



Succession in riparian communities of the lower Yellowstone River, Montana  
by Keith Webster Boggs

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in  
Biological Sciences  
Montana State University  
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Abstract:

Riparian plant communities of the lower Yellowstone River between Glendive and Sidney, Montana, were studied during the Summers of 1980 and 1981. These communities originally colonized sand and gravel bars deposited along the River channel. New sand deposits were invaded by *Salix* spp. and *Populus deltoides* Marsh. seedlings. This original community developed sequentially to willow thickets, to young cottonwood forests, and to mature cottonwood forests after about 3, 7, 34 and 92 years, respectively. While the mature cottonwood community is usually replaced by a grassland community (principally *Agropyron smithii* Rydb.) via a shrub community (*Rosa woodsii* Lindl. and *Symphori-carpos occidentalis* Hook.), it may be replaced by a *Fraxinus Pennsylvania* Marsh. plant community. Numbers of species with constancies of over 60% rose from 12 in the seedling community to 18 in the mature cottonwood community and declined to 13 in the grassland. Composition changes are documented in releve tables. *Populus deltoides* density fell rapidly from 48/M<sup>2</sup> at 3 years to 0.02/M<sup>2</sup> at 92 years; *Salix* spp. disappeared still more rapidly, with declines from 10/nr at 3 years to near 0/m<sup>2</sup> at 34 years. Aboveground biomass rose from 0.2 kg/m<sup>2</sup> at 3 years to 30 kg/nr at 60 years and declined to less than 0.5 kg/m<sup>2</sup> in near-climax grasslands; most of the large mass observed at mid-serie is living wood.. Belowground biomass rose from about 7 kg/m<sup>2</sup> at 3 years to over 30 kg/nr at 90 years and declined to about 19 kg/m<sup>2</sup> in grasslands; over half of this biomass was soil organic, matter in every community. Root/shoot ratios declined from 3/1 in the seedling community to 1/2 in the mature cottonwood community and rose again to 10/1 in the grassland. K, Na and N contents of the communities and ecosystem rose and fell with the rise and fall in its biomass. In contrast, P rose more rapidly in early succession and continued to rise slowly through the grassland stage. Management implications of logging and altered Streamflow are discussed.

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in

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MONTANA STATE UNIVERSITY  
Bozeman, Montana

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of a thesis submitted by

Keith Webster Boggs

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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## ABSTRACT

Riparian plant communities of the lower Yellowstone River between Glendive and Sidney, Montana, were studied during the Summers of 1980 and 1981. These communities originally colonized sand and gravel bars deposited along the River channel. New sand deposits were invaded by Salix spp. and Populus deltoides Marsh. seedlings. This original community developed sequentially to willow thickets, to young cottonwood forests, and to mature cottonwood forests after about 3, 7, 34 and 92 years, respectively. While the mature cottonwood community is usually replaced by a grassland community (principally Agropyron smithii Rydb.) via a shrub community (Rosa woodsii Lindl. and Symphoricarpos occidentalis Hook.), it may be replaced by a Fraxinus pennsylvanica Marsh. plant community. Numbers of species with constancies of over 60% rose from 12 in the seedling community to 18 in the mature cottonwood community and declined to 13 in the grassland. Composition changes are documented in relevé tables. Populus deltoides density fell rapidly from 48/m<sup>2</sup> at 3 years to 0.02/m<sup>2</sup> at 92 years; Salix spp. disappeared still more rapidly, with declines from 10/m<sup>2</sup> at 3 years to near 0/m<sup>2</sup> at 34 years. Aboveground biomass rose from 0.2 kg/m<sup>2</sup> at 3 years to 30 kg/m<sup>2</sup> at 60 years and declined to less than 0.5 kg/m<sup>2</sup> in near-climax grasslands; most of the large mass observed at mid-serie is living wood. Belowground biomass rose from about 7 kg/m<sup>2</sup> at 3 years to over 30 kg/m<sup>2</sup> at 90 years and declined to about 19 kg/m<sup>2</sup> in grasslands; over half of this biomass was soil organic matter in every community. Root/shoot ratios declined from 3/1 in the seedling community to 1/2 in the mature cottonwood community and rose again to 10/1 in the grassland. K, Na and N contents of the communities and ecosystem rose and fell with the rise and fall in its biomass. In contrast, P rose more rapidly in early succession and continued to rise slowly through the grassland stage. Management implications of logging and altered streamflow are discussed.

## INTRODUCTION

Recent studies of white-tailed deer (Odocoileus virginianus) on the lower Yellowstone River (Dusek 1981) required information about the riparian communities. A previous study of the area provided only qualitative data concerning plant communities (Stevens et al. 1978). The extent to which data from studies of similar floodplain vegetation in other localities (Everitt 1968, Hosner and Minckler 1963, Johnson et al. 1976, Keammerer et al. 1975, Ware 1949, Weaver 1960, Wikum and Wali 1974, Wilson 1970) could be applied to the lower Yellowstone River floodplain required determination.

The objectives of this study were to identify major riparian plant community types, qualitatively and quantitatively describe them, and describe their successional relationships. Community type descriptions were to include stand age, species lists with coverage estimates, woody plant densities, and plant and soil biomass and nutrient mass. The results of this study should be useful in the management of river flow, wildlife and agriculture on the floodplain.

Funding was provided by the Montana Department of Fish, Wildlife and Parks under Federal Aid in Wildlife Restoration, Montana Project W-120-R-12 and 13 and to a lesser extent by a Montana State University Faculty Creativity Grant (#2-6000-690).

## DESCRIPTION OF STUDY AREA

The Yellowstone River originates in northwestern Wyoming and flows north into Montana. It turns east and crosses the southern portion of Montana (Figure 1), then joins the Missouri River in western North Dakota. All major tributaries of the Yellowstone River have their origins in Wyoming and flow north. The tributaries, in the order in which they enter the Yellowstone, are the Clark Fork of the Yellowstone River, the Bighorn River, the Tongue River and the Powder River. The total drainage area of approximately 179,000 km<sup>2</sup> is nearly equally divided between Montana and Wyoming, with less than 1% lying in North Dakota (Stevens et al. 1978). The Yellowtail dam on the Bighorn River forms the only major reservoir in the Yellowstone drainage system.

Study sites were located on a 72 km stretch of floodplain between Glendive and Sidney, Montana (Figure 1). Specific study site locations are listed in Table 5. Elevations within the study area varied from 625 m above sea level at Glendive to 577 m at Sidney.

The Yellowstone River's main channel length in the study area is 101 km. Streamflow measurements obtained from a gauging station near Sidney (USGS Water Resources Data for Montana 1910 to 1980) show that the mean discharge is highest during the months of May, June and July and decreases dramatically between August and April (Figure 2). Average maximum discharge also peaks in May, June and July. The highest

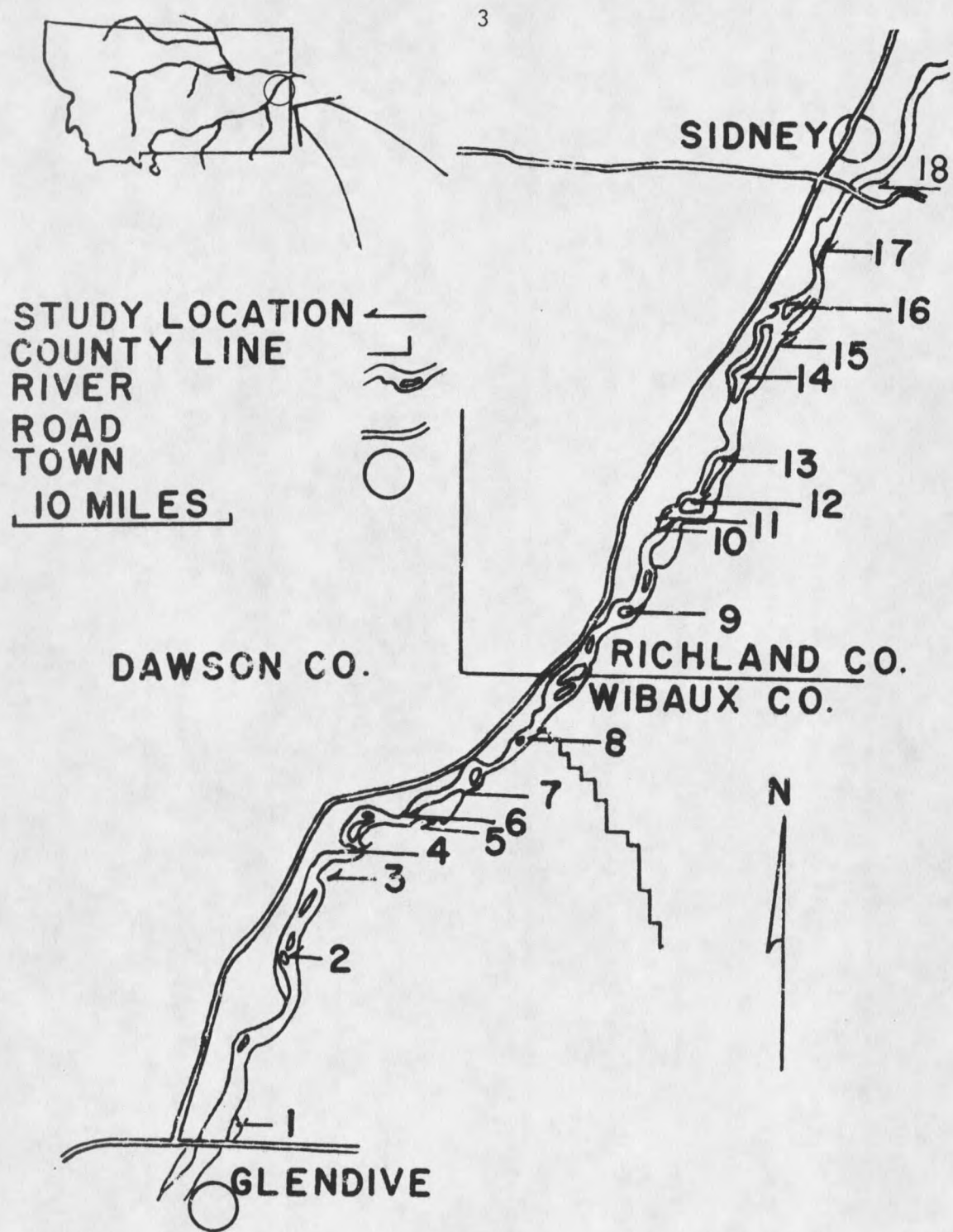


Figure 1. Map of the study area showing locations of specific study sites.

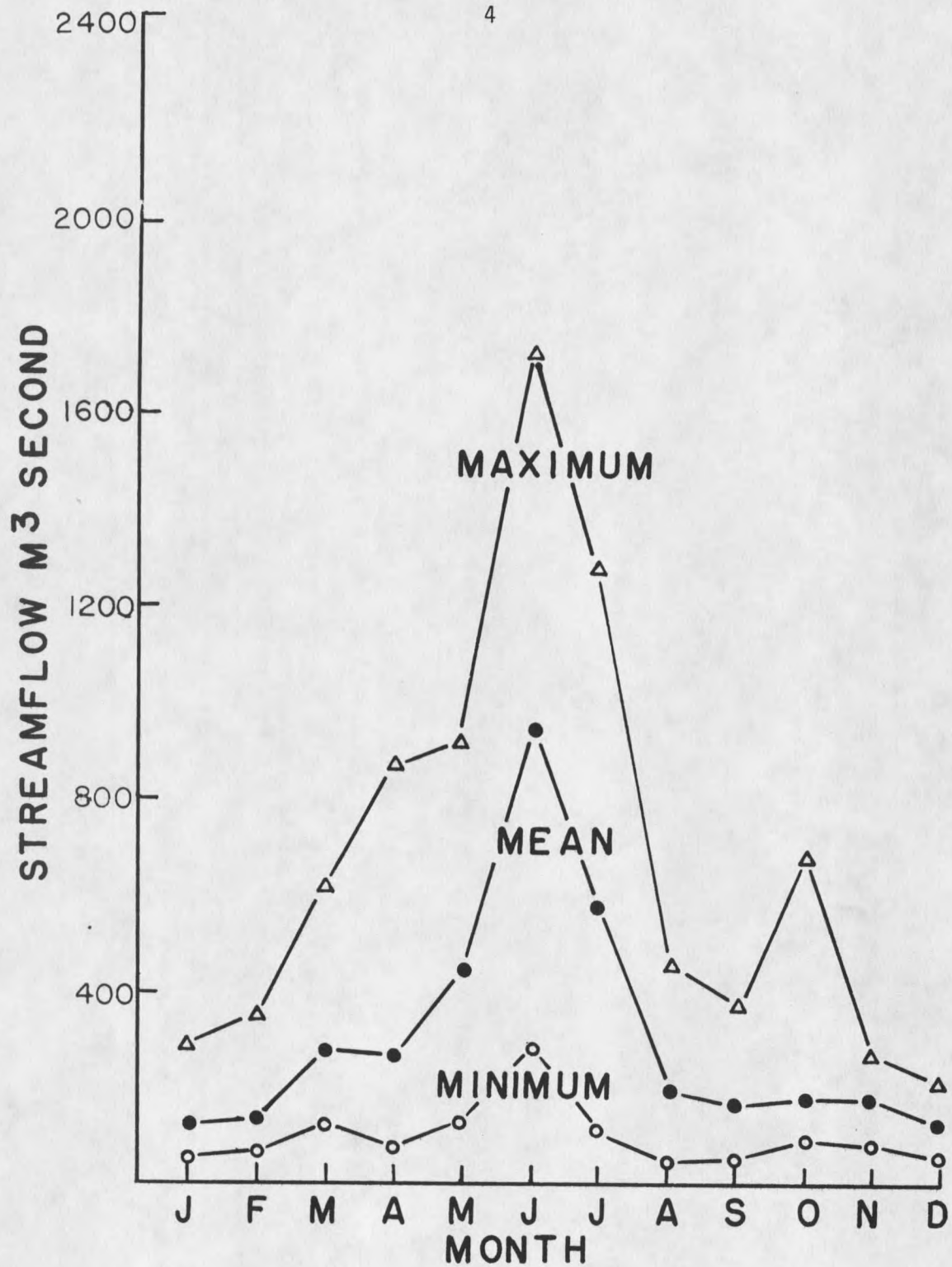


Figure 2. Mean, maximum and minimum Yellowstone River flow (m<sup>3</sup>/sec) at Sidney, MT, in the 1910-1980 period (USGS, 1910-1980).



flow ever recorded was 4,502 m<sup>3</sup>/s on June 2, 1921 and lowest flow was 13 m<sup>3</sup>/s on April 17, 1961.

The lower Yellowstone Valley lies along the western margin of the Williston Basin, a "broad shelf-low relief" geologic feature (Alden 1932). Marine sediments were deposited in the Williston Basin during the Paleozoic, Mesozoic and early Tertiary times. The Fort Union Formation, the latest sediment layer, was formed during the Paleocene Epoch (Veseth and Montagne 1980) and consists of soft nonmarine floodplain sediments derived from erosion of western Montana during the Laramide orogeny. During the Pleistocene continental glaciation, a lobe of glacial ice blocked the River valley at Intake, impounding the River flow to form a glacial lake with resultant deposition of fine sediments upstream (Alden 1932).

The landscape of the Williston Basin now consists of gently rolling hills, wide valleys, and flat divides with sandstone and clinker beds forming ridges and buttes (Veseth and Montagne 1980). Erosion by the Yellowstone River has formed a broad flat floodplain with an average width of 4.4 km in the study area. The floodplain broadens with distance downstream. The narrowest segment in the study area was 2.4 km at Glendive, the widest was 8.0 km at Elk Island.

Soils on the floodplain and low terraces are of the Trembles-Havrelon-Lohler association. This association is described by Pescaço and Brockmann (1980) as "deep, nearly level and gently sloping, well drained and moderately well drained fine sandy loams, silt loams, silty clay loams, and clays underlain by stratified fine sandy loam to silty

clay alluvium". This soil association forms a substrate for the plant communities identified below.

In the River, initial sedimentation leading to the formation of permanent land normally occurs with the formation of point bars. These originate on convex curves within the confines of the river channel. The opposing concave bank is cut, providing sediment for deposition on convex curves downstream (Matthes 1941). The channel thus meanders laterally across the floodplain. The channel width remains constant as vegetation colonizes the point bars and islands. Surface heights of new deposits rise as sediments are deposited on them by waters flowing over them at high-water times.

The lower Yellowstone River passes through a region which has a semi-arid climate (Thornwaite 1941). Climatic records for Glendive illustrate the precipitation and temperature fluctuations of the region (Figure 3, Ruffner 1971). Average monthly precipitation is highest in early summers with 8.1 cm falling in June, and drops during winters to 0.8 cm in December. The average annual precipitation is 30 to 35 cm. Temperatures fluctuate about an average monthly high of 23.7 degrees C in July to an average monthly low of minus 7.4 degrees C in February.

The present floodplain is occupied mainly by deciduous forests, grasslands and cultivated land. Immediately adjacent to the River, Salix spp. and Populus deltoides Marsh. (willow and cottonwood) seedlings and thickets are dominant. Mature Populus deltoides stands, grasslands (principally Agropyron smithii Rydb.) and shrublands (Rosa woodsii Lindl. and Symphoricarpos occidentalis Hook.) are scattered throughout the floodplain. Fraxinus pennsylvanica Marsh. (Green Ash)

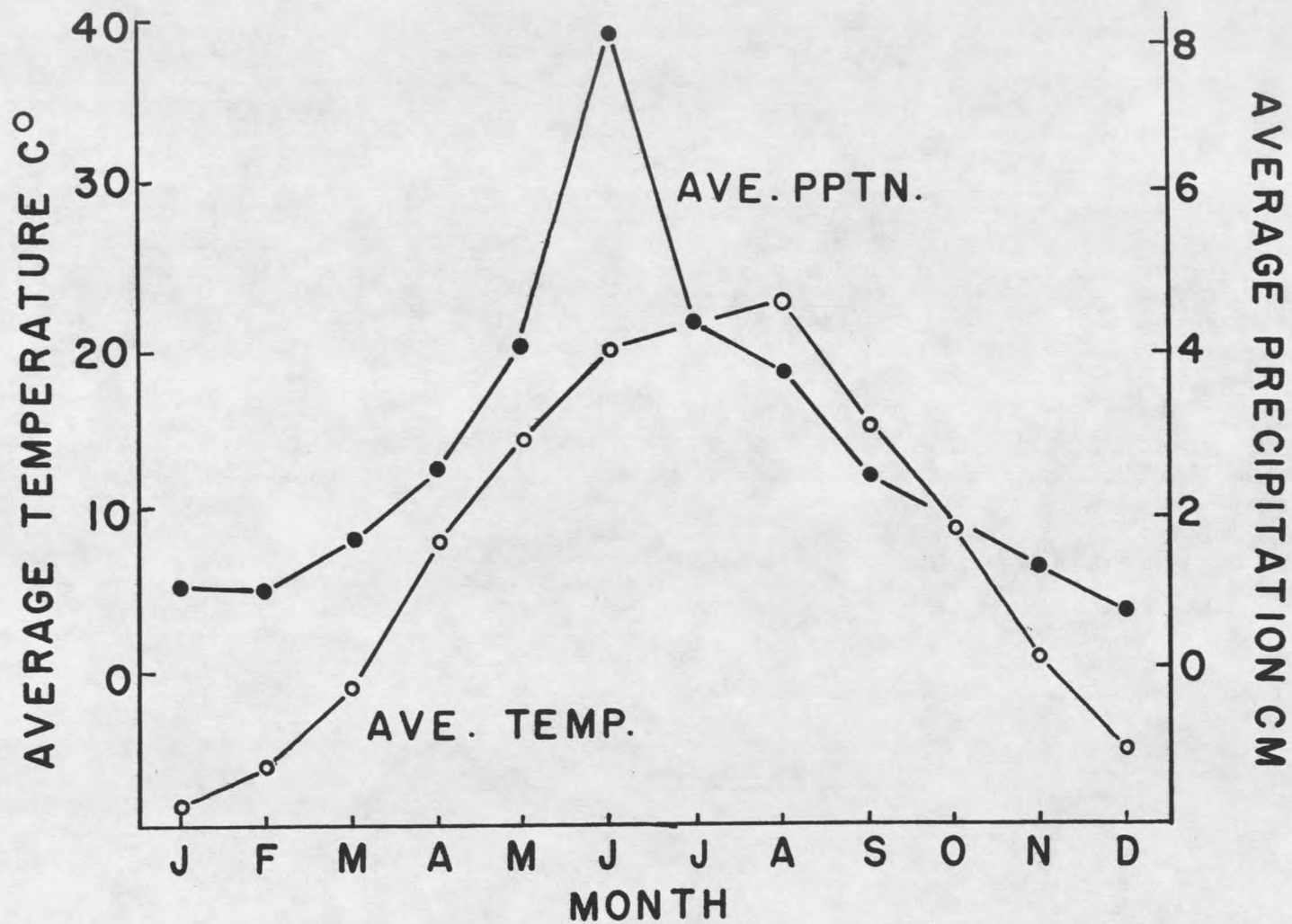


Figure 3. The average monthly temperature and precipitation at Glendive, MT (Ruffner 1971). The vertical scales are adjusted so evapotranspiration exceeds precipitation whenever the temperature line rises above the precipitation line (Walter 1973).

stands are commonly found at the edge of the floodplain. Marshes, which also occur here, were not studied. The semi-arid climate dominates floodplain vegetation where deep soil deposits lift the soil surface well above the water table, but ground water and flooding have a significant effect where soil deposits are shallow.

Man's impact on the floodplain vegetation stems mainly from agricultural use. Many once-forested lands, shrublands and grasslands have been cleared for cultivation. Most land not cultivated is used by sheep or cattle.

## MATERIALS AND METHODS

Reconnaissance during the early Summer of 1980 identified 12 major physiognomic plant community types. Seventy sites representing the major communities were selected for analysis. These were: 19 in the "sandbar" type, 9 "seedling" type, 8 "thicket" type, 9 "young cottonwood" type, 6 "mature cottonwood" type, 9 "shrub" type, 9 "grassland" type, 7 "green ash" type, 3 "willow-shrub" type and 1 "peach-leaved willow" type. A species list (Table 6) was also made for three "marsh" community types. Stand selection criteria were that each site represented one of the major community types indicated above, and that the sites showed no evidence of disturbance by fire, logging, recent grazing or other agricultural use. Measurements were taken to characterize each community type with respect to species composition, age, soil height, stand stratification and height, community composition (cover and/or density), biomass and nutrient masses.

### Species Composition

Complete plant species lists were kept for all sites. Species encountered in sites not sampled, including marshes, were separately recorded. Scientific names of plants follow Booth (1972) and Booth and Wright (1966) or, for species not listed by Booth, Van Bruggen (1976).

### Site Age

The age of forested sites was estimated by counting the annual rings of the largest Populus deltoides present. Growth rings were observed by cutting seedlings and saplings, or coring older trees at breast height. Four years were added to each core count to compensate for the time the tree took to grow to breast height (Wilson 1970).

### Stand Height

The height of the soil surface above the River water level was determined with a level and measuring tape. Since soil elevations were recorded at different times of the summer and since the River level varied throughout the summer, soil elevations are only approximate indicators of true height of the soil above the River level.

### Plant Cover

Horizontal cover was recorded for understory, shrub and overstory plants on a transect crossing the community perpendicular to the River. Graminoids, forbs, Artemisia ludoviciana Nutt., Toxicodendron rydbergii (Small) Greene, and vines were sampled with sixty step-points and presented as percent cover (Evans and Love 1957). Shrub cover was measured by calculating canopy coverage ( $\pi r^2$ ) of each shrub present in density plots (described below), summing and expressing the shrub coverage as a percent of the total plot area. Tree and sapling coverages were based upon ocular estimates.

Density of Woody Plants

Plots to sample the density of tree and willow species were located at three equally-spaced points on the cover transect. The number of trees and willows of each species was recorded in each plot. Seedlings, saplings and trees were defined by basal diameter as follows: seedlings were less than or equal to 0.5 cm, saplings were less than or equal to 6 cm, and trees were greater than 6 cm. Basal diameter was recorded for all saplings and the diameter at breast height (dbh) was recorded for all trees. Plot sizes used in various communities were as follows: seedling community 1 x 0.5 m; thicket community 2 x 3 m; young cottonwood community 5 x 5 m; mature cottonwood community 20 x 20 m; shrub community 1 x 5 m; willow-shrub community 4 x 10 m; the green ash and peach-leaved willow plots were 4 x 30 m. Thirty meter ash-willow plots were cut short if 20 trees were recorded before 4 x 30 m was reached and the actual plot length was recorded.

Density plots for shrubs (except Artemisia ludoviciana, Toxicodendron rydbergii and vines) were also placed at equidistant points along the transect. The minimum size of each plot was 1 x 5 m and the maximum size was 2 x 20 m, depending on which came first: 20 total shrubs or a maximum area of 40 square meters. Each shrub's crown diameter was recorded in one-decimeter units as the average of the widest crown measure and the crown measure perpendicular to it at its midpoint. Standing dead shrubs were not counted.

### Aboveground Biomass

Biomass was measured only in communities representing the sandbar through grassland sere. Time limitations prohibited measurements in the willow-shrub, peach-leaved willow and green ash communities.

Biomasses of graminoids, forbs, Artemisia ludoviciana, Toxicodendron rydbergii and vines were measured by harvest methods. All material in five 1 x 0.5 m plots equally spaced along the cover transect was clipped at ground level, combined, dried to constant weight at 60 degrees C and weighed. Biomasses of Populus deltoides and Salix spp. were measured similarly in the seedling community.

Tree and shrub biomasses were estimated by summing the weights of individual plants in each density plot. Because only a limited number of shrubs and trees could be harvested, weights of trees were determined from regressions relating weights of plant parts to a plant dimension (Whittaker and Woodwell 1968a). The method is outlined in the following six paragraphs.

Large, medium and small specimens of the shrubs Symphoricarpos occidentalis, Rosa woodsii and Artemisia cana Nutt. were collected in each of three sites. Crown diameter was measured and each shrub was separated into leaves, wood (branches) less than 0.5 cm in diameter and wood greater than 0.5 cm in diameter. These components were dried and weighed and their weights were regressed against crown diameter (Weaver 1977).

Nine specimens each of Salix fluviatilis Nutt. and Salix amygdaloides Anders. were collected from three locations. The basal diameter



of each Salix individual was recorded. Salix spp. were separated into leaves, wood less than 1 cm in diameter and wood greater than 1 cm in diameter. Each component was then dried and weighed. Subsamples of the larger specimens were used to determine the dry weight/wet weight ratios needed to convert wet weights to dry weights.

Similarly, five small Populus deltoides from the seedling and thicket communities were measured for basal diameter and the dbh of five Populus deltoides collected from the young cottonwood and mature cottonwood communities were measured. All specimens were separated into leaves, wood less than 1 cm in diameter, wood greater than 1 cm and less than 10 cm, wood greater than 10 cm in diameter, and weighed while wet. Subsamples were used to determine dry weight. Dry weights were regressed against diameters.

For each species, the logarithm of dry weight was regressed against the logarithm of diameter to create the graphs needed to estimate weights from an easily measured diameter (Whittaker and Woodwell 1968a). The regression parameters used to predict plant part masses are presented in Table 25 according to the formula  $y=mx+b$  where  $y=\log_{10}$  of the part weight in grams,  $b$ =the  $y$  intercept,  $m$ =the change in mass with changing diameter and  $x=\log_{10}$  of the plant diameter in cm. Plant diameter was canopy diameter for shrubs, basal trunk diameter for Salix spp. and small (0-6 cm basal diameter) Populus deltoides, and diameter at breast height for Populus deltoides larger than 6 cm basal diameter.

To measure the closeness of fit between two variables along a regression line, the correlation coefficient ( $r$ , Snedecor and Cochran

1980) and the estimate of relative error for a logarithmic regression (E, Whittaker and Woodwell 1968a) were calculated (Table 25).

Total biomass estimates of trees and shrubs in communities older than the thicket community are underestimated slightly because infrequently encountered species such as Juniperus scopulorum Sarg., Elaeagnus angustifolia L., Fraxinus pennsylvanica, Ribes spp. and Cornus stolonifera Michx. were not included.

#### Aboveground Dead Biomass

Litter mass was measured by harvesting three 1 x 0.5 m plots equally spaced along the cover transect, drying and weighing. Litter included all dead organic matter, including leaves and dead wood less than 10 cm in diameter lying on the ground or standing in the plot and reasonably distinct from the underlying soil.

Weights of dead Populus deltoides, whether standing or lying on the ground, were estimated by multiplying their pre-death weights, estimated with the weight-diameter regressions determined as described above, by a factor correcting for loss due to decomposition and subtracting weights of branches apparently lost to the litter component described above. This method is elaborated below.

To correct for decomposition, the dead trees were assigned to one of three categories: rotten, half-rotten or solid. The wood of rotten trees was weathered, rotted and could be kicked apart; half-rotten trees exhibited at least some sign of rot but the wood could not be kicked apart; solid trees showed no outward evidence of rot. Three to five samples for the 1-10 cm and greater than 10 cm diameter size

classes were collected from the rotten, half-rotten and solid categories. The samples were dried and weighed, their volumes were determined and wood density (gm/cc) was calculated. A mean for all the samples in each category was calculated. The ratio of rotten, half-rotten or solid wood density to live wood density provided a factor used to correct for decomposition.

To correct for loss of branches, dead trees were recorded as branchless (only the bole of the tree present), half-branched (the bole plus about half of the branches present) or fully-branched (the bole and most of the crown present). Weights of trees in the branchless category were calculated as wood greater than 10 cm in diameter from the Populus deltoides regression lines. Weights of trees in the half-branched category included the total of wood greater than 10 cm plus one-half of the 1-10 cm size class. Weights of trees in the fully-branched category included all wood larger than 1 cm in diameter. If the dbh of the tree was less than 1 dm, fully branched included all the 1-10 cm diameter wood, half-branched equaled three-fourths of the 1-10 cm wood and branchless equaled one half of the 1-10 cm wood.

The weights of individual dead Populus deltoides in the density plots were then determined by first calculating the weight of each dead tree as if it were alive by using the Populus deltoides tree regressions. Depending on which category the tree was recorded in--branchless, half-branched or fully-branched--some weight of the tree was subtracted from the overall weight. The weight of each tree was then multiplied by the appropriate dead weight/live weight ratio to convert

these data to rotten, half-rotten or solid weights. All dead tree weights were totaled for each plot.

Non-woody vegetation samples were dried in ventilated ovens (60 C) for two weeks, then weighed to the nearest gram. All woody biomass collected was weighed wet in the field to the nearest gram, or pound for large samples, then dried in ventilated ovens (60 C) for four weeks and reweighed. Dry weight/wet weight ratios were calculated to convert field weights of wet wood to dry weights.

#### Belowground Biomass

Belowground biomass consisted of four categories: root crowns and large roots greater than 1 cm, roots 1 cm to 0.1 cm in diameter, finer roots and soil organic matter. Due to pre-analysis grinding, soil organic matter included roots less than 1 cm in diameter.

Weights of large roots were measured by dimension analysis (Whittaker and Woodwell 1968a). Root systems of six Populus deltoides trees were either excavated or found pre-washed on gravel bars. Roots of each individual tree were separated into 1 to 10 cm and 10 cm or greater diameter classes, dried and weighed. Wherever systems were too large to dry, wet weights were converted to dry weights by multiplying by dry weight/wet weight ratios calculated from subsamples. A logarithm weight-logarithm diameter regression (Table 25) was prepared. Weights of roots greater than 1 cm diameter of all trees in each stand were estimated in a fashion paralleling the calculation of shoot biomasses.

Biomass of roots less than 1 cm in diameter, soil organic matter and soil nutrient concentrations were estimated from soil cores in the 0-10, 10-30 and 30-150 cm horizons. Five cores equally spaced along the cover transect were pooled for each horizon sampled. When the king tube sampler could not be driven beyond 120 cm, comparable samples were removed from the sides of a soil pit. Each sample was dried at 60 degrees C, mixed, weighed and subsampled (25% by weight) for laboratory analysis of elements and organic material present.

Biomasses of small roots (less than 1 cm in diameter) in the 0-10, 10-30 and 30-150 cm soil horizons were estimated by weighing, on an ash-free basis, volumetric samples washed from soil cores and expanding that value appropriately. Roots larger than 1 cm were discarded since they were separately estimated by dimension analysis. Roots and detritus were washed from the samples following the methods of Jackson (1956), except that soils were not presifted with a 6 mm screen. Roots, detritus and soil remaining on the washing screen were placed on pre-weighed Whatman 42 ashless filter paper. Roots, soil, detritus and filter paper were dried at 60 degrees C for two days. Roots and detritus were separated into size classes less than or equal to 1 mm and greater than 1 mm in diameter. Because roots and detritus greater than 1 mm in diameter were rare, they were combined across all stands of a type to calculate average biomass. Percent root in the sample remaining was ocularly estimated. The entire sample was then weighed, ashed and reweighed. Ash-free root biomass was calculated as (organic matter + filter paper + soil traces - filter paper - ash) times the percentage of root in the sample (Weaver 1982).

The organic matter content of soils acquired in volumetric cores was calculated as percent organic matter (gm/100 gm) times soil bulk density times volume of the soil layer considered. Organic matter contents were colorimetrically determined by the Montana State University Soil Testing Laboratory after dichromate oxidation (Sims and Haby 1970). Soil organic matter was estimated as total organic matter minus small root (0-1 cm diameter roots) organic matter.

#### System Nutrient Mass

Plant parts, litter and soils were analyzed for nitrogen, phosphorus, organic phosphorus of soil, potassium and sodium by the Montana State University Soil Testing Laboratory. The analytical results are summarized in Appendices K, M, N, O, P and Q. Only roots greater than 1 cm in diameter were removed from the soil samples, thus soil analysis also includes roots less than or equal to 1 cm in diameter.

Soil nutrient masses in each horizon were estimated by multiplying nutrient concentrations (gm/100 gm) by soil bulk density by the volume of soil in the horizon concerned. Stand-by-stand bulk density data are summarized in Table 26. Litter nutrient masses were determined by multiplying nutrient concentrations by litter weight.

Nutrient masses of plant parts were estimated by multiplying the nutrient concentration by plant part biomasses. Neither roots nor dead Populus deltoides were analyzed for nutrient contents (%). To adjust for this, fine root contents (0-1 cm) were assumed to equal twig (0-1 cm) contents of Populus deltoides and coarse root contents (1 cm+) were assumed equal to those of 1-10 cm wood. Similarly, nutrient

content (%) in live Populus deltoides wood greater than 10 cm in diameter was also used as an estimate of the nutrient content of dead trees.

Total nitrogen in both soils and plant material was measured by the Kjeldahl method (Bremner 1965). Potassium, sodium and phosphorus contents of plant material were measured by ashing samples and determining the quantities of elements released by spectrophotometric (P) or atomic absorption (K and Na) methods. Potassium and sodium were extracted from soils with 1 M ammonium acetate and measured by atomic absorption (Pratt 1965). Inorganic phosphorus was extracted with a 1 M sulfuric acid solution and measured spectrophotometrically (Olson and Dean 1965). Total soil phosphorus was determined by ashing, extracting with 1 M  $H_2SO_4$  and reading spectrophotometrically (Olson and Dean 1965). Organic phosphorus was assumed to be total phosphorus minus inorganic phosphorus (Saunders and Williams 1955).

## RESULTS AND DISCUSSION

Riparian communities of the Yellowstone River floodplain were readily distinguishable. These ranged from bare sandbars to willow thickets, to cottonwood forests and green ash forests, to grasslands. Data from my studies are used below to characterize these communities by composition, describe their seral relationships, speculate on forces driving the seral changes and measure changes in ecosystem contents of organic matter, nitrogen, phosphorus, potassium and sodium.

Figures 4 and 5 summarize the successional relations of the 12 plant communities which appear in the four seres identified, and which will be described below. The sere leading to the regional dry grassland climax dominates the floodplain. It began with Populus deltoides and Salix spp. seedlings colonizing newly-formed River sandbars together. The Salix spp. initially attained stature exceeding Populus deltoides seedlings, but they died out after about 20 years. Populus deltoides then assumed dominance but also disappeared after about 100 years because dying trees were not replaced by seedlings. Disappearance of Populus deltoides allowed a shrub community to invade and, eventually, a grassland community to assume dominance.

The green ash sere shared the sandbar through mature cottonwood communities (Figure 4) with the grassland sere but apparently has a green ash community climax. Fraxinus pennsylvanica first appeared in the young cottonwood community and steadily became more common up





































































































































































































