands are important to faunal diversity of the Great Plains depends on historic conditions (*e.g.,* Knopf *et al.*, 1988). In the northern Great Plains, cottonwood riparian woodlands along the Missouri River were established well before the influence of nonnative settlement (Rumble *et al.*, 1998). Cottonwood woodlands also provide economic values to the people in the northern Great Plains through wildlife habitat, shade and forage for livestock and firewood (Bjugstad and Sorg, 1984, 1985).

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Construction of dams on the Missouri River resulted in the direct loss of substantial areas of woodland riparian habitat, primarily the plains cottonwood woodland type. Cottonwood stands, not flooded dams that were constructed, have been affected by the altered hydrologic regimes of the river (Johnson *et al.*, 1976). The stabilized river channel is associated with extensive areas of cultivated flood plain (Bragg and Tatschl, 1977). Cottonwood riparian habitats will decline in the future because flooding that is required for regeneration of cottonwood is now controlled (Johnson, 1992). Early seral and late seral cottonwood woodlands are scarce (Bragg and Tatschl, 1977; Hesse, 1996).

Cottonwood riparian woodlands are important for neotropical migrant birds (Carter and Barker, 1993) and loss of these woodlands will decrease bird populations (Emmerich and Vohs, 1982) and reduce biodiversity (Johnson, 2002). Despite the importance of cottonwood woodlands to humans and wildlife, ecological information is lacking that quantifies the habitat relations of wildlife in the cottonwood riparian woodland. Few studies have evaluated bird communities in cottonwood woodland relative to succession. Emmerich and Vohs (1982) and Sedgwick and Knopf (1990) studied birds in mature cottonwood woodlands and Swanson (1999) studied birds in early seral cottonwood woodlands. However, we are unaware of any studies that attempted to integrate the bird relations among all seral stages of cottonwood woodlands. Federal land managers are required to understand and document the effects of their management on the surrounding environment National Environmental Policy Act of 1969 (Public Law 91-190, http://ceq.eh.doe.gov/nepa/regs/nepa/nepaeqia.htm). Determining management for cottonwood woodlands that is sustainable will require difficult decisions that are based on science. Consequently, our objectives were to describe quantitative relations between avifauna and the ecological patterns of succession in cottonwood woodlands along the Missouri River.

METHODS

Study area.—Cottonwood riparian woodlands occur along the Missouri River and its tributaries on the river floodplain. Spanning a time frame of about 30 y, the structure of these woodlands varies from seedlings and willows (*Salix* spp.) on recently flooded banks and sandbars, to dense sapling stands with co-existing willow and finally to fewer large diameter trees (Bragg and Tatschl, 1977). Green ash (*Fraxinus pennsylvanica*) or other trees will ultimately replace cottonwood (Bragg and Taschl, 1977). Descriptions of hydrologic and ecological relationships in cottonwood woodlands are provided in publications by Johnson *et al.* (1976) and Johnson (1992). Although cottonwood riparian woodlands are a disclimax, their temporal continuity on the landscape and value as a unique forest type for birds warrants description and quantification.

We studied 36 sites in seral stages of cottonwood habitats along the Missouri River between Pierre and Mobridge, SD, during 1990, 1991 and 1992. The seral stages (early, early intermediate, late intermediate and late) were classified using methods described by Uresk (1990) applied to cottonwood woodlands as part of a separate study by other scientists (unpublished seral stage classification for cottonwood, Rocky Mountain Research Station, Rapid City, SD). Our initial goal was to select 10 sites in each of four seral stages. However, final classification analyses for cottonwood resulted in uneven sample size distribution among seral stages with 6 sites in the late seral stage, 18 sites in the late intermediate seral stage, 4 sites in the early intermediate seral stage and 8 sites in the early seral stage (*e.g.*, Rumble and Gobeille, 2001). The center of each site was identified with a metal fence post.

Birds.—We estimated bird abundance at the center of each site using the variable circular-plot technique (Reynolds *et al.*, 1980) for data collection. Bird counts were conducted between sunrise and 1100 hours for three consecutive days constituting one sample session.

In 1990 we were able to complete one sample session between 25 June and 3 July. During 1991–92 we completed three bird count sample sessions between 19 May and 2 July. Subsequent bird count sample sessions were initiated usually within a week of finishing the previous session. However, count sessions at a particular site were separated by approximately 2 wk. Timing of bird counts was scheduled to maximize recording of breeding birds (Robbins *et al.*, 1989). We used five experienced observers that were trained at audio and visual identification of birds and estimating distances (Verner and Milne, 1989) before the study. Counts on individual sites within a bird count sample session were separated by 1 to 5 d. The daily order counts made at study sites and the observer that counted a particular site was rotated to maximize the number of species counted and minimize bias associated with counts (Verner and Milne, 1989). We identified all birds seen or heard during a 5-min interval and recorded species, sex, estimated distance to the bird and whether the bird was in or out of the prairie woodland habitat. We did not count birds when wind speeds exceeded 10 km/h or during rainy weather.

Vegetation.—On each study site we established a 20 × 40 m macroplot in which vegetative characteristics of the site were estimated once during the study. We estimated percent cover (Daubenmire, 1959) of total vegetation, grasses, forbs, shrubs and shrub species at 1-m intervals along two 30-m transects that were spaced 10 m apart. We counted the number of cottonwood seedling/saplings [<2.5 cm diameter-breast-height (dbh)] in two 1 × 30 m belt transects laid out adjacent to the two transects on which vegetative cover was estimated. We counted all trees and snags in the 20 × 40 m plot and recorded species and dbh. On sites where the density of small trees was sufficiently high that keeping track of individuals during counts was difficult, we subsampled either one-half or one-fourth of the macroplot. We estimated overstory canopy cover using a spherical densiometer (Griffing, 1985) at both ends and at the midpoint of transects described above. We measured foliage height density by counting the number of contacts from vegetation on a range pole in 0–0.5 m, 0.5–1 m and 1–2 m intervals [modified from Noon(1981)]. We calculated tree density/ha, tree basal area/ha and the density of small (13 cm–38 cm dbh) or large (>38 cm dbh) snags for each site. Heterogeneity indices were calculated as the standard deviation of measurements taken along transects or at sites.

Regulated water levels in the past resulted in some seral stages being restricted to narrow bands along the river channels. At these sites a 20 × 40 m macroplot would not fit within the seral stage selected, so we used a 10 × 40 m plot and sampled along transects that were 5 m apart.

Analyses.—The analyses below considered the bird count data as fixed-radius plots. The decision for the radius of the fixed-radius plot was made from the variable-radius field data and our experience post hoc. Only birds within 30 m of the count point and within the woodland were included in analyses of bird abundance in this study. Thirty m is an acceptable distance for skilled observers to estimate distance to within ±10%; accuracy declines beyond 30 m (Emlen, 1971; Verner and Ritter, 1988). We did not include observations of flying birds unless they landed in the woodland. We believe estimates of bird abundance in this study are accurate representations of relative use by birds in prairie woodlands along the Missouri River.

Bird species that occurred on ≤4 sites were not included in analyses comparing abundance among seral stages. However, we included all birds observed in woodlands in calculations of guild abundance, species richness and species diversity. Bird species richness was calculated as average number of species observed on a site per sample session (*see* above). We calculated species richness this way to provide an estimate of the number of species that would occur on a given site over a typical 3-d-sampling period for monitoring. Species identified as woodland obligates are from Ehrlich *et al.* (1988). Species diversity was calculated using the Shannon-Weiner formula. Abundance of individual bird species and guilds were averaged for days within sample sessions; sample sessions were averaged within years; and years were averaged for each site. We did not test for differences of bird abundance among sample sessions or years because our objective was to provide managers with habitat associations and short term bird abundances can be affected by factors other than habitat. Thus, our experimental unit was the site.

Results of bird abundance are discussed in terms of nest-substrate guilds (Root, 1967). Members of a particular guild share similar resource requirements, but may differ in other critical resource needs or in their ability to adapt to alterations of resources (Verner, 1984). Thus, managing for an indicator species within a guild may not represent other guild members (DeGraaf and Chadwick, 1984; Block *et al.*, 1987; Bayer and Porter, 1988). We use the guild concept for organizing species responses and abundance in guilds [whole guild concept (Verner, 1984)] and include tree, cavity, shrub and ground nesting guilds. Brown-headed cowbirds were not included in any guilds. Our data rarely adhered to homogeneity of variance and normality assumptions necessary for use of parametric statistics. Consequently, we used a multi-response permutation procedure (Mielke and Berry, 2001) to test differences in distributions of bird abundance, species diversity, species richness and richness of woodland obligates among seral stages. Multiple range tests among seral stages were based on the Peritz closure method (Petrondas and Gabriel, 1983), which maintains the Type I error rates at the specified α-level. P values of individual tests are not possible and significance is determined at the critical α. All tests were conducted using $\alpha = 0.10$. Scientific names of birds are from the American Ornithologist Union (2002) checklist and plant names follow those of the Great Plains Flora Association (1986).

RESULTS

Vegetation.—The following vegetation descriptions of seral stages did not include statistical tests and describe trends in vegetative characteristics among seral stages. Cottonwood woodlands were characterized by bands vegetation in seral stages; early seral stages were adjacent to the river and late seral stages were the farthest from the river on the flood plain. Table 1 includes the metrics for vegetation description of the seral stages of cottonwood woodlands. These seral stages could best be described as a gradation from many cottonwood and willow seedlings (52,428/ha and 61/ha, respectively) in the early seral stage to a few (116/ha) large (67 cm dbh) trees in the late seral stage. A shrub layer, usually comprised mostly of western snowberry, developed beneath the late seral cottonwood stands. Late seral stages of cottonwood extended across the flood plain sometimes for >400 m. The early intermediate and late intermediate seral stages were generally restricted to narrow bands near the river channel. The early seral stage in our study was restricted to drawdown areas resulting from low water levels during a drought in 1988 and 1989. Consequently, some early seral study sites were flooded by high water levels in 1992 and most will be flooded when the river returns to normal or above normal flows. The natural thinning of trees as stands progress from early intermediate to late seral stages resulted in a high density of snags 13–38 cm dbh in the intermediate seral stages. Because large diameter trees primarily occurred in the late seral stage, large snags (>38 cm dbh) were absent or rare in earlier seral stages. The high density of small and medium size trees in early intermediate and late intermediate seral stages resulted in these stages having higher overstory cover. However, there was more heterogeneity in overstory cover (patchiness) in the early and late seral stages. Foliage density <0.5 m was highest in the late seral stage, reflecting the increase of grasses and shrubs beneath stands of large mature cottonwood trees. Foliage density 0.5–1 and 1–2 m reflected the high density of

TABLE 1.—Averages (x̄ ± SE) of vegetative characteristics in cottonwood riparian woodlands along the middle Missouri River, 1990–1992

	Early n = 8		Early intermediate n = 4		Late intermediate n = 18		Late n = 6	
Variables	x̄	± SE	x̄	± SE	x̄	± SE	x̄	± SE
% cover vegetation <1 m tall	47.3	2.2	51.5	5.5	54.6	1.5	79.9	1.8
% grass cover	12.1	1.4	8.9	0.8	11.0	0.5	16.8	1.8
% forb cover	14.0	0.6	11.6	1.5	13.4	0.7	8.7	1.1
% shrub cover	12.8	1.5	10.2	2.6	12.5	1.0	17.6	2.1
% snowberry cover	0.4	0.1	0.3	0.1	6.9	0.9	5.0	0.5
Number of vegetation contacts <0.5 m	1.5	0.1	1.5	0.2	1.6	<0.1	2.3	0.1
Number of vegetation contacts 0.5–<1.0 m	2.3	0.2	1.2	0.2	2.0	0.1	1.7	0.1
Number of vegetation contacts 1.0–2.0 m	1.7	0.2	0.6	0.1	0.3	<0.1	0.2	<0.1
Number of cottonwood seedlings/ac	52,428.2	42,978.0	1042.3	214.9	123.5	9.9	2.5	2.5
Number of chokecherry seedlings/ac	0.0	0.0	0.0	0.0	6.2	1.5	14.6	4.2
Heterogeneity in vegetation <0.5 tall	1.4	0.1	1.3	0.1	1.4	0.1	0.9	<0.1
Heterogeneity in vegetation 0.5–<1.0 m tall	1.7	0.1	1.7	0.1	1.4	<0.0	1.4	<0.1
Heterogeneity in vegetation 1.0–2.0 m tall	1.4	0.2	2.7	0.2	3.2	0.1	2.7	0.4
Number of willow seedlings/ha	61.0	11.1	56.3	18.0	46.2	8.4	8.4	2.5
Number of cottonwood trees/ha	29.6	3.7	2471.4	93.9	949.7	29.4	116.5	8.6
Number of small snags/ha	0.0	0.0	6.2	3.2	52.1	4.4	0.0	0.0
Number of large snags/ha	0.0	0.0	0.0	0.0	0.7	0.2	6.1	2.5
Basal area (m^2)/ha of green ash	0.0	0.0	18.8	9.2	3.9	0.9	5.2	1.3
Basal area (m^2)/ha of cottonwood	0.0	0.0	217.4	33.2	332.6	10.0	766.0	41.9
Dbh of green ash (cm)	0.0	0.0	2.5	0.8	0.8	0.3	5.3	1.3
Dbh of cottonwood (cm)	1.3	0.3	7.6	0.6	17.0	0.5	67.3	2.0
% overstory canopy cover	13.0	1.1	59.2	2.6	58.7	0.9	48.5	3.6
Heterogeneity in overstory canopy cover	0.7	0.1	0.4	0.1	0.4	0.0	0.5	0.1

seedling/saplings in the early seral stage. The late seral stage of cottonwood had little vegetative cover between 1 m and the tree canopy.

Birds.—We observed 71 bird species in the cottonwood woodlands along the Missouri River between 1990–92 (Table 2; scientific names of birds will not be repeated in the text). Fifty-one (79%) species were woodland obligates (*see* Ehrlich *et al.*, 1988). Only 23 species were sufficiently distributed that we could conduct statistical analyses of their abundance among seral stages and, of these, all but the vesper sparrow were woodland obligates.

TABLE 2.—Common name, genus and species and nesting guild of birds seen during counts in cottonwood woodlands along the middle Missouri River, 1990–1992

Common name	Genus and species	Guild[1]
Turkey vulture	*Cathartes aura*	T
Ring-necked pheasant	*Phasianus colchicus*	G
Wild turkey[2]	*Meleagris gallopavo*	G
Killdeer	*Charadrius vociferus*	G
Spotted sandpiper	*Actitis macularia*	G
Upland sandpiper	*Bartramia longicauda*	G
Mourning dove[2]	*Zenaida macroura*	T
Black-billed cuckoo[2]	*Coccyzus erythropthalmus*	S
Yellow-billed cuckoo[2]	*Coccyzus americanus*	S
Short-eared owl	*Asio flammeus*	G
Common nighthawk	*Chordeiles minor*	G
Red-headed woodpecker[2]	*Melanerpes erythrocephalus*	C
Downy woodpecker[2]	*Picoides pubescens*	C
Hairy woodpecker[2]	*Picoides villosus*	C
Northern flicker[2]	*Colaptes auratus*	C
Eastern wood-pewee[2]	*Contopus virens*	T
Empidonax flycatchers[2]	*Empidonax* species	T
Eastern phoebe[2]	*Sayornis phoebe*	T
Say's phoebe[2]	*Sayornis saya*	L
Great crested flycatcher[2]	*Myiarchus crinitus*	C
Eastern kingbird[2]	*Tyrannus tyrannus*	T
Western kingbird[2]	*Tyrannus verticalis*	T
Loggerhead shrike[2]	*Lanius ludovicianus*	S
Bell's vireo[2]	*Vireo bellii*	S
Warbling vireo[2]	*Vireo gilvus*	T
Red-eyed vireo[2]	*Vireo olivaceus*	T
Blue jay[2]	*Cyanocitta cristata*	T
Black-billed magpie[2]	*Pica pica*	T
Tree swallow[2]	*Tachycineta bicolor*	C
Northern rough-winged swallow	*Stelgidopteryx serripennis*	L
Cliff swallow	*Hirundo pyrrhonota*	L
Black-capped chickadee[2]	*Poecile atricapilla*	C
White-breasted nuthatch[2]	*Sitta carolinensis*	C
House wren[2]	*Troglodytes aedon*	C
Eastern bluebird[2]	*Sialia sialis*	C
Veery[2]	*Catharus fuscescens*	G
Wood thrush[2]	*Hylocichla mustelina*	S
American robin[2]	*Turdus migratorius*	T
Gray catbird[2]	*Dumetella carolinensis*	S
Brown thrasher[2]	*Toxostoma rufum*	S
European starling[2]	*Sturnis vulgaris*	T
Cedar waxwing[2]	*Bombycilla cedrorum*	T
Yellow warbler[2]	*Dendroica petechia*	S
Black-throated green warbler[2]	*Dendroica virens*	T
American redstart[2]	*Setophaga ruticilla*	T
Ovenbird[2]	*Seiurus aurocapillus*	G
Common yellowthroat[2]	*Geothlypis trichas*	G
Wilson's warbler[2]	*Wilsonia pusilla*	G
Yellow-breasted chat[2]	*Icteria virens*	S

TABLE 2.—Continued

Common name	Genus and species	Guild[1]
Eastern towhee[2]	*Pipilo erythrophthalmus*	G
Chipping sparrow[2]	*Spizella passerina*	G
Field sparrow[2]	*Spizella pusilla*	G
Vesper sparrow[2]	*Pooecetes gramineus*	G
Lark sparrow[2]	*Chondestes grammacus*	S
Lark bunting	*Calamospiza melancorys*	G
Grasshopper sparrow	*Ammodramus savannarum*	G
Song sparrow[2]	*Melospiza melodia*	G
Chestnut-collared longspur	*Calcarius ornatus*	G
Rose-breasted grosbeak[2]	*Pheucticus ludovicianus*	T
Black-headed grosbeak[2]	*Pheucticus melanocephalus*	T
Blue grosbeak[2]	*Guiraca caerulea*	T
Indigo bunting[2]	*Passerina cyanea*	S
Dickcissel	*Spiza americana*	G
Red-winged blackbird	*Agelaius phoeniceus*	S
Western meadowlark	*Sturnella neglecta*	G
Brewer's blackbird[2]	*Euphagus cyanocephalus*	G
Common grackle[2]	*Quiscalus quiscula*	T
Brown-headed cowbird[2]	*Molothrus ater*	P
Orchard oriole[2]	*Icterus spurius*	T
Baltimore oriole[2]	*Icterus galbula*	T
American goldfinch	*Carduelis tristis*	T

[1] Guild symbols – T = tree nesting; C = cavity nesting; S = shrub nesting; G = ground nesting; L = ledges, cliffs, or crevices; and P = nest parasite

[2] Indicates birds that are woodland obligates from Ehrlich *et al.* (1988)

When averaged across all seral stages, we observed more ($P < 0.10$) tree nesting birds/site ($\bar{x} \pm \text{SE} = 3.9 \pm 0.4$) than birds in other nesting guilds. The second most abundant guild was the cavity nesting guild ($\bar{x} \pm \text{SE} = 3.2 \pm 0.7$ birds/site). Abundance of birds in the shrub and ground nesting guilds were similar ($\bar{x} \pm \text{SE} = 0.8 \pm 0.1$ and 0.8 ± 0.2 birds/site, respectively) among sites.

Bird species diversity was higher ($P \leq 0.10$) in the late and late intermediate seral stages than in the early seral cottonwood (Table 3). Bird species richness and richness of woodland obligates were greater ($P \leq 0.10$) in late and late intermediate seral cottonwood stands than early intermediate or early seral cottonwood. Total bird abundance differed only between early and late seral cottonwood ($P < 0.10$). Early and early intermediate seral cottonwood had less than half as many birds as the late-intermediate seral stage of cottonwood, but did not differ in total bird abundance ($P > 0.10$). Brown-headed cowbirds occurred in all seral stages and their abundance did not differ among seral stages despite appearing to have greater abundance in early intermediate and late intermediate seral stages ($P > 0.10$).

Bird abundance in the tree-nesting guild was greater ($P < 0.10$) in late and late intermediate seral stages than the early seral stage of cottonwood. However, abundance of some species of tree nesting birds was variable and statistical trends were not evident. For those species that exhibited differences among seral stages, abundance was usually greater in the late or late intermediate seral stages than early intermediate or early seral stages. However, orchard orioles were most abundant in the late intermediate and early intermediate seral stages followed by the late seral stage.

TABLE 3.—Bird species abundance (birds/ha) and diversity indices among seral stages of cottonwood riparian woodlands along the Missouri River, South Dakota 1990–92[1]

Guild/Species[2]	Early		Early intermediate		Late intermediate		Late	
	x̄ ±	SE	x̄ ±	SE	x̄ ±	SE	x̄ ±	SE
Tree nesting species								
Mourning dove	0.02	0.01A	0.10	0.03AB	0.55	0.15B	0.66	0.32B
Western kingbird	0.00		0.00		0.22	0.13	0.00	
Eastern kingbird	0.65	0.28	0.52	0.27	1.06	0.20	1.31	0.48
Blue jay	0.00		0.23	0.19	0.22	0.07	0.74	0.56
American robin	0.00		0.10	0.10	0.29	0.12	0.15	0.08
Warbling vireo	0.00A		0.07	0.07AB	0.34	0.14A	0.07	0.04AB
Black-headed grosbeak	0.22	0.07	0.53	0.17	0.27	0.07	0.41	0.24
Common grackle	0.03	0.03	0.16	0.10	0.16	0.10	0.00	
Orchard oriole	0.02	0.02A	0.49	0.22B	0.50	0.14B	0.26	0.15AB
Northern oriole	0.12	0.10A	0.36	0.11B	0.60	0.15BC	0.98	0.22C
American goldfinch[3]	0.24	0.14	0.39	0.39	0.03	0.02	0.00	
Tree nesting guild	1.93	0.75A	2.58	0.56AB	4.65	0.57B	5.08	1.08B
Cavity nesting species								
Downy woodpecker	0.00A		0.03	0.03A	0.39	0.26B	0.07	0.07AB
Red-headed woodpecker	0.00A		0.00A		0.05	0.02A	0.59	0.38B
Northern flicker	0.00		0.20	0.20	0.33	0.10	0.39	0.19
Black-capped chickadee	0.03	0.03	0.33	0.20	0.15	0.07	0.22	0.13
House wren	0.19	0.07A	0.82	0.29B	3.44	0.94B	3.10	0.75B
Cavity nesting guild	0.27	0.08A	1.21	0.25B	4.37	1.20B	4.98	1.27B
Shrub nesting species								
Brown thrasher	0.06	0.03	0.00		0.08	0.05	0.07	0.07
Bell's vireo	0.00		0.00		0.01	0.01	0.02	0.02
Yellow warbler	0.05	0.05A	0.00A		0.20	0.10AB	0.44	0.18B
Indigo bunting	0.03	0.03	0.03	0.03	0.17	0.11	0.02	0.02
Shrub nesting guild	0.11	0.05A	0.75	0.29B	1.07	0.17B	1.27	0.52B
Ground nesting species								
Eastern towhee	0.03	0.03	0.36	0.21	0.11	0.07	0.13	0.11
Common yellowthroat	0.17	0.15	0.10	0.10	0.15	0.08	0.00	
Vesper sparrow	0.03	0.03	0.00		0.13	0.07	0.24	0.19
Lark sparrow	0.39	0.17	0.23	0.13	0.15	0.08	0.70	0.44
Ground nesting guild	0.76	0.27	0.75	0.30	0.65	0.22	1.35	0.56
Brown-headed cowbird[4]	0.23	0.07	0.43	0.38	0.47	0.18	0.11	0.06
Total bird abundance	3.07	0.61A	5.3	0.79AB	10.75	1.53B	12.68	2.47B
Bird species diversity	2.32	0.22A	3.01	0.17AB	2.96	0.10B	3.19	0.12B
Bird species richness	4.47	0.30A	5.11	0.74B	8.04	0.58B	10.72	0.94B
Woodland bird richness	3.29	0.30A	4.81	0.83A	7.55	0.59B	9.58	0.83B

[1] Averages followed by different letters differed ($\alpha \leq 0.15$) among seral stages of cottonwood riparian woodlands, MRPP test

[2] Categories for guilds include all bird species observed within 30 m of the census point in the cottonwood woodlands

[3] Significant in overall test, but no differences were found in multiple comparisons

[4] Brown-headed cowbirds parasitize nests of other birds

Red-headed woodpeckers were abundant ($P < 0.10$) only in late seral cottonwood and were absent from early intermediate or early seral cottonwood stands. Downy woodpeckers were more ($P < 0.10$) abundant in the late intermediate seral stage than early or early intermediate seral stage. Downy woodpeckers were absent from early seral cottonwood and occurred in only one late seral cottonwood site. Abundance of house wrens was greater ($P < 0.10$) in early intermediate through late seral cottonwood than the early seral stage. Abundance of birds in the cavity-nesting guild was greater ($P < 0.10$) in the late seral stage than early intermediate or early seral stages and abundance of cavity nesting birds was also greater ($P < 0.10$) in the late intermediate sites than early seral sites.

Only three species of shrub nesting birds were sufficiently distributed to enable statistical tests. Although differences were not apparent, brown thrashers were uncommon and sporadically observed in other than the early seral stage. Abundance of yellow warblers differed among seral stages ($P = 0.08$), but no significant differences were apparent in the multiple range tests. Abundance in the shrub-nesting guild did not differ among early intermediate through late seral cottonwood, but was greater ($P < 0.01$) than in the early seral stage. No differences in abundance of birds in the ground-nesting guild were observed among seral stages.

DISCUSSION

In the absence of flooding, cottonwood is seral community of green ash (*Fraxinus pennsylvanica*) in the northern Great Plains (Hansen *et al.*, 1984). Increased occurrence of green ash in the late seral cottonwood supports the interpretation of Hansen *et al.* (1984). The cottonwood sites we studied have persisted for >60 y and the wildlife community associated with them differs from that in green ash woodlands (*see* Rumble and Gobeille, 1998, 2001). Historically, these areas would have been maintained as cottonwood because of reoccurring floods. Since dams were constructed in the 1950s, suitable conditions for reproduction of cottonwoods (*e.g.,* Johnson, 2000) occur only in very narrow bands adjacent to river channels. Without periodic flooding or other management, cottonwood woodlands will disappear or become green ash woodlands with a resulting loss of the associated wildlife community.

Vertical structure in vegetation communities results in greater bird diversity (MacArthur and McArthur, 1961). In cottonwood woodlands, the tree canopy was the primary source of habitat structure. Consequently, most of birds in cottonwood woodlands were obligates to the habitat created by these trees. Thus, the most abundant birds in cottonwood woodlands were tree nesting species. Shrub and ground nesting species comprised <30% of the bird species and <20% of bird abundance in cottonwood woodlands. In the northern Great Plains, the vegetation structure from various woodland types provides habitat for a large number of bird species (Emmerich and Vohs, 1982; Faanes, 1984; Hodorff *et al.*, 1988). Thus, the occurrence and abundance of birds in prairie woodlands is greater than in the surrounding grasslands (Faanes, 1984; Sieg, 1991) and tree plantings in shelterbelts cannot replace native cottonwood woodlands as bird habitat (Emmerich and Vohs, 1982).

Cottonwood woodlands are important for cavity nesting birds in the northern Great Plains. Although statistical patterns were not evident for some species, the trends observed in the cavity-nesting guild are likely representative of the expected patterns among seral stages of cottonwood. Cavity nesting birds depend on trees for nest habitat and cottonwood woodlands supported more cavity nesting birds than green ash, juniper (*Juniperus* spp.) or bur oak (*Querecus macrocarpa*) woodlands (Rumble and Gobeille, 1995, 1998; unpubl., Rocky Mtn. Res. Stn., Rapid City, SD). The density of secondary cavity nesting species, such as house wrens, is determined largely by primary cavity nesting species (Sedgwick and Knopf, 1992). Our data suggest that the loss of late seral cottonwood will reduce abundance of primary and secondary cavity nesting birds along the Missouri River. Sedgwick and Knopf (1990) predicted a decline in cavity nesting birds due to lack of cottonwood regeneration along the South Platte River. We predict a similar situation when the late seral cottonwoods die off. Other prairie woodland habitats cannot replace late and late intermediate seral cottonwood for cavity nesting birds. To support similar numbers of downy woodpeckers would require an area of early intermediated green ash 13 times greater than that of late seral cottonwood (Rumble and Gobeille, 1998; this study). Similarly, it would require 3.5 times more early intermediate green ash to provide for similar numbers of red-headed woodpeckers as late seral cottonwoods. However, early intermediate green ash woodlands arising from retrogression (loss of shrub community and lack of regeneration) of late seral green ash is not sustainable (Rumble and Gobeille, 1998). These conditions in early intermediate green ash woodlands result from overgrazing or disease (Boldt *et al.*, 1978). In addition, our data suggest that twice as much late seral green ash would be required to provide similar for numbers of house wrens as occurred in late seral cottonwood.

Cottonwood riparian woodlands also provided habitat for bird species that were rare in the other woodland types. Species that are uncommon to rare in South Dakota such as Bell's vireo, American redstart and ovenbirds occurred in habitats similar to early intermediate cottonwood elsewhere along the Missouri River (Swanson, 1999). These species also occurred in low abundance in our study.

Late seral cottonwood habitats are approaching the end of their life expectancy along many rivers and riparian areas in South Dakota. Few areas of early seral cottonwood, indicative of regeneration, occur. Poor seedling establishment and senescence of old cottonwood stands will eventually lead to the loss of most cottonwood riparian habitats (Johnson, 1992; McDonald and Sidle, 1992; Snyder and Miller, 1992). Loss of late seral cottonwood woodlands will occur first and represent the loss of very valuable bird habitat that may also be important in the management of neotropical migrants (Carter and Barker, 1993). We concur with Emmerich and Vohs (1982) that other woodland types such as green ash cannot replace the cottonwoods as bird habitat. Cottonwood woodlands are the only woodland type along the Missouri River in which abundance of brown-headed cowbirds was not related to abundance of other birds (unpubl., Rocky Mtn. Res. Stn., Rapid City, SD), suggesting that cowbirds were not effective nest parasites in this woodland type.

MANAGEMENT IMPLICATIONS

The plains cottonwoods along the major rivers and tributaries of the northern Great Plains are important to the biodiversity of this region (Johnson *et al.*, 1976; Reily and Johnson, 1982; Johnson, 1992; McDonald and Sidle, 1992; Snyder and Miller, 1992). Cottonwood woodlands provided habitat for different bird community than green ash woodlands (Rumble and Gobeille, 1998). The cavity nesting guild in cottonwood woodlands was more abundant than in other woodland types in this region. The prognosis is that cottonwood woodlands will decrease in abundance and distribution, while green ash woodlands will increase (Johnson, 1992). Our study revealed evidence of successional trends toward green ash replacing cottonwood woodlands along the Missouri River. We observed a lack of cottonwood regeneration and, by far, the largest expanses of cottonwoods were associated with the late seral stage. Along the upper Missouri River and its tributaries, the only representation of cottonwood woodlands will be the narrow bands along the river channels if the large gallery forests on the floodplain are lost. Thus, substantial woodland habitat will be lost. Mitigation that includes planting green ash cannot replace cottonwood woodlands on a one-for-one area basis for all bird species.

Creative methods for regenerating the cottonwood forests will be necessary to maintaining the avian habitat provided by these woodlands. Many of the trees in late seral cottonwood were >80 y old during our study, suggesting that many late seral cottonwood woodlands may be near the terminal end of their occurrence. The effectiveness of selective irrigated flooding, mechanical scalping, pitting or beavers for regenerating cottonwoods in tributaries of the Missouri needs investigation. Timing and sequence of planting male and female cottonwood trees to ensure new regeneration and the effectiveness of such treatments also need investigation.

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Errata

Table 1, page 169, from Rumble and Gobeille, Avian Use of Successional Cottonwood (*Populus deltoids*) Woodlands Along the Middle Missouri River, Vol.152 No.1, 2004, has an error in Basal area (m^2)/ha of cottonwood. The corrected table is presented below

Table 1.—Averages ($\bar{x}$ ± SE) of vegetative characteristics in cottonwood riparian woodlands along the middle Missouri River, 1990–1992

	Early n = 8		Early intermediate n = 4		Late intermediate n = 18		Late n = 6	
Variables	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
% cover vegetation <1 m tall	47.3	2.2	51.5	5.5	54.6	1.5	79.9	1.8
% grass cover	12.1	1.4	8.9	0.8	11.0	0.5	16.8	1.8
% forb cover	14.0	0.6	11.6	1.5	13.4	0.7	8.7	1.1
% shrub cover	12.8	1.5	10.2	2.6	12.5	1.0	17.6	2.1
% snowberry cover	0.4	0.1	0.3	0.1	6.9	0.9	5.0	0.5
Number of vegetation contacts <0.5 m	1.5	0.1	1.5	0.2	1.6	<0.1	2.3	0.1
Number of vegetation contacts 0.5–<1.0 m	2.3	0.2	1.2	0.2	2.0	0.1	1.7	0.1
Number of vegetation contacts 1.0–2.0 m	1.7	0.2	0.6	0.1	0.3	<0.1	0.2	<0.1
Number of cottonwood seedlings/ha	52,428.2	42,978.0	1042.3	214.9	123.5	9.9	2.5	2.5
Number of chokecherry seedlings/ha	0.0	0.0	0.0	0.0	6.2	1.5	14.6	4.2
Heterogeneity in vegetation <0.5 tall	1.4	0.1	1.3	0.1	1.4	0.1	0.9	<0.1
Heterogeneity in vegetation 0.5–<1.0 m tall	1.7	0.1	1.7	0.1	1.4	<0.0	1.4	<0.1
Heterogeneity in vegetation 1.0–2.0 m tall	1.4	0.2	2.7	0.2	3.2	0.1	2.7	0.4
Number of willow seedlings/ha	61.0	11.1	56.3	18.0	46.2	8.4	8.4	2.5
Number of cottonwood trees/ha	29.6	3.7	2471.4	93.9	949.7	29.4	116.5	8.6
Number of small snags/ha	0.0	0.0	6.2	3.2	52.1	4.4	0.0	0.0
Number of large snags/ha	0.0	0.0	0.0	0.0	0.7	0.2	6.1	2.5
Basal area (m^2)/ha of green ash	0.0	0.0	18.8	9.2	3.9	0.9	5.2	1.3
Basal area (m^2)/ha of cottonwood	0.0	0.0	11.4	1.7	17.5	0.5	40.2	2.2
Dbh of green ash (cm)	0.0	0.0	2.5	0.8	0.8	0.3	5.3	1.3
Dbh of cottonwood (cm)	1.3	0.3	7.6	0.6	17.0	0.5	67.3	2.0
% overstory canopy cover	13.0	1.1	59.2	2.6	58.7	0.9	48.5	3.6
Heterogeneity in overstory canopy cover	0.7	0.1	0.4	0.1	0.4	0.0	0.5	0.1