RESPONSE OF RIPARIAN SHRUBS TO DECLINING WATER AVAILABILITY

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ABSTRACT

Community dominance, productivity, and grazing effects were recorded in a cottonwood sere along the Yellowstone River. The sere progressed from seedlings of Great Plains cottonwood (Populus deltoides) *and sandbar willow* (Salix exigua), *to cottonwood forests with a dense shrub understory, and then to grasslands. Total shrub canopy cover and biomass rose as sandbar willow matured, declined as they died, rose again as shrubs developed under the cottonwood canopy, and declined as grasslands dominated.*

INTRODUCTION

Our objectives were to document changes in plant composition, net primary productivity, and potassium mass, and to observe the effects of grazing on shrub composition in a cottonwood sere. Vegetation growing on new alluvial deposits nearer the stream may be contrasted with that on older deposits farther inland to recognize and measure successional processes (Jenny 1980; Leopold and others 1964; Stevens and Walker 1970). The sere described here progresses from seedlings of Great Plains cottonwood establishing on newly deposited alluvium, to a thicket of sandbar willow and cottonwood, to cottonwood forest, to a shrubland dominated by western snowberry (*Symphoricarpos occidentalis*) and woods rose (*Rosa woodsii*), and then to a self-perpetuating grassland dotted with silver sagebrush (*Artemisia cana*). The cottonwood-to-grassland sere is one of the dominant riparian seres in this region of the Northern Great Plains.

The study area was located on a 72-km stretch of floodplain along the lower Yellowstone River in Montana. It is the longest undammed river in the arid Western United States and has a floodplain whose water-erosion-deposition dynamics are intact. The region has a semiarid climate (Thornwaite 1941) supporting grass and shrub vegetation on the uplands.

METHODS

The study plan was to first identify the sere and seral stages during reconnaissance of the study area. Seven successional stages were identified on the floodplain and are presented in a chronosequence: sandbar, cottonwood seedling, cottonwood sapling, cottonwood pole, mature cottonwood, shrub, and grassland. Sixty-six stands representing the sere were located along the length of the study area. One transect, 60 m in length, was placed in each stand. The following variables were recorded or sampled along the transect in each stand: plant species list, canopy coverage, cottonwood age, elevation of the land surface relative to the river surface, density of the dominant woody vegetation, harvest plots of herbaceous species, and soil cores to 15 dm deep.

Percent cover of understory plants was measured with 60 step points along the transect in each stand. Shrub cover was calculated by summing areas (Pi $\cdot$ r^2) of all shrubs present in density plots (described later) and dividing by total plot area. Tree canopy cover was estimated ocularly.

Stand age was estimated by counting the rings of typical cottonwood trees cut at the base (seedlings and saplings) or cored at breast height (pole and mature trees).

Elevation of the land surface relative to the river surface was used to determine rate of alluvial deposition. Stand elevation was determined with a measuring rod and hand level.

Tree and shrub densities per stand were recorded. These density measurements were later used to calculate total biomass of each stand. Aboveground biomass was estimated for five stands per stage by summing the mass of the tree, shrub, herb, and litter components. Individual tree and shrub mass was determined using allometric equations, and herb and litter mass was measured by harvesting a subsample of the stand. Dry mass of individual cottonwood trees in each stand was estimated from a tree dry mass/stem diameter regression using 10 cottonwood trees of various sizes (Boggs 1984). The mass of the tree layer was determined by estimating the dry mass of each tree from its diameter, summing across all trees in the density plots, and adjusting to a square-meter basis (Kira and Shidei 1967; Whittaker and Woodwell 1968). Sandbar willow, peach-leaved willow (*Salix amygdaloides*), western snowberry, woods rose, and silver sagebrush were similarly estimated using numbers and crown diameters of shrubs in the density plots. Aboveground mass for grasses, forbs, and litter was determined by harvesting, drying, and weighing the material present in five 0.5-m^2 plots spaced equally along the transect line in each stand.

Belowground biomass was estimated for the same five stands per stage used for aboveground biomass. The following categories were measured: root crowns, roots with diameters >1 cm, and soil organic matter. To estimate the mass of root crown and roots >1 cm we used a root mass/stem diameter regression constructed from six

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cottonwood trees either excavated or found prewashed on sandbars (Boggs 1984). Total soil organic matter was estimated from three soil cores (0-15 dm in depth) from each transect. The cores were dried, ground (with roots), and analyzed for organic matter colorimetrically after dichromate oxidation (Sims and Haby 1970).

Net primary productivity was taken as the rate of change in standing crop implied by biomass and age estimates on the chronosequence plots. Because net primary production (kg/m²/yr) is change in mass per unit of time, it can be estimated as the slope of a line resulting when standing crop (kg/m²) is plotted against time.

The same five stands per stage used for biomass estimates were used for the potassium mass estimates. The plant contribution was determined by multiplying the estimated biomass component mass by potassium concentrations. For each species, five samples of leaves from wood of diameter classes 0-1, 1-10, and >10 cm were analyzed for potassium, and the results averaged. Potassium concentrations in roots <0.1 cm in diameter were assumed to equal 0-1-cm twig concentrations and >1 cm root concentrations were assumed to equal those of 1- to 10-cm branches. Potassium was determined by ashing samples and determining quantities of the nutrients released by spectrophotometric methods (Olson and Dean 1965).

Soils sampled for root mass and organic matter were used for potassium analyses and soil potassium mass estimates. The mass of soil potassium per stand was estimated by multiplying potassium concentrations (g/100 g) from the soil by soil bulk density by the volume of soil. Bulk density was estimated by dividing soil mass by sample volume; volumes were calculated by multiplying core area by core depth and adjusting to a square-meter basis. Potassium was extracted from soils with 1 *M* ammonium acetate and measured by atomic absorption (Pratt 1965).

The effects of grazing on the shrub component were determined by observations in stands of known grazing intensity, ranging from light to heavy grazing.

RESULTS AND DISCUSSION

Because cottonwood seedlings were recorded only on recent alluvial deposits, and all cottonwood stands were even-aged, cottonwood age was a direct measure of stand age. This was consistent with reports from other parts of the Great Plains (Johnson and others 1976; Moss 1938). With the death of the oldest cottonwood trees, the relatively precise cottonwood chronology ceased.

Trees and shrubs that appeared in over 60 percent of the stands of any stage are listed with cover estimates in table 1. In the cottonwood seedling stage, sandbar willow, peach-leaved willow, cottonwood, and herbaceous seedlings colonized new alluvial deposits of silt, sand, and gravel. Cottonwood, willow, and shrub cover averaged 27 ± 5 SE. Sandbar willow and cottonwood also dominated the cottonwood sapling stage. Due to the loss of sandbar willow between the cottonwood sapling and cottonwood pole stages, cottonwood dominated the cottonwood pole stage with an average canopy cover of 66 ± 4 SE. The undergrowth had a scattering of shrubs including woods rose and western snowberry with an average canopy cover of 5 ± 1 SE. Cottonwood canopy cover decreased to 40 ± 4 SE in the mature cottonwood stage. The shrub understory component increased dramatically to 19 ± 4 SE. The stand's appearance became one of widely spaced, dying cottonwoods.

With the disappearance of cottonwoods either of two communities assumed dominance: a shrub stage composed of woods rose and western snowberry or a green ash (*Fraxinus pennsylvanica*) forest. Stands supporting green ash were uncommon in the study area and consequently are not presented. Shrubs in the shrub stage had an average canopy cover of 23 ± 2 SE (table 1). Few dead shrubs were observed in the mature cottonwood stage, while ocular estimates of percent dead shrubs in the shrub stage ranged from 20 to 50 percent. The shrub stage was seral to a self-perpetuating grassland stage dominated by western wheatgrass (*Elymus smithii*) and prairie sandreed (*Calamovilfa longifolia*), and dotted with silver sagebrush. The herbaceous cover averaged 67 ± 3 SE and silver sagebrush averaged 1 ± 0 SE.

Table 1—Canopy coverage of trees and shrubs which occurred in >60 percent of the stands in six seral stages. The stages include: seed (cottonwood seedling), sapling (cottonwood sapling), pole (cottonwood pole), mature (cottonwood mature), shrub (shrub), and grass (grassland)

Plant species	Habit	Canopy coverage ($\bar{X}$±SE)					
		Seed	Sapling	Pole	Mature	Shrub	Grass
Populus deltoides	Tree	21±3	30	66±4	40±4	<1	—
Salix exigua	Shrub	5±2	30	—	—	—	—
Salix amygdaloides	Tree	1±1	5	<1	<1	—	—
Toxicodendron rydbergii	Shrub	—	—	<1	12±3	3±1	<1
Vitis riparia	Liana	—	—	<1	4±2	—	—
Ribes aureum	Shrub	—	—	<1	<1	<1	—
Parthenocissus inserta	Liana	—	—	<1	1±0	<1	<1
Ribes setosum	Shrub	—	—	—	—	<1	—
Rosa woodsii	Shrub	—	—	<1	12±3	14±2	<1
Fraxinus pennsylvanica	Tree	—	—	<1	<1	<1	—
Symphoricarpos occidentalis	Shrub	—	—	<1	6±2	8±1	<1
Artemisia ludoviciana	Shrub	—	<1	<1	<1	<1	2±1
Artemisia cana	Shrub	—	—	—	—	—	1±0

Estimates of water availability were made using the elevation of the ground surface above the river water surface, and changes in potassium mass. The rate of alluvial deposition during the 0- to 20-yr period was 0.11 m/yr, which rapidly raised the ground surface level above the river water surface to approximately 2.2 m (fig. 1). The rate of alluvial deposition was less thereafter, 0.01 m/yr, raising the ground surface level to 3.0 m at 110 yr. The rapid increase in ground surface level produces a corresponding decrease in flooding frequency.

Potassium is loosely bound by soils and organic matter and is easily delivered by river and groundwater, and leached by precipitation. Groundwater from the adjacent uplands and river water account for the majority of water and potassium inputs into the ecosystem. Ecosystem contents of organic and ammonium acetate extractable potassium rose, leveled off, and fell in time (fig. 2). Approximately 0.05 kg/m² was initially deposited on new alluvial bars, rose to 0.35 kg/m² in the mature cottonwood stage, and fell to 0.25 kg/m² in the grassland stage. This suggests that water availability is highest during the period of rapid alluvial deposition, and when the community is horizontally and vertically nearest the river. The river water imports are surely due to periodic flooding, a high water table, and pumping from the water table by the relatively deep-rooted cottonwood. During the conversion of the cottonwood forest to grassland, potassium loss from the total ecosystem, about 100 g/m² (fig. 2), may be influenced by the release of 40 g/m² stored in cottonwood biomass. Leaching of potassium by precipitation (30-35 cm/yr), which has been steady through succession, the loss of cottonwoods pumping potassium from the water table, and reduced flooding may account for most of the potassium loss.

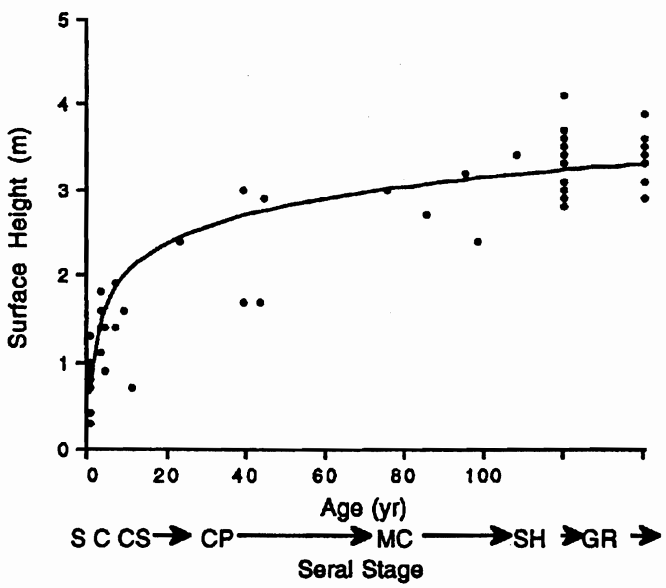

Figure 1—Ground surface elevation above the river water level. Letters represent the seral stages: sandbar (S), cottonwood seedling (C), cottonwood sapling (CS), cottonwood pole (CP), mature cottonwood (MC), shrub (SH), and grassland (GR).

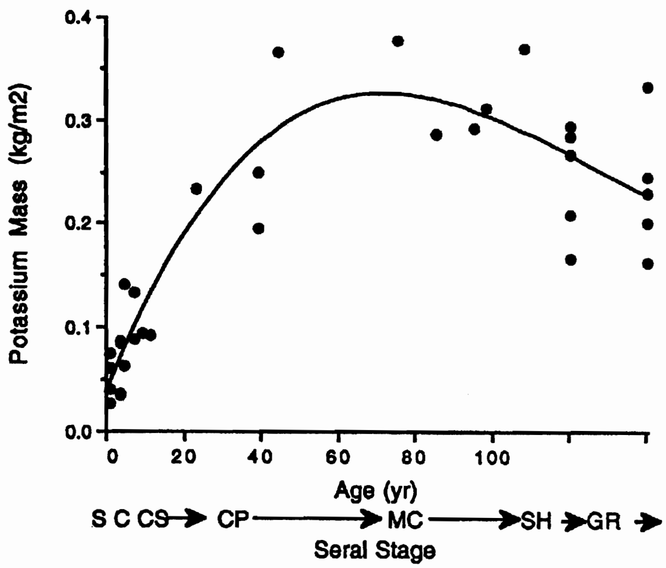

Figure 2—Ecosystem content of potassium (K). Totals include contents of soil and plant materials, both living and dead, and above and below ground. Letters represent the seral stages: sandbar (S), cottonwood seedling (C), cottonwood sapling (CS), cottonwood pole (CP), mature cottonwood (MC), shrub (SH), and grassland (GR).

Total biomass increased as the cottonwoods matured and decreased dramatically with the loss of cottonwoods. Changes in aboveground biomass by lifeform illustrate changes in community composition. Willow mass first dominated the sandbars; after 10 yr cottonwood mass exceeded that of willow (fig. 3). As cottonwood stands thinned after about 100 yr, understory shrubs, primarily woods rose and western snowberry, reached their greatest live biomass. As the shrub stage is replaced by the grassland stage, shrub biomass decreased with the loss of snowberry and woods rose. The massive dominance of cottonwood in the 20-100 yr period was understated in figure 3 due to the division of its biomass by 20. Whereas water availability is highest in the early seral stages, community biomass is limited by the degree of community development and reaches its peak as the cottonwood forest matures. With the eventual death of the cottonwoods, aboveground biomass is limited by the lack of regeneration of any tree species in the shrub and grassland stages. Cottonwood trees evidently tap the water table, but as they die they are eventually replaced by species, such as silver sagebrush and western wheatgrass, that have far lower transpiration requirements.

Aboveground net primary production was positive (0.4 kg/m²/yr) when the ecosystem was young, approached neutral in the 80- to 110-yr period, was negative as the cottonwood forests died, and approached neutral in the shrub and grassland stages. Aboveground net primary productivity in the sandbar-through-mature cottonwood stages is below that of other temperate forests. The steepest upward slope (0.4 kg/m²/yr) is below the 0.6 to 2.5 kg/m²/yr range reported for temperate deciduous

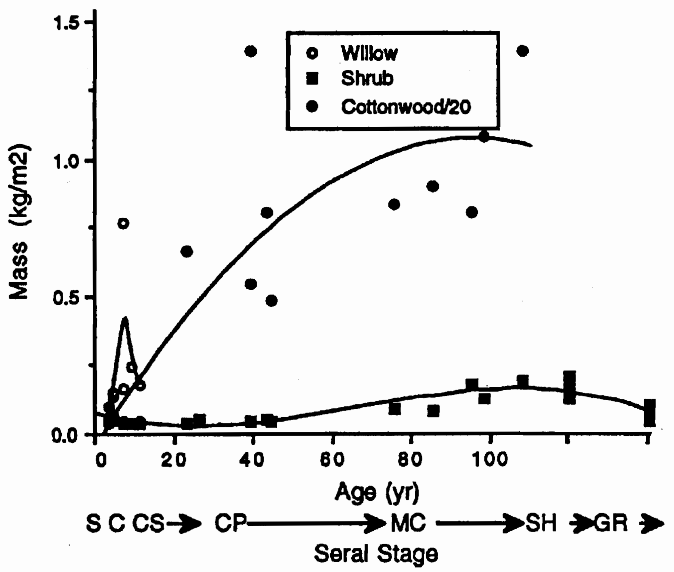

Figure 3—Aboveground mass of cottonwood (*Populus deltoides*), willow (*Salix* spp.), and shrubs. Note the division of cottonwood by 20. Letters represent the seral stages: sandbar (S), cottonwood seedling (C), cottonwood sapling (CS), cottonwood pole (CP), mature cottonwood (MC), shrub (SH), and grassland (GR).

forests (Art and Marks 1971; Whittaker 1975). This low production rate can be attributed to a number of causes including: physical removal of organic matter by flood waters, saturated cold anaerobic soil conditions during flooding, and the loss of cottonwoods without regeneration. Approximately 50 percent of the aboveground organic matter is lost with conversion of the mature cottonwood stage to shrub and grassland stages.

On sites that are relatively ungrazed, the understory of the mature cottonwood forest will contain a diverse, dense shrub layer dominated by redosier dogwood (*Cornus stolonifera*), western serviceberry (*Amelanchier alnifolia*), common chokecherry (*Prunus virginiana*), western snowberry and woods rose, various species of willows (*Salix* spp.), and currants and gooseberries (*Ribes* spp.). With moderate grazing, there will be an increase in western snowberry and woods rose, with a corresponding decrease in both the abundance and canopy cover of redosier dogwood, western serviceberry, common chokecherry, and various species of currants and gooseberries. If the disturbance continues, the more palatable shrubs will be eliminated leaving woods rose and western snowberry, which can form a nearly impenetrable understory. However, if the disturbance is severe enough, shrubs can be eliminated and the understory will be converted to an herbaceous one dominated by species such as Kentucky bluegrass (*Poa pratensis*), common timothy (*Phleum pratensis*), and smooth brome (*Bromus inermis*). During the process of converting from a diverse, dense shrub understory to an herbaceous understory, the stand will open up, resulting in a drier site. Once the stand has converted from a shrub-dominated understory to one that is dominated by a variety of introduced herbaceous species, the ability to return the site to its former state (shrub dominated) is very difficult. It may be possible, but it will require a drastic change in management. Therefore, if the manager wants to maintain the stand in a shrub-dominated understory state, change the management on the site before the site is degraded.

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