

WOODLAND EXPANSION IN THE PLATTE RIVER, NEBRASKA: PATTERNS AND CAUSES¹

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Abstract. This research was conducted to identify the factors that have permitted *Populus–Salix* woodland to expand into the formerly active channels of the Platte River and its two major tributaries, the South and North Platte rivers. The research included: pre-settlement vegetation reconstruction based on the General Land Office survey notes, a statistical comparison between historic rates of woodland expansion from aerial photographs and environmental variables, and a field study of seedling demography to isolate the factors controlling recruitment and survival in the modern river.

Woodland expansion began in the South and North Platte rivers around 1900 and spread downstream into the Platte River. By the late 1930s, vegetation had occupied most of the former channel area of the South and North Platte rivers and was expanding into Platte River channels. Rates of channel loss in the Platte River have been as great as 10%/yr during droughts. By 1986, channel-to-woodland proportions were relatively uniform throughout the Platte River system.

Statistical models indicated that sandbar succession to woodland was regulated by three environmental factors: June flows, summer drought, and ice. June flow regulated seedling recruitment and initial survival because it coincided with the main *Populus–Salix* seed germination period. Historic reductions in flow at this time for irrigation and to fill reservoirs exposed much of the riverbed and elevated recruitment and seedling survivorship. Late-summer seedling survival was regulated by factors that affect seedling water balance, including river stage, seedling elevation in the riverbed, and rainfall.

Winter conditions exerted the largest effect on seedling survivorship. Dominant factors were air temperature, streamflow, and seedling elevation in the riverbed. Lowest survivorship occurred during cold, icy winters with relatively high flow and when most seedlings were growing on low sandbars.

The dominant historic trend, of losses in channel area and gains in woodland area, has ceased in recent years. No significant declines in channel area have occurred since 1969; in several reaches channel area has significantly increased since 1969. Comparatively small changes in channel and woodland proportions are expected in the future as long as water use and climate do not change markedly. The steady state has developed because flows have come into balance with active channel area, thereby reducing recruitment and increasing the mortality of tree seedlings. Because of the importance of wide, unvegetated channels to certain avifauna, it may be desirable to manage future flows to ensure no further reduction in channel widths, even if narrowing is only temporary.

Dominance by *Populus* and *Salix* on new sandbars can be explained by life history characteristics. These include large and dependable seed crops that are effectively dispersed by wind and water to optimal germination sites; rapid germination; rapid root and height growth to withstand flooding, drought, and sedimentation; tolerance of low soil fertility; and the ability of *Salix* to reproduce vegetatively. Pioneer vegetation and geomorphic processes (principally sedimentation) facilitate succession on floodplains by modifying the highly variable riverbed environment suitable for early successional species into relatively stable surfaces favorable for recruitment of later successional species.

Much of the extensive *Populus–Salix* woodlands that now occupy the Platte River will be replaced by later successional tree and shrub species with lower associated faunal diversity. Maintenance of the current biotic diversity may require artificial regeneration, as is taking place along other river systems in western North America.

The response of the Platte River to altered flow differed from that of other rivers. This divergent response despite similar disturbances points out the complex interrelationships among plants and hydrogeomorphic processes operating on floodplains and the difficulties associated with understanding, generalizing, and predicting the effects of human modification of streamflow on natural ecosystems.

Key words: demography; geomorphology; hydrology; management; *Populus*; primary succession; remote sensing; riparian woodland; *Salix*; sandbar colonization.

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FIG. 1. Aerial photograph comparison of woodland and channel extent in the Platte River (Nebraska) near the Shelton Bridge (Zone 1), in 1938 (left) and in 1986 (right).

INTRODUCTION

Plant colonization and survivorship patterns are especially complex on floodplains because of a highly dynamic disturbance regime (Wistendahl 1958, Lindsey et al. 1961, Johnson et al. 1976, Nanson and Beach 1977, McBride and Strahan 1984, Hupp and Osterkamp 1985, Streng et al. 1989, Stromberg et al. 1991). The interaction between plant life history traits (e.g., arrival time, growth rate, tolerance to flooding) and the timing, intensity, and scale of hydrogeomorphic disturbances largely determines colonization patterns (Wolman and Leopold 1957, Everitt 1968, Viereck 1970, Keeley 1979, Conner et al. 1981, Hupp 1982, Hupp and Osterkamp 1985, Walker et al. 1986, Harris 1987, Walker and Chapin 1987). Major floods associated with ice and heavy siltation cause high mortality of trees, thereby dramatically affecting forest phyto-mass and composition along elevational gradients (Hosner 1960, Lindsey et al. 1961, Sigafos 1964, Viereck 1966, Bedinger 1971, Johnson et al. 1976, Nanson and Beach 1977, Yanosky 1982). Unusually low flows associated with drought also may cause tree mortality, especially of young recruits, due to intolerably low soil moisture or high surface soil temperatures (Horton et al. 1960, McBride and Strahan 1984, Streng et al. 1989).

Thus, colonization rates, successional trajectories, and the extent and composition of floodplain vegetation are a product of the natural mix of disturbance factors.

Major changes in the vegetation of floodplains in the past half century, especially in the arid and semi-arid regions of western North America, have been attributed to human alteration of natural flow regimes. In the American Southwest, declining populations of *Populus fremontii* Wats. correlate with changes in the magnitude and seasonal timing of flows caused by dams (Ohmart et al. 1977, Fenner et al. 1985, Bradley and Smith 1986, Rood and Mahoney 1990). The absence of a naturally declining river stage, which exposes moist sandbars and banks during a short seed dispersal period, has sharply reduced recruitment of the native *Populus*. Simultaneously, the more stable flows from reservoirs may have favored the spread of exotic species, especially *Tamarix chinensis* (Horton et al. 1960, Turner 1974, Everitt 1980, Turner and Karpiscak 1980, Brothers 1984, Ohmart et al. 1988), which has a life history less dependent on flood events.

Regulation of the Missouri River in the northern Great Plains by dams also has been implicated in the absence of recruitment of *Populus deltoides* Marsh., as well as in a decline in tree growth rate and reduced

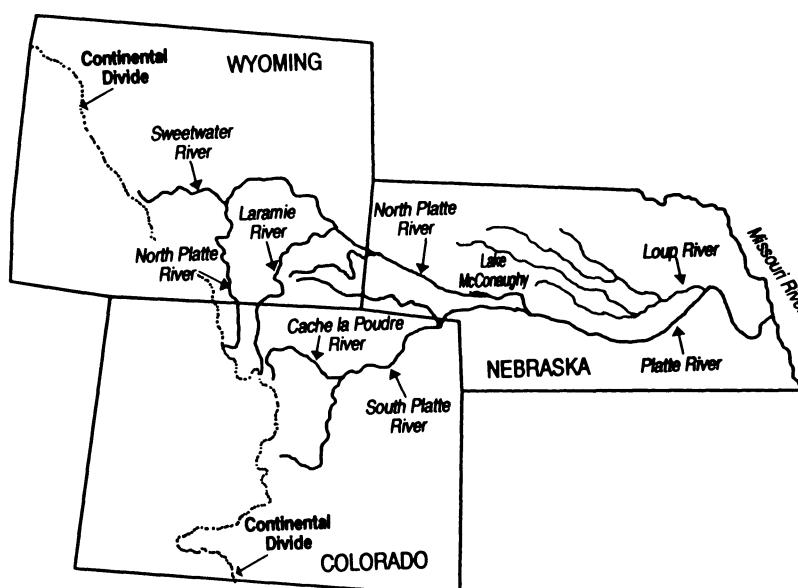


FIG. 2. The Platte River Basin in Colorado, Wyoming, and Nebraska.

sapling survivorship of certain later successional trees (*Ulmus americana*, *Acer negundo*) (Johnson et al. 1976, Reily and Johnson 1982). *Populus-Salix* forests have historically dominated the Missouri River floodplain because of past rapid lateral accretion (point bar deposition) of the river. The precipitous decline in meandering rate after dam construction resulted in a loss of sites for *Populus-Salix* colonization and has been projected to shift forest composition toward later successional species (Johnson 1992).

Although a frequent response of western rivers to flow alteration has been a decline in pioneer *Populus* forests, the opposite has occurred in the central Great Plains along developed rivers such as the Platte and the Arkansas. For example, the Platte, South Platte, and North Platte rivers have been transformed from sparsely wooded pre-settlement conditions with wide, unvegetated channels to a modern condition with extensive *Populus-Salix* woodlands lining much narrower channels (Fig. 1) (Frith 1974, Williams 1978, FWS 1981, Currier 1982, Currier et al. 1985, Sidle et al. 1989). Similar changes have occurred in the Arkansas River (Nadler and Schumm 1981).

The increases in woodland along the Platte River system have been accompanied by numerous environmental changes, including the cessation of prairie fires, elimination of the bison, and extensive water resources development (Currier 1982). The latter includes construction of irrigation and hydropower diversions and dams, and direct pumping of groundwater and river water for irrigation and municipal water supplies. Collectively these have reduced streamflow and altered other hydrologic characteristics of the Platte River system (Williams 1978, USGS 1983, Hadley et al. 1987).

The primary purpose of this research was to identify

the specific factors that have permitted *Populus-Salix* woodland to expand into the formerly active, unvegetated channels of the Platte River system. The problem was divided into three components. First, the pre-development vegetation was reconstructed from the field notes and plat maps of the General Land Office Survey (GLO; contracted by the Surveyor General of the United States) to serve as a reference for post-development changes. The second component was a statistical comparison between the past rates of woodland change and environmental variables, including flow and climate. The third component was a 4-yr demographic field study of *Populus-Salix* births and deaths in Platte River channels in permanently marked plots. Survivorship patterns were then related to river flow and climate. This research component identified the existing environmental control over *Populus-Salix* recruitment and survivorship in the modern river and the prospects for continued change in woodland and channel area.

Collectively, the research contributes to our knowledge of the basic mechanisms of primary succession and the role of humans in affecting hydrology, colonization patterns of pioneer species, and the dominant vegetation associated with rivers in western North America. Specific comparison is made between the Platte and the upper Missouri River, which have exhibited strongly contrasting vegetation responses to flow regulation.

GENERAL ENVIRONMENT

Physiography and geomorphology

The Platte River lies wholly in Nebraska; its two major tributaries, the North and South Platte rivers, both originate high in the Rocky Mountains of Colorado (Fig. 2). The North Platte River (drainage area:

80 000 km²; Kircher and Karlinger 1983) flows from its headwaters northward into central Wyoming, then southeastward into Nebraska. The South Platte River (drainage area: 62 900 km²; Kircher and Karlinger 1983) flows northeastward through Colorado to meet the North Platte River at North Platte, Nebraska (Fig. 2). From this point, the Platte River flows for 501 km until it meets the Missouri River.

The rivers bisect north-south trending climatic zones as they flow through the Great Plains. For example, mean annual temperature increases sharply from the mountain peaks (-1.8°C , mean annual temperature at Mount Evans, Colorado; calculated from NOAA weather data 1984–1988) to the high plains near Denver, Colorado (10.1°C ; from NOAA data 1951–1980), while mean annual precipitation initially decreases along the same elevational gradient but then increases steadily eastward from Denver (38.9 cm; from NOAA data 1951–1980) to Ashland, Nebraska (74.5 cm; from NOAA data 1951–1980) near the confluence of the Platte and Missouri Rivers. The temperature gradient is the result of the declining elevation of the watersheds from ≈ 4300 to 430 m, while the trend of increasing precipitation eastward reflects the declining influence of the rain shadow of the Rocky Mountains.

Other mountain rivers and streams contribute to the flow of the Platte River, including the Laramie River, Sweetwater River, Saint Vrain Creek, Big Thompson Creek, and the Cache la Poudre River. Tributaries that originate in the Great Plains at lower elevations are mostly ephemeral but occasionally provide substantial flow to the Platte River via the South Platte River (Matthai 1969, Osterkamp and Costa 1987).

Historically the large majority of flow in the Platte River system above the Loup River (Fig. 2) was derived from snowmelt in the Rocky Mountains (Eschner et al. 1983). Increased diversion of snowmelt for irrigation in the upstream portions of the basin may have increased the proportional effect of local extreme climatic events such as strong summer thunderstorms on hydrogeomorphology and vegetation dynamics in downstream reaches.

The Platte, North Platte, and South Platte rivers are classified as braided streams, defined by Leopold and Wolman (1957) as those that flow in two or more anastomosing channels around alluvial islands. Braided streams are steeper, wider, and shallower than undivided reaches carrying the same flow (Leopold and Wolman 1957) and are produced under conditions of a steep stream gradient, an ample supply of relatively coarse sediments, and high flows (Schumm 1977, Osterkamp 1978). The Platte River has a steep slope (0.00135 m/m at Odessa, Nebraska; Kircher 1983), wandering thalweg, and friable banks and islands because of the lack of fine bed material ($<15\%$ silt and clay; W. C. Johnson, *unpublished data*). In contrast, the Missouri River is classified as a meandering stream in part because of its gentle gradient (0.00016 m/m at

Omaha, Nebraska; Osterkamp and Hedman 1982), single thalweg, and erosion-resistant banks (mean silt + clay content of 71%, Johnson et al. 1976). Furthermore, the Platte River is relatively shallow, rarely exceeding 2 m, while the Missouri River is much deeper (average depth at Omaha, Nebraska, of 11.6 m; Osterkamp and Hedman 1982).

The Platte River forms a large bend in central Nebraska known as the Big Bend Reach (Fig. 2). That portion between the towns of Lexington and Shelton (see Fig. 5) was designated by the U.S. Fish and Wildlife Service in 1982 as critical habitat for the Whooping Crane (*Grus americana*), a rare and endangered bird which passes through Nebraska during migration between Canada and Texas. *Populus* and *Salix* seedling demography was monitored within this specially designated reach of the Platte River.

Vegetation

The steep climatic gradient in the watershed causes corresponding west-to-east changes in general vegetation. Evergreen forest (principally *Pinus*, *Picea*, and *Abies*) predominates in the Rocky Mountains, while at lower elevations in the Great Plains the rivers flow mainly through grassland vegetation of several types: short grass in the drier west (*Bouteloua*–*Buchloe*) and mixed grass (*Andropogon*, *Bouteloua*, *Buchloe*) and tall grass (*Andropogon*, *Panicum*, *Sorghastrum*) in the more humid east (Kaul 1975). Within the grassland region, deciduous forest (principally *Populus* and *Salix*) is generally restricted to floodplains and other wetlands. The west-to-east trends in vegetation are locally complicated by variation in geology, topography, soils, and disturbance regime.

The earliest system-wide records of the pre-development vegetation (\approx mid-19th century) indicated a mosaic of drier grassland away from river channels, meadow and marsh vegetation on low terraces near the river, and woodland/shrubland on islands and banks. The scattered nature of the woodland in the braided Platte River contrasted sharply with the meandering Missouri River, which was densely forested on low terraces prior to settlement (Weaver 1960, Johnson et al. 1976).

The modern wetland vegetation associated with the Platte River is divisible into grass/sedge meadows (e.g., *Carex*, *Andropogon*, *Panicum*, *Agrostis*, *Calamagrostis*) on low-lying lands outside the high riverbanks and on some large islands; open- and closed-canopied woodland (*Populus deltoides* Marsh., *Salix amygdaloides* Anderss., *Fraxinus pennsylvanica* Marsh., *Acer negundo* L., *Ulmus americana* L.); shrub vegetation (*Salix* spp., *Amorpha fruticosa* L.) along channels and on small river islands; and ephemeral vegetation forming in late summer on low sandbars as flows decline (Currier 1982). Dominant sandbar plants are annuals (e.g., *Cyperus*, *Echinochloa*, *Eragrostis*, *Xanthium*),

which quickly germinate and fruit in late summer. Seedlings of pioneer tree species (*Populus*, *Salix*) often occur with the annuals.

History of water development

The Platte River has a long and complex history of water development that co-occurred with post-settlement ecological changes. The earliest water development for agriculture occurred upstream along the South and North Platte Rivers. Simple irrigation ditches were hand-dug along the South Platte River as early as the mid-1800s (McKinley 1938). With the rapid increase in the number of ditches following the discovery of gold in 1858 near Denver, Colorado, and no significant reservoir storage, summer flows were overappropriated (water rights exceeded flow) by the early 1880s (Eschner et al. 1983, Hadley et al. 1987). Full appropriation of summer flows along the North Platte River did not occur until about 1915 (Eschner et al. 1983, Knopf and Scott 1990).

Dams were built to increase the supply of irrigation water. Reservoir storage was greatest on the North Platte River. Four major mainstem dams were completed on the North Platte River between 1910 and 1956; cumulative water storage in 18 reservoirs was $\approx 8000 \text{ hm}^3$ (U.S. Bureau of Reclamation 1982). The South Platte River basin has smaller storage capacity (3400 hm^3 in 60 reservoirs; U.S. Bureau of Reclamation 1982), primarily in the form of off-channel reservoirs. Flows in the South Platte River have been augmented substantially by transbasin diversions of surface water, primarily from the North Platte River and Colorado River watersheds. In 1974 these diversions totaled 460 hm^3 (Gerlek 1977). Transbasin diversions into the North Platte River amounted to only $\frac{1}{10}$ of this amount (Eschner et al. 1983).

Canal irrigation also began along the Platte River in the mid-1800s but was not as extensive as in the more arid westerly tributaries (Eschner et al. 1983). No mainstem reservoirs were constructed on the Platte River except for small impoundments behind diversion dams. Water diverted at the confluence of the North and South Platte rivers, however, formed a series of off-channel reservoirs used principally for recreation, irrigation, and hydropower. Groundwater in all three basins has been actively exploited for cropland irrigation and for municipal and industrial uses in recent decades (Knopf and Scott 1990).

Water development has affected streamflow in the three rivers. The South and North Platte River hydrographs show divergent time-series patterns. Annual instantaneous peak flow and annual mean discharge in the South Platte River at Kersey, Colorado, appear to have increased with time since 1900 (Fig. 3). In contrast, mean and peak flows have declined sharply during the period of record in the North Platte River at North Platte, Nebraska (Fig. 3). Peak and mean flows

are now only one fourth to one half of those at the start of this century. Flows, however, have stabilized following the end of the major dam-building period in the early 1940s (Fig. 3).

The greater mainstem reservoir storage on the North Platte River and larger transbasin diversions into the South Platte River largely explain the divergent historic hydrographs; however, a decline in peak and mean flows from pre-development levels also may have occurred in the South Platte River but prior to the first hydrograph data. The flow record for the South Platte River began in 1901 at Kersey, Colorado, almost a half century after canal irrigation began. Thus, flows in both rivers may have declined similarly, the South Platte prior to and the North Platte during the period of record.

Downstream in the Platte River, higher low flows followed reservoir construction (Kircher and Karlinger 1983, Hadley et al. 1987). Higher low flows in summer are typical of rivers with upstream flow regulation caused either by controlled releases from dams or by return flows from irrigation (Williams and Wolman 1984). Most gaging stations have recorded fewer days with no recorded flow following development (Williams 1978).

Mean and peak flows in the Platte River also have changed from pre-development levels (Fig. 4). Mean peak flow during 1957–1970 at Overton, Colorado, the gage station with the longest record, was $\approx 30\%$ of that during 1909–1927 (Williams 1978); however, peak flows in the 1970s and 1980s increased sharply from unusually large snowmelt inflows from the Rocky Mountains. The Overton data also indicated comparable reductions in mean annual discharge (Fig. 4). Water development also may have altered sediment transport patterns. It is known, for example, that sediment scavenging by reservoirs causes channel degradation below dams (Williams and Wolman 1984); evidence for this effect throughout the Platte River system is lacking because of the absence of historic cross-section data.

METHODS

Pre-settlement woodland conditions

The records of the United States Survey of the Public Lands were obtained on microfilm from the Nebraska Department of Survey in Lincoln, Nebraska. The geographic scope of the pre-settlement analysis ranged from the downstream end of the Big Bend Reach of the Platte River in Nebraska (Range 9W; near the current city of Grand Island) upstream along the North Platte River to the Nebraska–Wyoming state line (Range 58W; upstream of Scottsbluff, Nebraska) and along the South Platte River almost to Greeley, Colorado (Range 62W) (Fig. 5). The date of the surveys in Nebraska ranged from 1859 (Range 9W) to 1881 (Range 58W), the date of the survey later moving westward. Dates for the

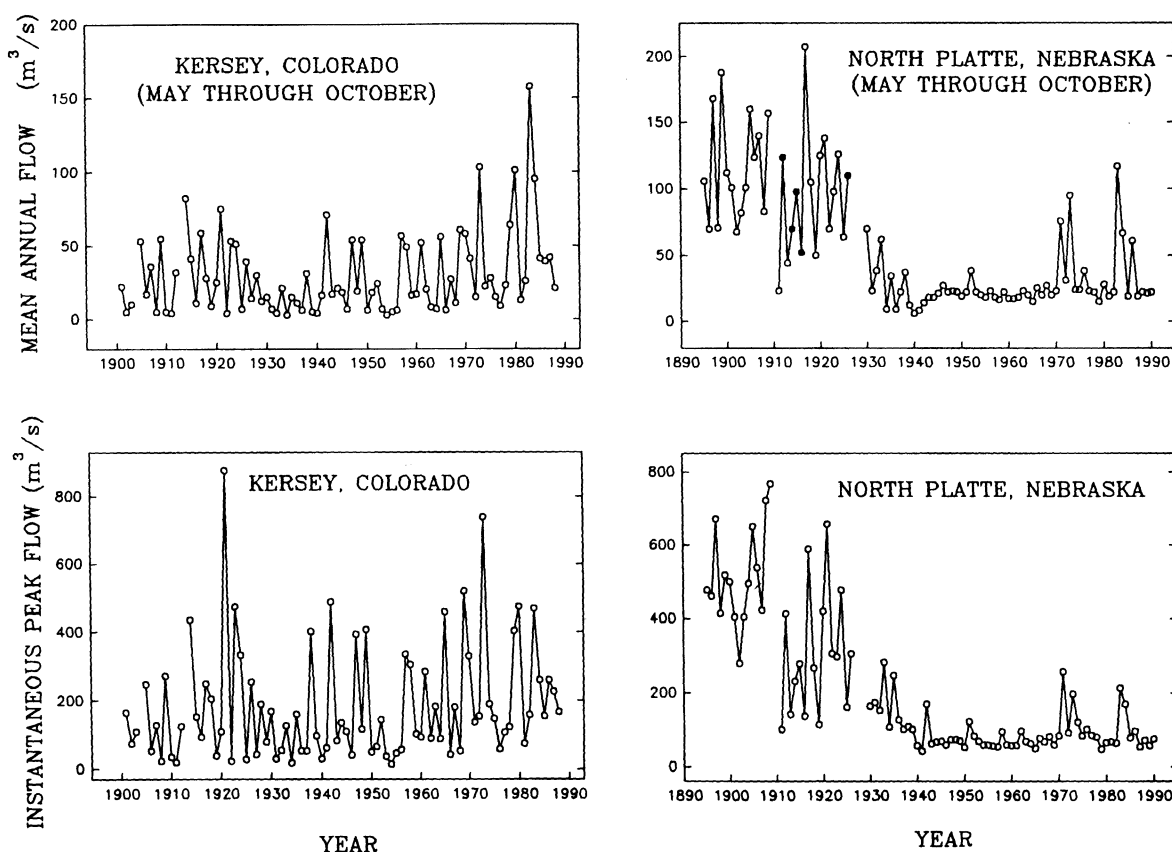


FIG. 3. Comparison of historic seasonal mean and annual peak flow between the South Platte (left, Kersey, Colorado) and North Platte rivers. Darkened symbols denote years with incomplete data from May through October. Mean flow was based on seasonal data (May–October) because the early records did not include flows during the winter. No data were available for 1910 and 1927–1929 at North Platte and for 1904 and 1913 at Kersey. Data are from USGS gages at Kersey and North Platte.

survey of the South Platte River in Colorado ranged from 1866 (Range 64W) to 1873 (Range 44W).

Both the field notes and the plat maps were examined. Entries in field notebooks included measurements of trees used to “witness” the survey corners and lines (Minnick, n.d.). Each witness tree was identified by the surveyors to species, its distance and angle from a line or corner determined, and its diameter measured. Witness trees occurring on the outside banks of the Platte River, its riverine islands, and along the banks of some tributary streams near the Platte River (e.g., Wood River) were included in the sample.

Sampling biases and misidentification of trees by surveyors have been found in other regions. Criteria for selection of witness trees were size and age of the tree, species longevity, distance from the survey corner, and conspicuousness in the stand (Grimm 1984). Because of the scattered nature of trees along the Platte River in pre-settlement times, many of these biases were minimal, since surveyors had few trees from which to pick. Also, misidentification of trees probably rarely occurred along the Platte River because of the low species diversity and morphological distinctiveness of

most species. The most significant bias was probably for size; Grimm (1981) detected a bias toward trees in the mid-size range (diameter at breast height: 25–36 cm).

Later resurveys of two closed military reservations along the Platte River in Nebraska were also examined because river islands were more carefully surveyed and vegetation more completely described than during the original survey. These included the Fort Kearny Island Reservation (Ranges 14–16W) and Fort McPherson (Range 28W), resurveyed in 1877 and in 1897, respectively.

Time series aerial photograph analysis

Historic changes in channel area and riverine vegetation were determined from a time series of aerial photographs. Sixteen reaches, ranging in length from 2 to 11 km, were selected for sampling (Table 1). These included 12 reaches on the Platte River and two each on the North Platte and South Platte rivers (Fig. 5). Reaches were selected to represent the spatial heterogeneity in environment introduced into the modern river by water development projects such as above and

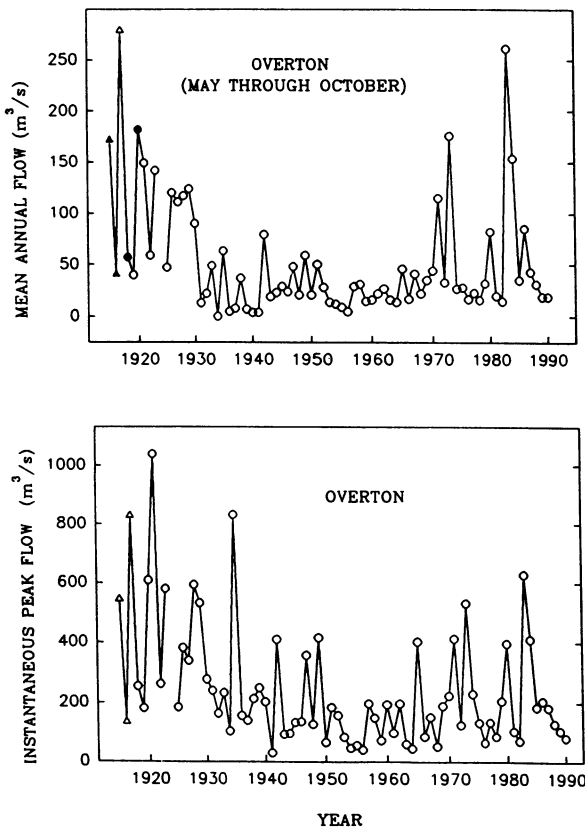


FIG. 4. Historic seasonal mean and annual peak flow at Overton on the Platte River. Triangles indicate data from the Elm Creek gage (near Overton) and circles indicate the Overton gage data. Darkened symbols denote years with incomplete data from May through October. No data were available for 1924. Data are from the USGS gage at Overton.

below major water diversions, water returns, and reservoirs. Local, within-reach variation was reduced by excluding areas with extensive river-margin sandpits, diversion dams, or bridge crossings (except for the Shelton Bridge reach). Some minor diversions and returns were included, out of necessity, in upstream sample reaches due to their high density.

A photograph interval of 5–8 yr was judged to be optimal for detecting vegetation changes. Longer intervals may have masked short-term, yet important, variation in change rates, while vegetation changes may not have been evident during shorter intervals. The most complete series of aerial photographs consistent among reaches was used for the Platte River. Except for the Brady reach, the series began in 1938 and ended in 1986, with intervening dates of 1951, 1956 or 1957, 1963, 1969, and 1978. The widest photograph interval was 13 yr (1938–1951) and the narrowest 5 yr (1951–1956). Black-and-white photographs were chosen for consistency among dates. The photograph dates for the South Platte and North Platte rivers often differed from those on the Platte River. The series began in either

TABLE 1. General characteristics of reaches used in time series aerial photograph analysis.

River and reach name	State	Nearest rangeline	Length (km)	No. sample points
Zone 1—Platte River				
Wood River	Neb.	12W	6.2	555
Shelton Bridge	Neb.	13W	2.0	175
Shelton	Neb.	14W	6.2	337
Kearney-East	Neb.	15W	6.0	373
Overton	Neb.	19W	2.0	796*
Zone 2—Platte River				
Kearney-West	Neb.	16W	3.7	788*
Odessa	Neb.	18W	4.5	624
Zone 3—Platte River				
J-2 East	Neb.	20W	2.5	382
J-2 West	Neb.	21W	2.0	263
Zone 4—Platte River				
Cozad	Neb.	23W	6.0	324
Gothenburg	Neb.	24W	3.0	833*
Brady	Neb.	25W	4.2	295
Zone 5—North Platte River				
Hershey	Neb.	32W	3.9	313
Bridgeport	Neb.	44W	4.5	492*
Zone 6—South Platte River				
Sedgwick	Col.	46W	7.0	238
Balzac	Col.	55W	11.0	417

* Double-sampled.

1937 or 1939 and ended in either 1978 or 1986. Photograph scale was $\approx 1:12\,000$ for photographs from 1951–1986, while earlier photographs were at an approximate scale of 1:24 000. Reaches were assigned to zones based on geographic proximity and similarity of historical trends in rates of woodland expansion (Table 1).

Data were collected by affixing a grid over the sample area of the first photograph of the time series. At each grid intersection occurring between the high banks of the river the cover type was identified. Five broad cover types were used: active channel (unvegetated sand and water), low vegetation (vegetation < 1 m tall occurring between high banks on exposed riverbed and islands), sparse forest (widely spaced trees with non-contiguous crowns), dense forest (densely spaced trees with contiguous crowns), and open land (tended, unwooded land on banks or on large islands between major river channels—mainly land in agriculture). The grid scale resulted in an average of ≈ 100 sample points per river kilometre. Because of differences in reach length, sample size ranged from 175 to 624 points for once-sampled reaches (Table 1).

Use of the computer program AUTOCAD (Autodesk 1985) allowed the sample grid from the first photograph in the series to be relocated on successive photographs. In this way, the same locations were resampled. Digitization of common reference (control) points on each photograph of the time series enabled

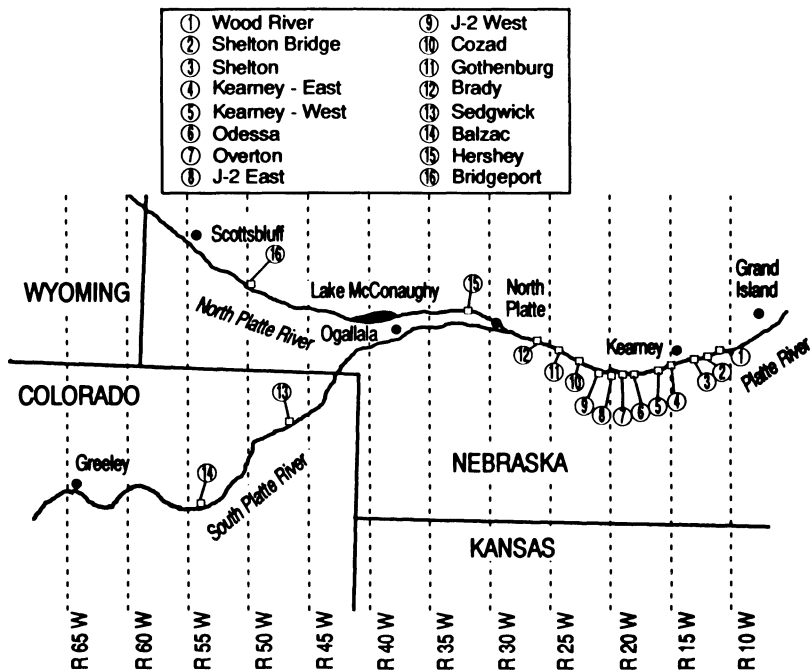


FIG. 5. Location of rangelines (R) in central and western Nebraska in relation to the Platte River and other geographical features. Numbered locations were reaches used in the historic photograph analysis. Demography of *Populus* and *Salix* was studied in reaches 3 (Shelton) and 6 (Odessa).

the program to adjust and match the scales of successive photographs. Control points used most often were permanent farm buildings. The mean error in relocating the same non-control point features on successive photographs ranged among reaches from 2.3 ± 0.7 to 5.6 ± 5.6 m (mean ± 1 SD).

Complete change matrices were constructed for each successive pair of photograph dates in each reach. The change matrix showed all shifts in cover categories that occurred, i.e., the number of sample points in one category that shifted to another category during the time interval. This method allowed not only estimation of the parameters routinely used in photogrammetry (changes in the proportional area of each category over time) but also the origin of the losses and gains in each category. For example, a cover category may have remained stable (i.e., be in steady state) in total area while still exhibiting dynamic behavior by having losses to and gains from other cover categories.

One reach in each of four of the six major zones was double-sampled to obtain an estimate of variance. A second sample was obtained by moving the grid within the same reach boundaries and recalculating the change matrix. This procedure enabled calculation of confidence limits and other expressions of statistical variance for numbers in the change matrix or calculated from the matrix.

Total channel width of the unvegetated river channels (islands excluded)—a linear, not an area, measurement—also was estimated within the same sample

reaches. Width was measured along ten parallel-running transects in each reach for each photograph date using an electronic digitizer and AUTOCAD (Autodesk 1985).

Statistical analysis of channel/woodland change rates

General.—Multiple regression analysis was used to identify possible causes of historic changes in channel and woodland area. Six Platte River reaches were selected: Wood River, Shelton, Kearney-West, Odessa, Cozad, and Gothenburg (Fig. 5). Hydrologic data were from the closest USGS gages with long-term flow records: Grand Island, Odessa, Cozad, and Brady. Flow at Wood River and Shelton was estimated from the Grand Island gage, Kearney-West and Odessa from the Odessa gage, Cozad from the Cozad gage, and Gothenburg was the average of flow at the Cozad and Brady gages.

Dependent variables.—Four dependent variables were selected (Table 2). CHANAREA was the average annual rate of change in channel area during each time interval. This variable was calculated from the change matrix as the percentage of change in the number of channel sample points divided by the number of years in the photograph interval. CHANAREA was positive when channel area increased (vegetation decreased) and negative when it decreased (vegetation increased).

The other dependent variables were obtained by decomposing the net change in channel area into its two components, rate of vegetation erosion (gains to chan-

TABLE 2. Variables used in the multiple regression analysis relating environmental factors to historic rates of change in channel and woodland area.

	Dependent variables
CHANAREA:	Mean annual % change in active channel area
COLONIZ:	Mean annual rate (%) of vegetation establishment from active channel
EROSL:	Mean annual rate of loss (%) of low vegetation to active channel
EROSA:	Mean annual rate of loss (%) of all vegetation to active channel
	Independent variables
JUNE:	Mean June flow (average for period)
JUNEMIN:	Minimum June flow (average for period)
WJUNEF:	Weighted June flow (average for period; see <i>Methods: Statistical analysis . . . : Independent variables: Flow variables for explanation</i>)
JA:	Mean flow during July and August (average for period)
WIDTH:	Total active channel width
ICE:	Values of the ice index (average for period; see <i>Methods: Statistical analysis . . . : Independent variables: Flow variables for explanation</i>)
DURAT:	Duration of peak flows; days within 20% of peak
PEAK:	Maximum peak flow between February and July (single value for period)
PEADUR:	JPK3·DURAT (average for period)
FJPEAK:	Average peak flow between February and July (average for period)
JPK1:	Peak flow 15 May–15 July (average for period)
JPK2:	Peak flow outside 15 May–15 July (average for period)
JPK3:	Maximum peak flow 15 May–15 July (single value for period)
JPK4:	Maximum peak flow outside 15 May–15 July (single value for period)

nel from vegetated categories) and rate of plant colonization (losses from channel to vegetation via succession). Certain environmental variables may correlate more strongly with one of the components than with the net change.

The rate of colonization (variable name COLONIZ) was computed as the percentage of channel sample points that shifted to the low-vegetation category divided by the time interval. Two erosion variables were created. One (variable name EROSL) was the percentage of low-vegetation sample points that shifted to channel, divided by the time interval. The second erosion variable (EROSA) was based on losses from all vegetated categories (low vegetation, sparse forest, dense forest), not just the more erodible low-vegetation category.

Independent variables. — 1. *Ice index.* — An ice index (ICE) was computed for each winter from 1938 through 1986 using a two-component relationship: air temperature and flow. The formation of ice and its effectiveness in removing tree seedlings would be expected to

increase as air temperature decreases and flow increases. Scores for each winter were calculated as follows. First, episodes when the mean daily air temperature was -10°C or colder during December–March were determined from NOAA (National Oceanic and Atmospheric Administration) weather data from Kearney and Gothenburg. If an episode of cold weather occurred for 3–5 d between -18° and -10°C , a score of 3 was assigned to the episode. If an episode of the same length class was below -18°C , a score of 5 was assigned. Higher scores were given to episodes with duration >5 d: 4 for temperatures between -10° and -18°C and 6 for those below -18°C .

For each cold episode less than the -10°C temperature and 3-d duration thresholds, flow during and up to 2 wk after was assigned a score. For the Grand Island and Odessa gages, maximum flows 14–42 m^3/s were assigned a score of 1, 42–85 m^3/s a score of 2, and >85 m^3/s a score of 3. Flows <14 m^3/s were assigned a value of 0. The flow range was scaled differently for Cozad because of the much narrower channels there, i.e., low flows with ice in a small channel could be as effective in removing vegetation as high flows with ice in a wide channel. The range for each flow class was reduced by 37% (the width ratio between Cozad and Odessa in 1938).

The scores for both factors in each cold weather episode were summed for each year. The scoring weighted temperature twice as heavily as flow. The average yearly ice scores ranged among photograph intervals from ≈ 20 through 45.

2. *Flow variables.* — Eight peak-flow variables were assembled (FJPEAK, PEAK, DURAT, JPK1–4, PEADUR; Table 2). These reflected both the magnitude (FJPEAK, PEAK, JPK1–4) and the duration (DURAT, PEADUR) of peak flows. Variables for peak flows during 15 May–15 July corresponded to the approximate seed dispersal period for *Populus* and *Salix*. DURAT would reflect differences between floods of the same magnitude, but with either sharp (short-duration) or flat (long-duration) peaks. The variable PEADUR combined magnitude and duration by multiplying JPK3 by DURAT.

The variable JA characterized late summer, low-flow conditions, while three variables (JUNE, JUNEMIN, WJUNEF) were constructed to represent flows during the seed germination period (Table 2). JUNE was a measure of riverbed exposure during the time when most *Populus* and *Salix* seeds were dispersed. JUNEMIN was the average minimum June flow for a period. Weighted June flow (WJUNEF) gave greater weight to late-June flows nearer the end of the seed dispersal period, which would be more effective than earlier peaks in removing an entire seedling cohort.

3. *Channel width.* — This variable accounted for any effect that differences in width among reaches may have had on rates of vegetation change. For example, rates of woodland expansion in two reaches with the same

flow should be higher in the reach with the greater active channel width, since more substrate would be exposed (assuming similar riverbed cross sections).

Statistical methodology.—The data from the six sites and six time intervals were analyzed using multiple regression analysis (SAS Institute 1985). Models were selected using the all-possible-regressions approach (PROC RSQUARE). When the number of variables was too large for the RSQUARE procedure, stepwise procedures were first used to select the candidate variables. These variables and additional ones that indicated relationship with the dependent variable were then used in the RSQUARE procedure.

Graphical and follow-up analyses of residuals were run to assess the fit of the model and to check for oddities in the data. Two problems occurred. First, the relationships between the explanatory variables and the response variable were not always linear. Logarithmic transformation of the explanatory variable proved most satisfactory. Second, there were two extremely large increases in channel area in the COLONIZ data set for Cozad and Gothenburg in period 6 (1978–1986). Checks on the values indicated that the points were not outliers. The influence of these extreme points was assessed in two ways, first by deleting them from the data set and recalculating the regression equation, and second by computing separate equations for the reaches above (Cozad, Gothenburg) and below (Odessa, Kearney-West, Shelton, Wood River) the J-2 return.

Tree seedling demography

Site selection.—The demographic analysis was confined to the central Platte River. Two sample reaches were chosen to include the widest variety of ecological conditions over a relatively short distance (2–3 km). Specifically, reaches were chosen which included multi-channelled sections of both wide and narrow channels, a variety of riverbank conditions (forest, field, meadow), and a wide range of island and sandbar sizes. Sandbars were viewed as basic experimental units representing different sets of environmental conditions, although not always homogeneous throughout. Sites that included bridges or water diversions were not considered.

Reaches near Shelton and Odessa (Fig. 5) were selected based on the above criteria. The Shelton reach (upstream of the Shelton Bridge) was studied the most intensively with the largest number of sample plots, while Odessa (upstream of the Odessa bridge) served as a check or reference reach to see how well demographic patterns observed at Shelton could be extended to narrower portions of the central Platte. The Odessa reach is circumvented by the Kearney diversion and canal, which has a maximum capacity of $\approx 8 \text{ m}^3/\text{s}$. The canal returns water to the Platte River above the Shelton reach. This is one reason why flows at Shelton are frequently greater than they are upstream at Odessa.

Total active channel width was $\approx 85 \text{ m}$ greater at Shelton than at Odessa in 1986.

Field methods—tree seedlings.—Prior to sampling 1985, 1987, and 1988 cohorts, reconnaissance of all channels in the sample reaches was conducted to locate each landform (usually newly formed sandbars or recently disturbed banks) with first-year tree recruitment. New recruitment on sites with well-established, perennial vegetation (e.g., *Populus-Salix* forest, *Salix* thickets) was not included in the sample.

Each landform was temporarily flagged, numbered (119 at Shelton in 1985), and its general physiographic characteristics recorded (elevation: low, medium, or high; position of seedlings on landform: perimeter or middle; size of adjacent or surrounding channel: small, medium, or large). These three characteristics were used as strata from which to select sampling sites.

Approximately equal numbers of sites were selected in each stratum, where possible, thus obtaining a sample of a wide range of conditions in which seedlings grew. For strata with excess sites, an adequate number was selected randomly. Otherwise, all sites flagged were sampled. In some years, a disproportionately large number of sites occurred in small and medium channels because seedlings were largely absent from the widest channels.

The goal was to maintain ≈ 50 sample plots (25 sites) in the Shelton reach and 10–20 plots (5–10 sites) in the Odessa reach. Establishment of few plots per landform allowed more landforms to be sampled, thereby maximizing the range of environmental variation covered by the plot network.

Sites selected were revisited and plots established. The landform was gridded into numbered cells the approximate size of the sampling frame (1.5 m^2). Plots were then located in (usually) two cells whose numbers were randomly drawn, one at a low point on the landform and the other at a high point.

Each site (i.e., landform) was identified by placing a numbered site marker made of rebar (metal rod) downstream of the site. Plot locations at each site were marked with rebar, which fit through the center of the circular sampling frame. Azimuth and distance from each site marker to the plot rebar were recorded to assist in relocating the plots or to reconstruct the plots if the rebars were removed or buried.

Tree seedlings (*Populus deltoides*, *Salix* spp., *Fraxinus pennsylvanica*, *Acer negundo*, *Ulmus americana*, and *Catalpa speciosa* Warder) were counted in all six sectors of the sampling frame; when seedlings were especially dense, counts were made in only two or three of the sectors selected randomly. Numbered plastic tags were attached to a subsample of the seedlings to estimate population turnover (concurrent mortality of some individuals and reproduction by vegetative means of others) between sampling intervals. *Salix* seedlings were not identified to species because of the difficulty in distinguishing taxa at this stage.

The elevation of plots relative to river stage was determined using a surveyor's rod and level. Measurements were made to the nearest 0.031 m (0.1 foot). The plots were placed on the same relative elevational scale by accounting for changes in stage within and between days in which plots were installed or remeasured. In 1985 and 1986 these adjustments were based on USGS (United States Geological Survey) stage height data from the Kearney gage corrected for the time required for flow at the gage to reach the study area. In 1987 and 1988 elevation adjustments for plots were made based on stage change data from shallow wells dug on the river bank in each reach. The wells were lined with plastic pipe, and stage changes recorded continuously by Stevens gages. The gage data were checked throughout the study by surveys of river elevation near benchmarks installed in 1985. In 1989 elevation adjustments were made from repetitive surveys at the benchmarks during the sample days.

The initial network of sample plots of 1985 cohort seedlings was installed at Shelton in November 1985. The field work was shortened due to ice formation in the river. The sample plot network for this cohort was completed at Shelton and initiated and completed at Odessa during May 1986. In 1987 and 1988 new plots were installed in early to mid-July. No new plots were added to the network in the summer of 1986 because new recruitment was absent.

Measurements were scheduled at the end of a period when a single environmental factor predominated (May: end of ice period and leaves present; July: after peak flows and most seedling recruitment; September: end of summer drought) to help identify specific causes of seedling mortality (see Table 3 for sampling dates). Two winter visits were also made to the Shelton site in 1988 to estimate ice coverage and thickness on sample plots.

Estimates of ice coverage were made from three central Platte River bridges, Kearney, Elm Creek, and Overton, between 15 December 1987 and 29 February 1988. The presence, absence, and percentage of ice cover was estimated in each 6 m wide bridge section extended 12 m into the river.

The demographic data were related statistically to environmental factors using simple correlation and multiple regression analyses. Seedling mortality rate was calculated by sampling interval in two ways: (1) by averaging plot-specific mortality rates across cohorts ("average" mortality rates) and (2) by pooling all seedling cohorts ("proportional" mortality rates). Plot mortality rate also was calculated and defined as the percentage of sample plots that lost their entire population of tree seedlings during an interval. Mortality was event oriented rather than gradual within each interval; therefore mortality rates were calculated by interval (which varied in length according to season) rather than by a discrete time period (i.e., days, weeks). *Populus* and *Salix* seedlings were pooled for most anal-

TABLE 3. Sampling dates and period designation numbers for Shelton and Odessa (Nebraska) study sites, 1985–1989. Winter visits were also made to Shelton on 28 January and 10 March 1988.

Year	Period	Shelton		Odessa	
1985	1	17–18	November	...	
1986	2	16–18	May	19	May
	3	10–11	July	9	July
	4	29	September	28	September
1987	5	19	May	20	May
	6	28	June	...	
	7	9	July	...	
	8	11–14	July	15	July
	9	14–16	September	17	September
1988	10	9–10	May	11	May
	11	10–11	June	...	
	12	6–9	July	8	July
	13	19–20	September	21	September
1989	14	17	May	16	May
	15	13	June	...	
	16	8	August	9	August

yses because of their extremely similar life history traits (Fowells 1965).

The Statistical Analysis System (SAS 1985) was used to sum all individual within-plot mortalities and to calculate a mean and standard error of each type of mortality estimate for each sample date. These means were unweighted, in that an 80% mortality rate in a plot with 10 seedlings contributed as much as an 80% rate in a plot with 500 seedlings. Because plots with very few seedlings might have an unduly large effect on mean mortality and variance, plots with <5 seedlings were deleted from the average mortality estimates.

Some analyses were performed by separating the data into 1st-yr and older cohorts. Sometimes mortality rates were <0 because seedlings may have vegetatively reproduced or germinated late. Negative mortality rates were set equal to zero by assuming that negative mortality meant that no or few seedlings actually died during the interval. This was supported by trends observed in tagged populations.

The proportional mortality rates for Shelton were used in the statistical analysis of demographic patterns. For winter, all seedling ages were lumped, while for spring/summer, seedlings older than one growing season were used. The Shelton data (not the Odessa data) were used because of the larger sample size. Data were divided into three groups by season (winter, spring, and summer). Mortality estimates for each season ($n = 4$ for winter and spring; $n = 3$ for summer) were correlated with a series of environmental variables (see the Appendix).

The goal was to construct winter variables that affected ice formation and thickness in the river (air

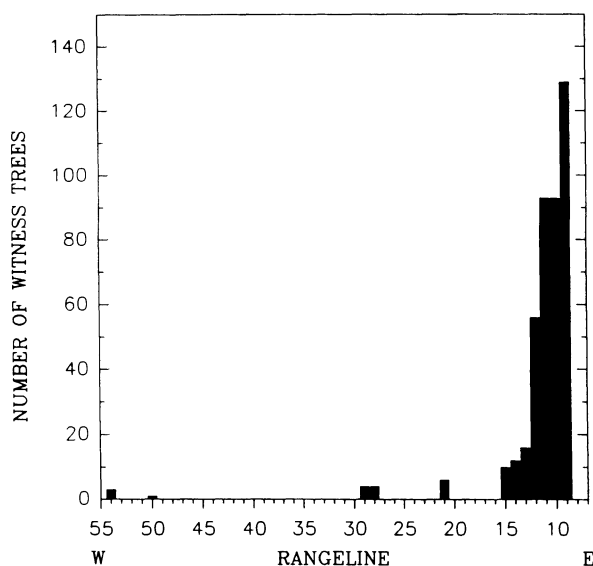


FIG. 6. Geographic distribution of witness trees from Range 9W (Grand Island, Nebraska) to Range 54W (in Nebraska, near the Wyoming state line).

temperature), height at which ice formed in the riverbed (flow), and scouring potential at ice breakup (flow and plot elevation). The indices (e.g., ice index) integrated several factors (primarily air temperature and flow) that could have affected seedling mortality. Some indices were structured to represent discrete events involving ice formation and flow rather than using average values over an entire period or season.

Spring and summer variables included rainfall, air temperature, flow, and elevation (Appendix). Other variables were constructed to estimate important discrete events (e.g., length of drought, consecutive rain-free days).

Seedling mortality also was calculated by channel size (small: <25 m wide, medium: 25–50 m wide, and wide: >50 m wide) to identify differences among channels in their potential for woodland expansion. An index of plot survivorship (rate of plot loss per sample interval) was calculated for 1987 and 1988 cohorts as the percentage of plots lost (i.e., when the last seedling has died) divided by the number of sampling intervals.

Field and laboratory methods—tree seeds.—The sampling objective was to determine the dispersal period and the relative abundance of seeds dispersed, not to estimate seed deposition rates on the ground or water. Both airborne and waterborne seeds were sampled in 1987 and 1988 and their germinability determined. Airborne seeds were trapped in “Tree Bug-Lok” adhesive (Transworld Adhesive and Chemical Corporation), a sticky substance spread on wire screen frames (four sided, each side 23 × 76 cm) suspended from tripods to within 0.5 m of the ground. Trap sites were on exposed banks away from tall vegetation. Larger traps of about twice the surface area (each side 29 ×

122 cm) were used at Shelton in 1988. Deposition (capture) rates were standardized by trap area.

Traps for airborne seeds were set out at ≈1-wk intervals, the seeds identified and counted at the end of each sampling period, and subsamples returned to the laboratory for germination tests. Sampling was not conducted on rainy days, because no airborne seeds were evident.

Populus deltoides seeds were collected in a rectangular-shaped plankton net with the lower rim held just below the water surface. A 1.07 m wide net was used at Shelton, and a 0.79 m wide net was used at North Platte. The mesh size for both nets was 1 mm. *Populus* seeds ranged in length from 3 to 5 mm. *Salix* seeds were too small (<1 mm long) to be collected in this manner. Waterborne *Populus* seeds were collected at ≈1-wk intervals. The length of time that the net was held in the river was recorded and varied according to the abundance of seed. Seeds in net samples were counted and subsamples (≈50 seeds/lot when possible) returned to the laboratory for germination tests.

Seeds were collected at two sites, North Platte and Shelton, Nebraska, to determine how seed dispersal patterns varied geographically. At North Platte four seed traps were used, and net samples were taken at two locations in the river. Six seed traps were established at Shelton because of the wider river there; net samples were taken at three locations, each in a different channel.

Germinability was determined by placing seeds on moistened filter paper in petri dishes in the dark at ≈29°C in a temperature-controlled chamber. Counts of germinated seeds were made after ≈48 h.

RESULTS

Pre-settlement woodland vegetation

Composition and geographic distribution.—A total of 431 witness trees was enumerated in the General Land Office (GLO) survey notes along the Platte River system in Nebraska west of Grand Island. Witness trees were most frequent in the downstream (easterly) portion of this reach (Fig. 6). The largest number of trees (129) per 9.7-km (6-mile) segment occurred between Ranges 9W and 10W (west of the 6th principal meridian), upstream of Grand Island. Beyond Range 15W numbers were sporadic, with the majority of segments without witness trees.

The surveyors' witness tree records and general field notes (see *Methods: Pre-settlement woodland conditions*, above) indicated that trees occurred both on outside river banks and on islands in the lower half of the central Platte, i.e., below Kearney. Farther west, in the upper half of the central Platte, the few trees recorded grew on islands in the river, not on banks. Farther upstream, along the South Platte River in Colorado, references to woodland were rare and few witness trees were recorded. Thus, riparian woodland decreased

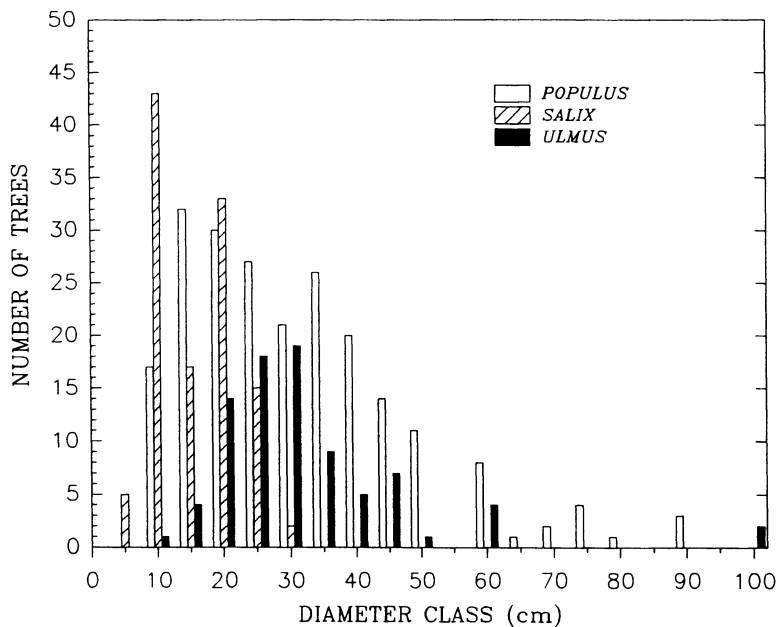


FIG. 7. Size (diameter) distributions for the major species of witness trees recorded along the Platte River system in Nebraska during the General Land Office Survey (late 1850s to late 1880s). Size classes were 5-cm intervals (i.e., 0–5 = 5-cm-diameter class, >5–10 = 10-cm class, etc.).

sharply from the central Platte River upstream into the lower portions of the South and North Platte rivers.

Numerous references were made to evidence of tree cutting prior to the survey along or near the central Platte in Nebraska. The following notebook entries are representative:

1) “The margin of the streams or channels of the Platte has been quite well timbered with cottonwood and elm but it has been nearly all cut down and carried away leaving only scattered timber” (Range 9W, Township 10; 1866)

2) “. . . banks of island have timber all cut off.” (Range 20W, Township 8; 1862)

3) “The wood has been mostly all taken off the islands but there are yet many young trees of cottonwood and elm.” (Third Standard Parallel through Range 29W; 1869)

Three species of witness trees dominated the Platte River woodlands between Ranges 9W and 58W during early settlement. Cottonwood (*Populus deltoides*) was the most frequent, comprising 218 of the 431 witness trees (Fig. 7). American elm (probably *Ulmus americana*) exhibited the widest size range (diameter: 10–100 cm) and was the largest in diameter. Willow trees (probably *Salix amygdaloides*) were numerous but much smaller in size.

From one to two individuals of minor species were recorded as witness trees. Box elder (*Acer negundo*), ash (*Fraxinus pennsylvanica*) and oak (*Quercus macrocarpa* Michx.) occurred in central Nebraska, while pine (*Pinus ponderosa* Laws.) and cedar (probably *Juniperus*

scopulorum Sarg.) occurred as witness trees in westernmost Nebraska.

The absence of trees in the 0–5 cm size class for most species (Fig. 7) suggested that surveyors selected against small trees (Grimm 1984). The shape of the size-class distributions for larger trees (>15-cm-diameter class) indicated relatively stable regional population structure (Goff and West 1975).

Islands.—Study of the field notes revealed that most small islands were not surveyed and therefore not drawn on plat maps. Knowledge of the actual pre-settlement mix of riverine islands was important because islands not found on the plat maps have been assumed to represent evidence of channel narrowing and woodland expansion when they appear in the first basin-wide photographs in the late 1930s. The following excerpts document the abundance of small islands:

4) “The Platte River is a very shallow stream, and may be crossed at any point most seasons of the year. It is filled with islands of all sizes, which mostly have some cottonwood and willow on them.” (Range 20W; 1865)

5) “I see numerous other islands north, too small to survey. I then waded across the whole of the South Platte River (south fork of the Platte River near old Ft. McPherson), examining the islands which appear large, but find them mostly long and narrow and of very slight value, not worth surveying. The islands which are covered with grass, brushes [sic] and small trees, are very permanent in their appearance, and not subject to overflow.

TABLE 4. Proportion of bank-to-bank channel width in the unvegetated (active) category on 1937 and 1938 photographs of reaches on the South Platte, North Platte, and Platte rivers. Data are arranged from east (downstream) to west (upstream).

Reach name (Range)	Proportional area (%)
Platte River	
Wood River (R12)	54
Shelton (R14)	64
Kearney-East (R15)	44
Kearney-West (R16)	80
Odessa (R18)	54
Cozad (R23)	55
Gothenburg (R24)	29
Brady (R26)	50
North Platte River	
Hershey (R32)	38
Bridgeport (R44)	16
South Platte River	
Sedgwick (R47)	13
Balzac (R55)	10

“Timber cottonwood, cedar, elms—thick growth of brush on islands. River full of small islands and sandbars with very little water.” (Range 28W; 1899)

6) “The river at this point is very shallow, quicksand bottom and filled with immense numbers of small islands covered with timber and brush.” (Range 29W; 1869)

Islands were not surveyed for several reasons. First, small islands were thought to have no agricultural value. Second, they were so numerous as to be too costly to survey individually. The instructions to the General surveyors of the U.S. Public Lands (1864) state, “Many

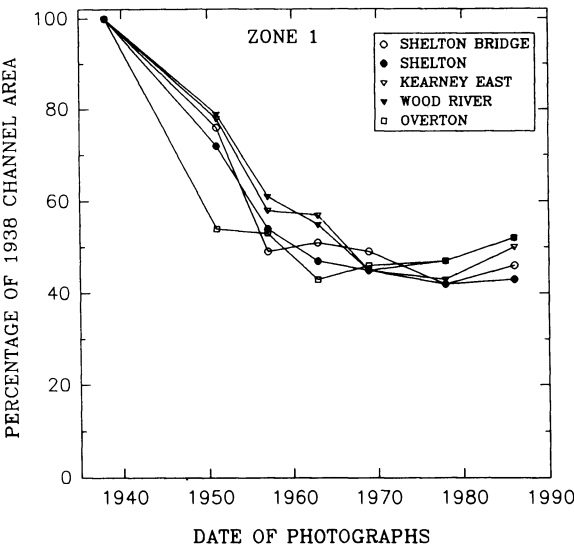


FIG. 8. Changes in active channel area in Zone 1 reaches from 1938 through 1986. Starting channel area in 1938 was set equal to 1.

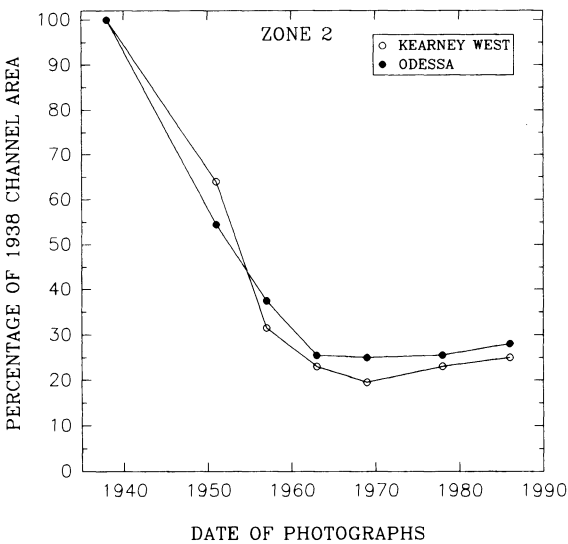


FIG. 9. Changes in active channel area in Zone 2 reaches from 1938 through 1986. Starting channel area in 1938 was set equal to 1.

applications are received at this office for the purchase of small unsurveyed islands which were omitted when the adjacent lands were surveyed. These islands are usually of too little value to justify the Government in incurring the expense of survey; but where a party desires the survey made and is willing to pay for the cost thereof in advance . . . , it may be done . . . ” (cf. Minnick, n.d.). Third, some islands were not surveyed because the river was not actually crossed by the surveyors. Fourth, there may have been bias against small islands depending on the method by which surveyors measured distances across river channels. More islands were surveyed when distances were chained rather than triangulated.

One quantitative estimate of the extent to which islands were left off the original survey was made by comparing the plat map (1897) with a later map (1899) based on a more detailed island survey of the Platte River near Fort McPherson (Range 28W). The average proportion of the river width comprised of islands was 4.2% for the original map and 11.5% for the island survey—a difference of $\approx 7\%$. The resurvey field notes also indicate that numerous very small islands were still not measured on the special island survey; these probably would have accounted for at least several additional percentage points. Thus, for this 9.7-km (6-mile) reach, the total active channel width would have been perhaps 10% (or more) less than as depicted on the original plat maps.

Post-settlement changes in channel and woodland area

Changes in channel area.—The changes in the active channel–woodland mosaic between the time of the GLO surveys and the first extensive aerial photographs of

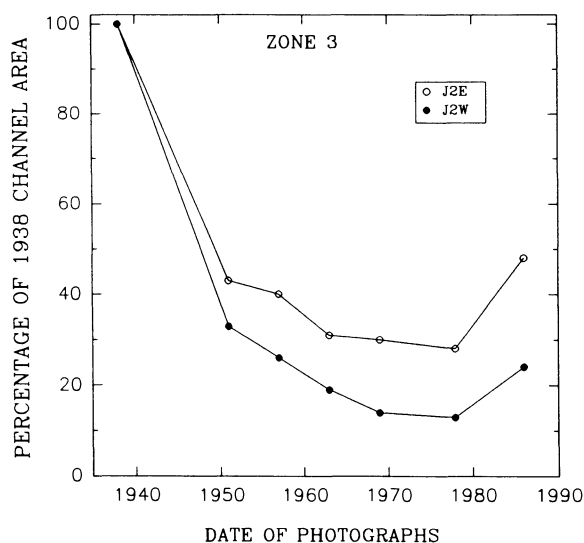


FIG. 10. Changes in active channel area in Zone 3 reaches from 1938 through 1986. Starting channel area in 1938 was set equal to 1.

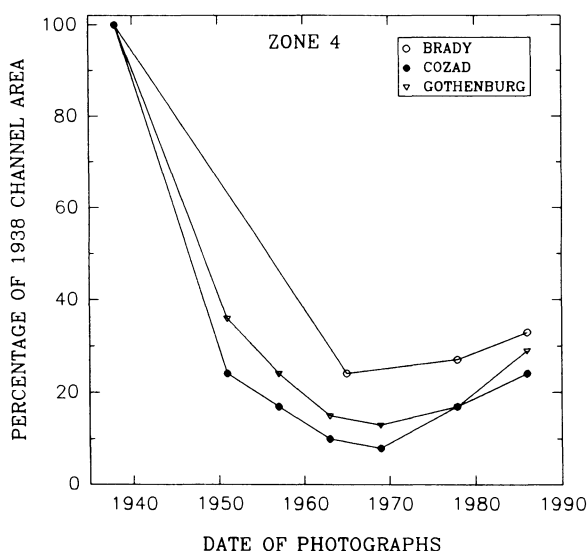


FIG. 11. Changes in active channel area in Zone 4 reaches from 1938 through 1986. Starting channel area in 1938 was set equal to 1.

the river (late 1930s) cannot be accurately reconstructed. Some resurveys conducted in the early 1900s to settle disputes over the ownership of islands in the North Platte River indicate that woodland began to expand into the North Platte River about 1900.

Woodland expansion occurred earliest in upstream reaches. By the late 1930s, aerial photographs showed that much of the pre-settlement active channel in the North and South Platte rivers had succeeded to woodland. For example, <20% of the total channel width remained unvegetated by 1937–1938 in the upstream tributaries (except Hershey), while >50% of the width remained unvegetated in most Platte River reaches downstream (Table 4).

Woodland expansion rates since the late 1930s have been highly variable in space and time. All Zone 1 reaches (Table 1) showed a sharply declining channel area between 1938 and 1951 (Fig. 8), a gradually slowing rate of loss from 1951 to 1978, and a slight increase in the last photograph date. Overall, channel area in 1986 for Zone 1 reaches was \approx 50% of that in 1938 (Fig. 1).

Zone 2 reaches were closer to the Kearney diversion and had higher initial rates of channel loss than in Zone 1 (Figs. 8 and 9). Channel area in 1956 was only 30–40% of the 1938 area. By the mid-1960s, however, channel area had essentially stabilized (Fig. 8) at \approx 25% of that in 1938.

Zone 3 reaches showed contrasting rates of channel change (Fig. 10). Channel area below the J-2 Return (J-2 East) declined less sharply than did the upstream reach. Between 1978 and 1986, both reaches exhibited dramatic increases in channel area. The channel area of J-2 West in 1986 was its largest since 1938.

The reaches in Zone 4 showed the largest post-1938

declines in channel area (Fig. 11). Channel area at Cozad had declined to 7% of its 1938 area by 1969. After 1969, channel area increased substantially at all three reaches. By 1986 it had more than tripled at Cozad and Gothenburg, resulting in channel area \approx 25% of that in 1938.

Trends for the two reaches on the North Platte River (Zone 5) ranged from a large decline in channel area below to a moderate increase above Lake McConaughy (Fig. 12). Hershey (below Lake McConaughy) showed marked declines in channel area similar to those for

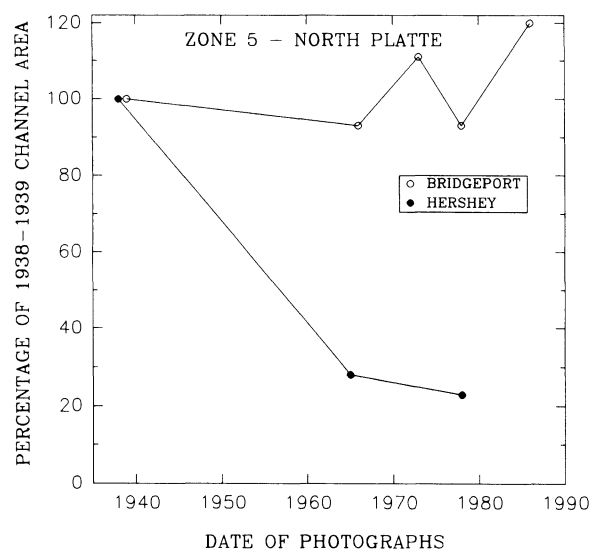


FIG. 12. Changes in active channel area in Zone 5 reaches from 1938 through 1986. Starting channel area in 1938 was set equal to 1.

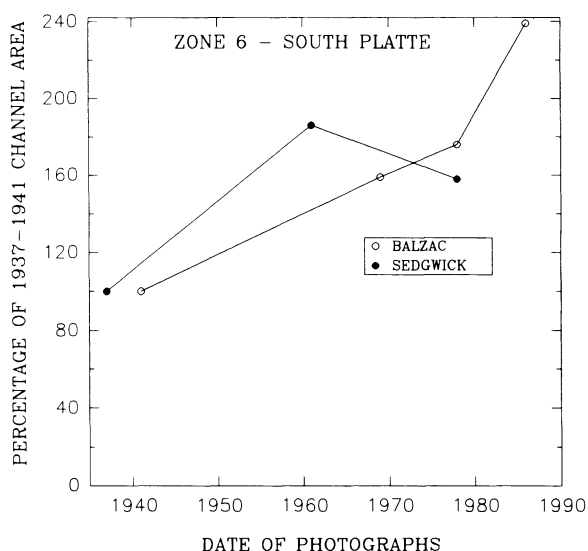


FIG. 13. Changes in active channel area in Zone 6 reaches from 1937 through 1986. Starting channel area in 1937 was set equal to 1.

Zone 4, with channel area $\approx 20\%$ of its 1938 area by the late 1970s. In contrast, unvegetated channel area at Bridgeport above Lake McConaughy exhibited two episodes of reduction each followed by noticeable increases. Historic trends in channel area apparently are highly variable from place to place in the North Platte River (McDonald and Sidle 1992).

Both reaches in Zone 6 (South Platte River) showed increases in channel area since the late 1930s (Fig. 13). Channel area at Balzac increased steadily over time; 1986 area was over twice the 1939 values. Channel

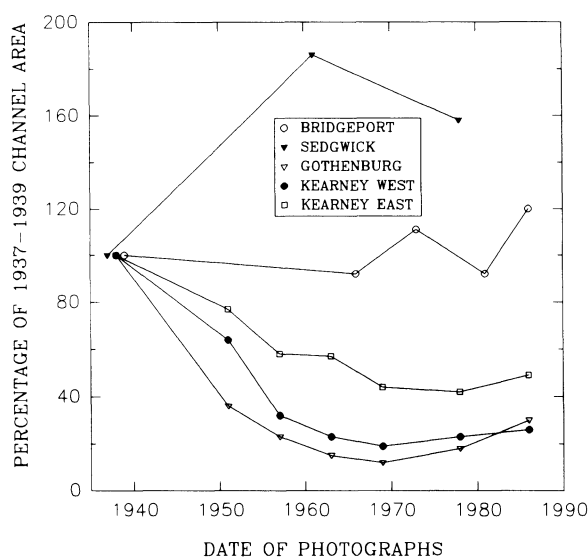


FIG. 14. Changes in active channel area for five representative double-sampled reaches (1 each from 5 zones) from 1937 through 1986. Initial channel area was set equal to 1. Reach names in the key are ordered from west (top) to east (bottom).

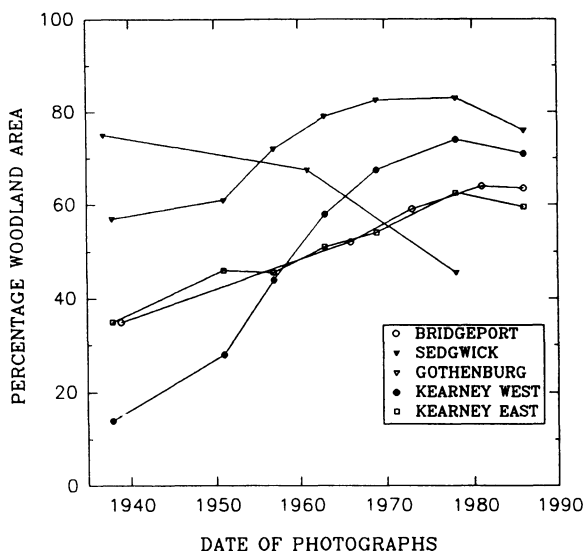


FIG. 15. Changes in woodland cover for five representative reaches (1 each from 5 zones) from 1937 through 1986. Initial channel area was set equal to 1. Reach names in the key are ordered from west (top) to east (bottom).

area for Sedgwick in 1979 was ≈ 1.5 times the 1939 area. The relatively consistent increases in Zone 6 reaches contrasted strikingly with those in other zones.

A composite graph with one curve from each of five zones clearly shows the dichotomy between post-1938 channel dynamics on the North and South Platte rivers vs. the Platte River (Fig. 14). Channel area generally was stable or sharply increased with time along the upstream tributaries (but recall Hershey in Fig. 12), while in all cases downstream in the Platte River, channel area was at a maximum in the earliest photographs (late 1930s) and declined thereafter.

Changes in woodland area.—Woodland area in the double-sampled reaches (Fig. 15) generally was the inverse of channel area because most channel area losses were gains to the low vegetation and woodland categories via natural succession. Kearney-West exhibited the sharpest increase. Bridgeport and Kearney-East exhibited virtually identical curves despite being located hundreds of kilometres apart and on different rivers. A large proportion of the woodland increase at Bridgeport was from the low vegetation rather than from the unvegetated channel category, which explains the significant increase in woodland but rather stable channel area.

Sedgwick (South Platte River) exhibited a contrasting trend of rather sharply declining woodland area over the period 1937–1978 (Fig. 15). This reach had the highest initial (1937) proportion of woodland among the zonal representatives.

All reaches showed declines in woodland area during the last photograph interval (Fig. 15). The largest decline occurred over a longer time at Sedgwick; declines in the other reaches for shorter intervals were more

TABLE 5. Channel area (as a proportion of floodplain area) from 1966 to 1986 for five double-sampled reaches.* The ANOVA *P* values are for overall differences among years.

Reach	ANOVA <i>P</i>	Date of photographs					
		1966	1969	1973	1978	1981	1986
Gibbon	.724	...	0.610 ^A	...	0.592 ^A	...	0.591 ^A
Kearney-West	.001	...	0.161 ^A	...	0.183 ^B	...	0.202 ^C
Overton	.033	...	0.158 ^A	...	0.157 ^A	...	0.171 ^B
Gothenburg	.024	...	0.042 ^A	...	0.040 ^A	...	0.082 ^B
Bridgeport†	.082	0.139 ^A	...	0.181 ^B	...	0.159 ^{AB}	0.189 ^B

* Analysis of variance was used to test for differences in channel area across each time series within each reach. Differences between years were tested using the least significant difference (LSD) test. Channel area proportions were arcsine transformed prior to analysis. Numbers in a time series were the same superscript letter are not significantly different at the .05 level. Reaches are arranged in order from east to west (upstream).

† For Bridgeport, although differences were significant at .05 in LSD, significance can only be claimed at .082 from the ANOVA.

modest, from ≈8% at Gothenburg to only 1–3% in the other Platte River reaches. These declines in woodland were generally somewhat smaller than the corresponding increases in channel area, indicating that some channel sample points formerly were non-forest cover categories (i.e., low vegetation, agriculture).

Statistical analysis of channel area/width changes.—Analysis of the double-sampled reaches showed no statistically significant declines in channel proportion since 1969 (Table 5). In contrast, significant increases in channel proportion occurred at four of the five reaches. Channel area at Kearney increased steadily and significantly between 1969–1978 and 1978–1986. Gothenburg only widened significantly between 1978 and 1986 and doubled in channel area.

Patterns of change in channel width based on linear measurements were similar to those based on area measurements (Table 6). For example, no reach exhibited a significantly narrower channel in 1986 than in 1969 or 1978; some reaches showed significant widening between 1978 and 1986. Two of the reaches exhibited significant short-term narrowing during the time series (Bridgeport and Wood River), but both widened later. These analyses indicate that the sharp and steady narrowing pattern evident during the first part of the time series has not continued in recent years.

Annual rates of channel area change.—Average an-

nual rates of change in channel area were calculated for each photographic period for use as dependent variables in multiple-regression analyses. Plots of these values clearly distinguish periods of low, moderate and high rates of change in channel area (Figs. 16–18). Negative values correspond to periods of decrease, while positive values correspond to periods of increase in channel area.

Curves for Zone 1 reaches generally rose toward the 0 line with increasing photograph date, indicating a shift with time towards more stable channel area (Fig. 16). Channel area loss rates for Zone 2 reaches were higher than in Zone 1 reaches early in the time series, especially between 1951 and 1956 (Fig. 16). The 10%/yr average reduction in channel area in the Kearney-West reach between 1951 and 1956 was the largest rate of channel loss of any interval in any reach.

Whereas Zone 2 reaches exhibited the highest negative change rates in the data set, Zone 3 reaches exhibited some of the highest positive values of ≈10% average annual gain in channel area between 1978 and 1986 (Fig. 17). These reaches exhibited the most contrasting time series, with high rates of channel loss early in the time series and high rates of channel increase late in the time series.

Change rates for Gothenburg and Cozad (Zone 4) paralleled those of Zone 3 (Fig. 17). Prior to 1969, rates

TABLE 6. Channel width (in metres) since 1965 for nine reaches along the North Platte and Platte rivers in Nebraska.* The ANOVA *P* values are for overall differences among years.

Reach	ANOVA <i>P</i>	Date of photographs							
		1965	1966	1969	1973	1978	1981	1986	1989
Wood River	<.001	287.1 ^A	...	182.8 ^B	...	272.1 ^A	...
Shelton	>.50	351.6 ^A	...	334.9 ^A	...	327.0 ^A	...
Kearney-East	>.50	320.9 ^A	...	322.2 ^A	...	312.3 ^A	...
Odessa	>.50	225.1 ^A	...	223.4 ^A	...	239.4 ^A	...
J-2 East	<.001	228.3 ^A	...	247.1 ^A	...	338.2 ^B	...
Cozad	<.001	96.1 ^A	...	114.7 ^A	...	190.4 ^B	...
Gothenburg	<.001	71.5 ^A	...	69.2 ^A	...	148.1 ^B	...
Hershey	>.50	84.9 ^A	81.7 ^A	82.5 ^A
Bridgeport	<.001	...	133.7 ^A	...	186.2 ^B	...	156.4 ^C	194.7 ^B	...

* Differences between years in channel width were tested using analysis of variance and a test of least significant difference (LSD). Numbers in a time series with the same superscript letter are not significantly different at the .01 level.

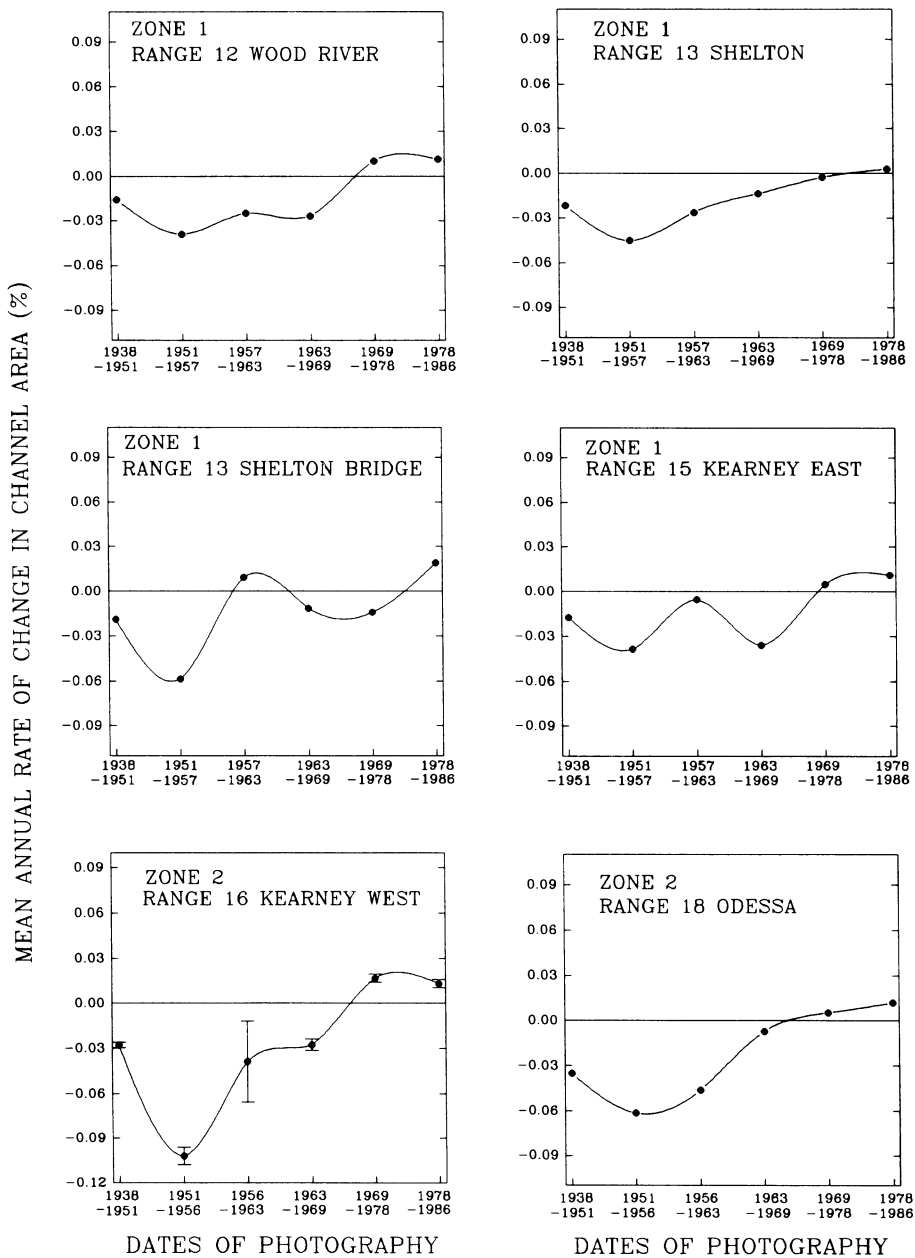


FIG. 16. Average annual rate of change in channel area for Zone 1 and 2 reaches. Negative values indicate channel area decrease; positive values indicate channel area increase. Curves were smoothed using the cubic spline function in Sigma-Plot 5.0 (Jandel Scientific, San Rafael, California, USA). Vertical bars for double-sampled reaches are standard errors of the mean.

were moderate and steady, causing large cumulative declines in channel area. After 1969, rates rose sharply above the 0 change line. The rate of almost 14%/yr for Gothenburg between 1978 and 1986 was the largest rate of channel area increase across all dates and sites. The two North Platte reaches (Zone 5) had strongly contrasting trajectories of change (Fig. 18). Zone 6 reaches on the South Platte River were unique because most of the values in the series were positive (Fig. 18).

System-wide trends.—A steep and statistically sig-

nificant east-west gradient ($P < .001$) existed in the proportion of the floodplain occupied by unvegetated channel in the late 1930s (Fig. 19). Channel proportion ranged from $\approx 70\%$ of the floodplain in downstream (easterly) reaches to $\approx 10\text{--}20\%$ in the upstream (westerly) reaches. The direction of the trend sharply contrasted with the pre-development pattern of decreasing woodland westward.

By 1986 this strong gradient was no longer apparent (Fig. 19). The result of slight increases in channel area

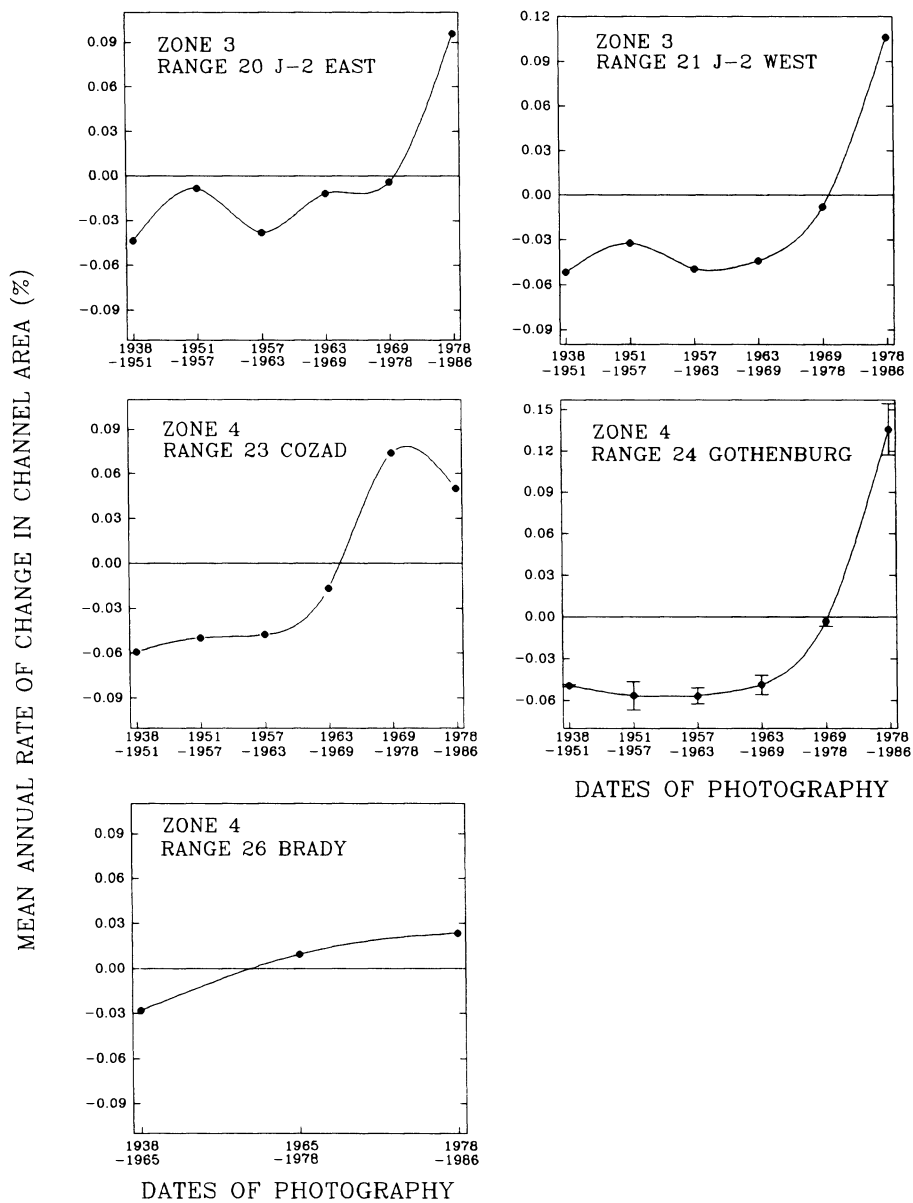


FIG. 17. Average annual rate of change in channel area for Zone 3 and 4 reaches. Negative values indicate channel area decrease; positive values indicate channel area increase. Curves were smoothed using the cubic spline function in Sigma-Plot 5.0 (Jandel Scientific, San Rafael, California, USA). Vertical bars for double-sampled reaches are standard errors of the mean.

in most westerly reaches and a dramatic reduction in the easterly reaches produced a distinct flattening of the regression line and some increase in proportional width variation resulting in a nonsignificant east-west trend.

The photographic record indicates that the river system has become more homogeneous from east to west in the mix of channel and woodland categories. Significant woodland expansion occurred first in upstream reaches of the North and South Platte rivers, which was followed later in time by a comparable expansion downstream in the Platte River. Thus, the changes have cascaded with time downstream from west to east.

Causes of woodland succession

Several statistically significant and ecologically meaningful models resulted from the multiple-regression analysis that related historic rate of change in channel area to environmental factors (Table 7). Sets of environmental variables were found to significantly correlate with two of the four vegetation (dependent) variables: COLONIZ (rate of establishment of new vegetation patches from channel) and CHANAREA (net change in channel area). Both models were improved by dividing the data into two groups, one including reaches below and the other reaches above the J-2 Return.

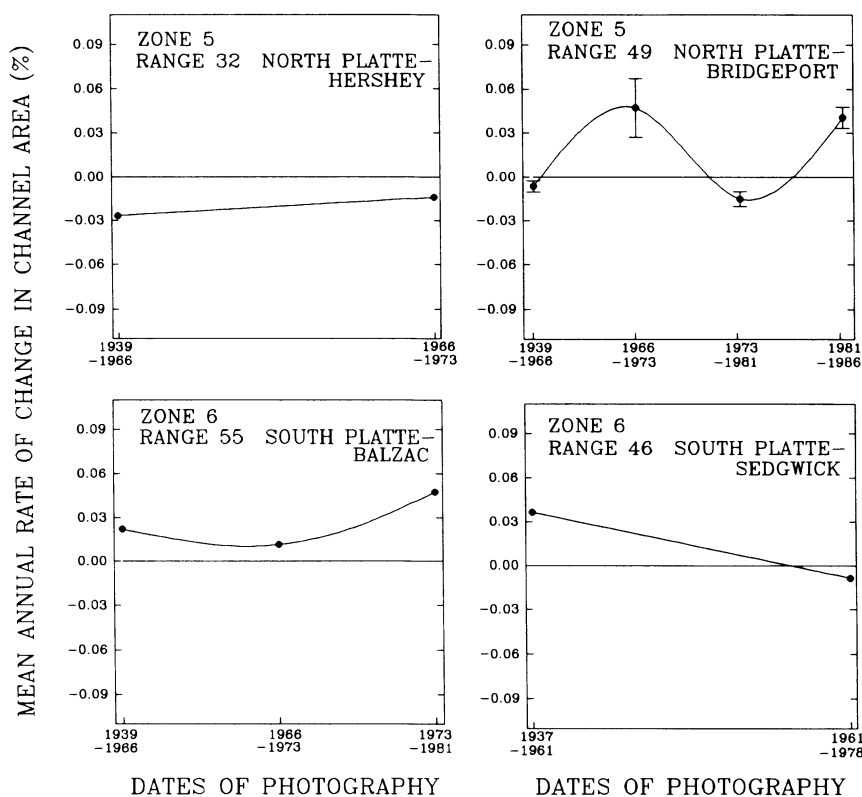


FIG. 18. Average annual rate of change in channel area for Zone 5 and 6 reaches. Negative values indicate channel area decrease; positive values indicate channel area increase. Curves were smoothed using the cubic spline function in Sigma-Plot 5.0 (Jandel Scientific, San Rafael, California, USA). Vertical bars for double-sampled reaches are standard errors of the mean.

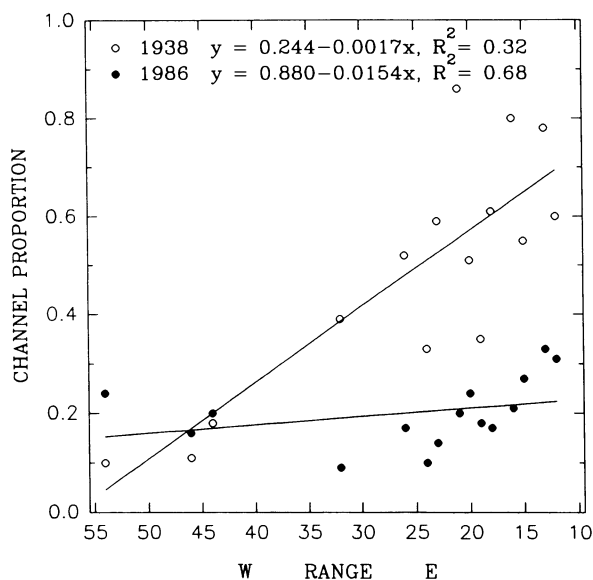


FIG. 19. Relationships between 1938 (○) and 1986 (●) channel area and reach location from west (Range 54W) to east (Range 12W). Regression for 1938 area was statistically significant ($P < .001$), while it was nonsignificant ($P > .05$) for 1986 area.

Four of the 14 environmental variables appeared as significant factors in the models: JUNE, JPK3, ICE, and WIDTH. The log-transformed equivalents (e.g., natural log of June flow, LJUNE) were usually stronger, indicating a curvilinear relationship between most vegetation and environmental variables.

Erosion/colonization.—The spatio-temporal pattern of colonization was best explained by a two-variable model: LJUNE and LPK3 (Table 7). Both were inversely correlated with colonization, indicating that the formation of new vegetation patches was favored by lower mean and peak flows during the seed dispersal period. LJUNE and LPK3 were of comparable strength in the model. The erosion models were considerably weaker than the colonization models, and included factors more difficult to interpret ecologically.

Splitting of the colonization data into reaches above or below the J-2 Return produced a stronger model for the downstream sites ($R^2 = 0.933$; Table 7). LPK3 was the dominant explanatory variable, as it was for the pooled model, but ICE entered as a second significant but weaker variable. This model suggested that over 5–10 yr time intervals, ice may have reduced overall colonization rates.

Net change in channel area.—The statistical model

TABLE 7. Statistically significant regression models. Independent variables are listed from left to right in decreasing order of importance in explaining variation in the dependent variable.

Dependent variable	Independent variable*		Error df	R ²	P
COLONIZ	LJUNE	LPK3	33	0.771	.0001
COLONIZ					
Downstream reaches (O, K, S, W)†	LPK3	ICE	21	0.933	.0001
EROSA	LJUNE	JPK3	33	0.608	.0001
CHANAREA					
All reaches	LJUNE	LWIDTH	33	0.756	.0001
Upstream reaches (G, C)†	LJUNE	LWIDTH	9	0.770	.0013
Downstream reaches	LJUNE	LWIDTH	21	0.866	.0001

* Variable names are translated in Table 2. The “L” prefix indicates the log-transformed variable.
† O = Odessa, K = Kearney-West, S = Shelton, W = Wood River, G = Gothenburg, C = Cozad; see Table 8 for models.

that best explained historical variation in the net change (%) in channel area (CHANAREA) included two environmental variables: LJUNE and LWIDTH. The model was significant ($P < .0001$) and accounted for 75.6% of the variation in CHANAREA (Table 7). LJUNE was positively correlated, while LWIDTH was negatively correlated with CHANAREA. Thus, rates of channel area loss were higher during periods of lower June flow and in wider reaches. LWIDTH was a significant, yet minor, component of the model.

The relationship of LJUNE and LWIDTH was strengthened by producing separate models for upstream and downstream reaches. R^2 increased to 0.866 for the upstream reaches and to 0.770 for the downstream reaches (Table 8).

The graphic relationship between CHANAREA and JUNE (linear scale) is shown in Fig. 20, together with

the regression line from the model $CHANAREA = B_0 + B_1 JUNE$. CHANAREA values ranged from $-10\%/yr$ at Kearney-West during period 2 to almost $15\%/yr$ at Gothenburg during period 6 (Fig. 20). Mean June flows (multi-year averages) ranged among photo intervals from ≈ 10 to $140\text{ m}^3/s$.

The regression line (Fig. 20) showed channel area change loss rates of $5\%/yr$ at mean June flows of $\approx 15\text{ m}^3/s$. Channel change rate was slightly positive (i.e., channel widening) at mean June flows near $120\text{ m}^3/s$. The regression line crossed the no-net-change line (i.e., in channel width/area) at $\approx 80\text{ m}^3/s$ (from model $CHANAREA = B_0 + B_1 LJUNE$; Table 8), suggesting that flows in this range would result in relatively stable channel widths.

The flow estimate of $80\text{ m}^3/s$ to prohibit woodland expansion was an average of all reaches and did not

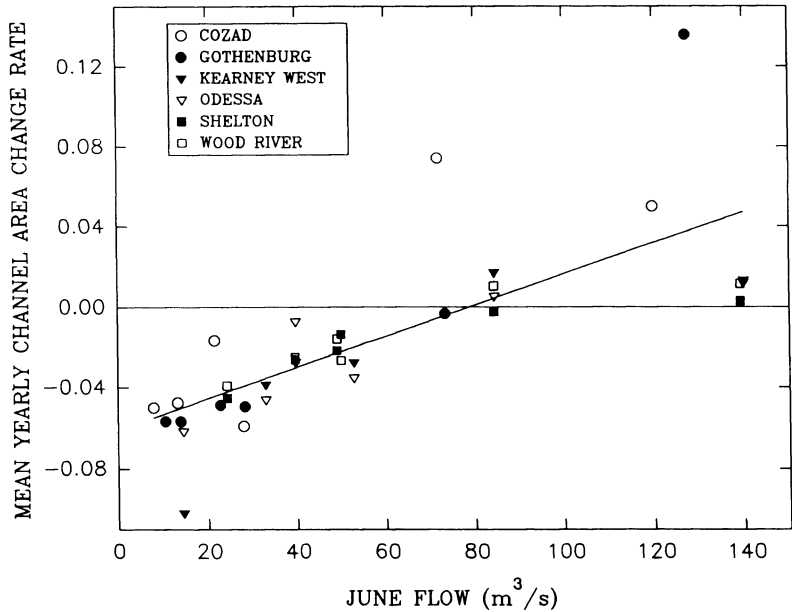


FIG. 20. Relationship between mean yearly channel area change rate and mean June flow. Negative values indicate channel narrowing and positive values indicate channel widening. Regression line is a least-squares fit.

TABLE 8. Active channel widths for six Platte River reaches, and estimation of mean June flow needed for no net change in channel width. Two flow estimates are given: one using mean channel width for each reach (1938–1986) and a second using 1986 channel width.

Site	Channel width (m)				Mean June flow to maintain channel width (m³/s)	
	1938–1986 mean width		1986 width		At 1938–1986 mean width	At 1986 width
	Mean	ln _e mean	Mean	ln _e mean		
Gothenburg	127.1	4.845	88.4	4.482	36.4	31.3
Cozad	126.8	4.843	114.6	4.741	36.4	34.8
Odessa	443.2	6.094	242.9	5.493	101.8	77.4
Kearney-West	387.1	5.959	247.8	5.513	95.8	78.1
Shelton	389.2	5.964	292.6	5.679	96.0	84.2
Wood River	325.5	5.785	243.5	5.495	88.6	77.5
Models:						
C, G	$0.0844 - 0.0515 \text{ LJUNE} + 0.0208 \text{ LWIDTH } R^2 = 0.771$					
O, K, S, W	$0.0614 - 0.0328 \text{ LJUNE} + 0.0148 \text{ LWIDTH } R^2 = 0.866$					

take into account existing differences in total channel width. Reach-specific estimates of mean June flow to maintain 1986 channel width ranged from 31 m³/s for Gothenburg, the narrowest reach (88 m), to 84 m³/s for Shelton, the widest reach (293 m) (Table 8). The range for the downstream half of the Big Bend reach of the Platte River was ≈75–85 m³/s. As a check on the relationship, mean June flow during period 5 (1969–1978) was 84 m³/s, and the channel area change rate was 0.00743, indicating slight widening but a value statistically indistinguishable from 0 ($P > .05$) (0 was the value calculated from the regression equation). Use of mean channel widths over the 1938–1986 period in the equation for each reach resulted in larger required June flows to produce stable channel widths (Table 8).

The flow range calculated for 1986 widths does not mean that flows need to be within this range each year

to produce stability in total channel width. Mean flow was within this range during 1969–1978, but annual June flows exhibited considerable year-to-year variation. Mean June flows during this period at Odessa ranged from 4 to 308 m³/s, while peak flows ranged from 16 to 507 m³/s.

A natural event occurred in 1986 that enabled evaluation of the effectiveness of flows in the 75–85 m³/s range in preventing seedling recruitment in the active channel. Mean June flow was 81 m³/s at Odessa and 87 m³/s at Kearney. Flow in early June at Odessa was <60 m³/s (minimum of 18 m³/s) until mid-June when it rose sharply to a peak of 183 m³/s on 20 June (Fig. 21). Flow then steadily declined to end the month at ≈60 m³/s. Field reconnaissance at both sites in mid-July at the end of the seed dispersal period revealed that no 1986 cohort tree seedlings were present on sandbars.

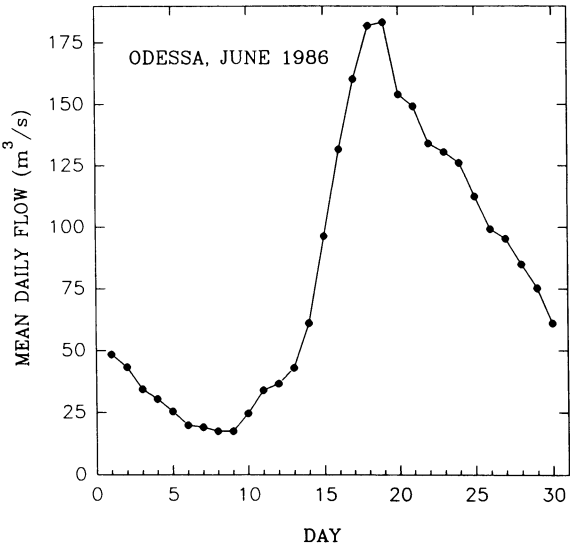


FIG. 21. Mean daily flow at Odessa, Nebraska, for June 1986 (USGS gage data).

Populus and Salix demography

Seed dispersal period—airborne.—The airborne seed dispersal period in 1987 spanned slightly <2 mo from mid-May to just before mid-July. Rates of capture of airborne *Populus* seeds were already moderately high (≈5 seeds/trap-hour) at Shelton on 16 May (Fig. 22). Peak rates for *Populus* occurred in early June (1 June at Shelton and 8 June at North Platte). The time of peak dispersal was similar between seed species (Fig. 22). *Salix* seeds, however, were an order of magnitude more numerous than were *Populus* seeds. The last airborne seeds were collected in early July (6 or 10 July) at both sites (Fig. 22). Overall rates of capture (≈0.1–0.2 seeds/trap-hour) were lowest at that time. The dispersal curve was right-skewed, with the peak occurring before mid-season. Sticky traps were active a total of 227.2 trap-hours at Shelton and 389.5 trap-hours at North Platte.

The 1988 dispersal period was virtually identical to 1987. At Shelton, *Populus* dispersal began in mid-May

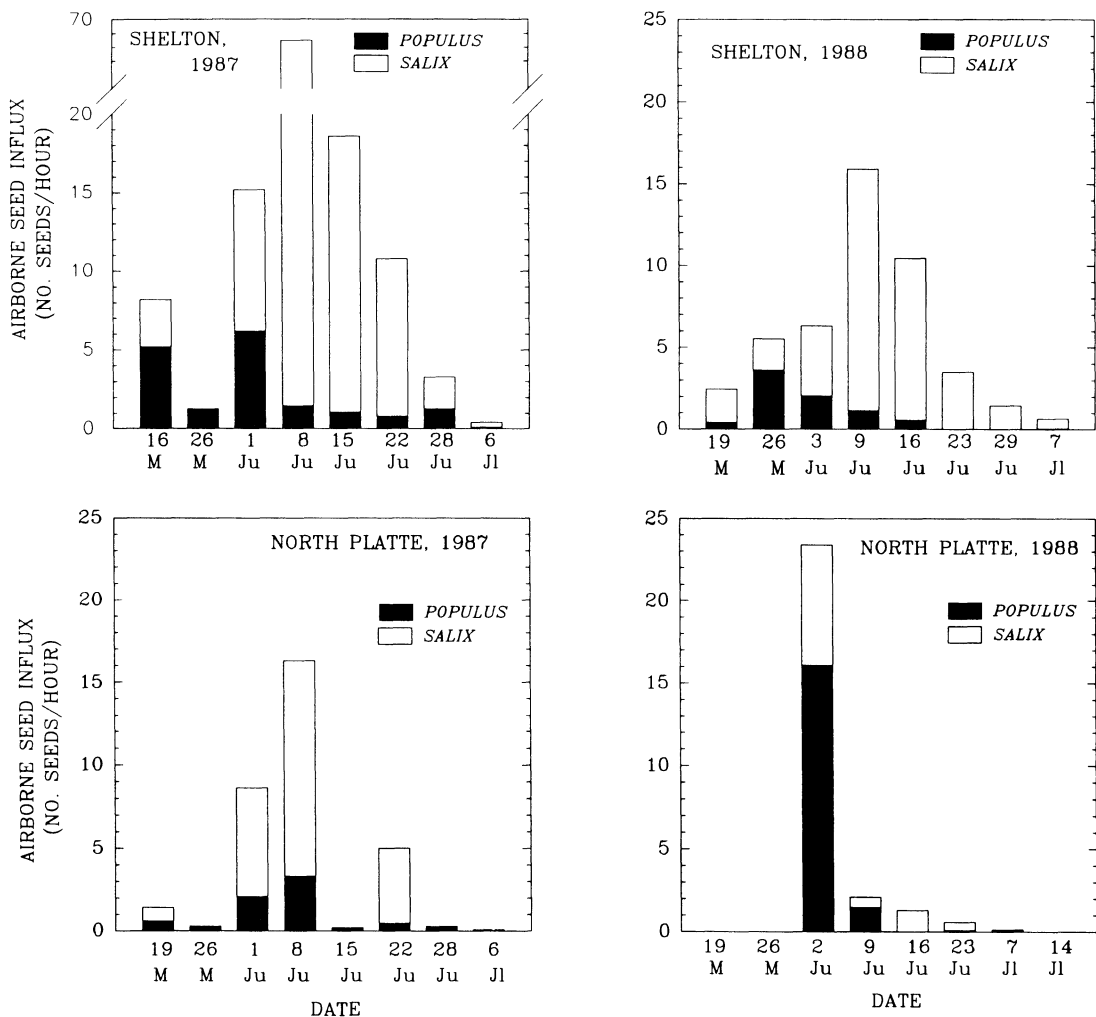


FIG. 22. Rate of airborne *Populus*, *Salix*, and combined seed dispersal (seeds per trap-hour) at Shelton and North Platte, Nebraska, field sites in May–June 1987 and 1988.

and peaked in late-May (Fig. 22). *Populus* seed capture rate reached 3.6 seeds/trap-hour on 26 May, but fell to <0.1 seed/trap-hour by 23 June. No airborne *Populus* seeds were trapped after 7 July (sampling continued through 28 July). A similar seasonal pattern occurred for *Salix* in 1988, except that capture rates generally were lower than in 1987 (Fig. 22). Trap-hours in 1988 totaled 300.1 at Shelton.

The seed dispersal period was 1–2 wk shorter at North Platte than at Shelton in 1988 because of a later starting date for both genera and an earlier ending date for *Salix* (Fig. 22). Peak capture rate for *Populus* was higher at North Platte than at Shelton in 1988. Trap-hours at North Platte in 1988 totaled 105.9.

Seed dispersal period—waterborne.—*Populus* seeds were dispersed by water in vast numbers in 1987, up to ≈340 seeds/net-minute (Fig. 23). Waterborne dispersal began in mid-May and peaked in late May–early June at Shelton. The rate of waterborne dispersal was affected by stage changes. For example, the later peak

capture at North Platte was probably caused by seeds being washed off sandbars by a heavy rain the evening before sampling. Heavy rains near Kearney in early July also probably increased waterborne dispersal rates on 13 July at Shelton (Fig. 23).

Waterborne seed dispersal continued in very low amounts a week or so after airborne dispersal (Figs. 22 and 23). Some seeds were transported by the river as late as 27 July (Fig. 23). The dispersal period in water was probably prolonged by redistribution of older seeds. Net-hours in 1987 totaled 4.1 at Shelton and 6.7 at North Platte.

Waterborne and airborne seed capture rates peaked at the same time in 1988 (Figs. 22 and 23). Peak capture rate at Shelton was 105 seeds/trap-minute, about 1/3 of the maximum capture rate in 1987. After 9 June, waterborne dispersal was low and intermittent.

Seed dispersal in 1988 at North Platte was a week later than at Shelton (Fig. 23). As at Shelton the capture rate at North Platte dropped off precipitously in early

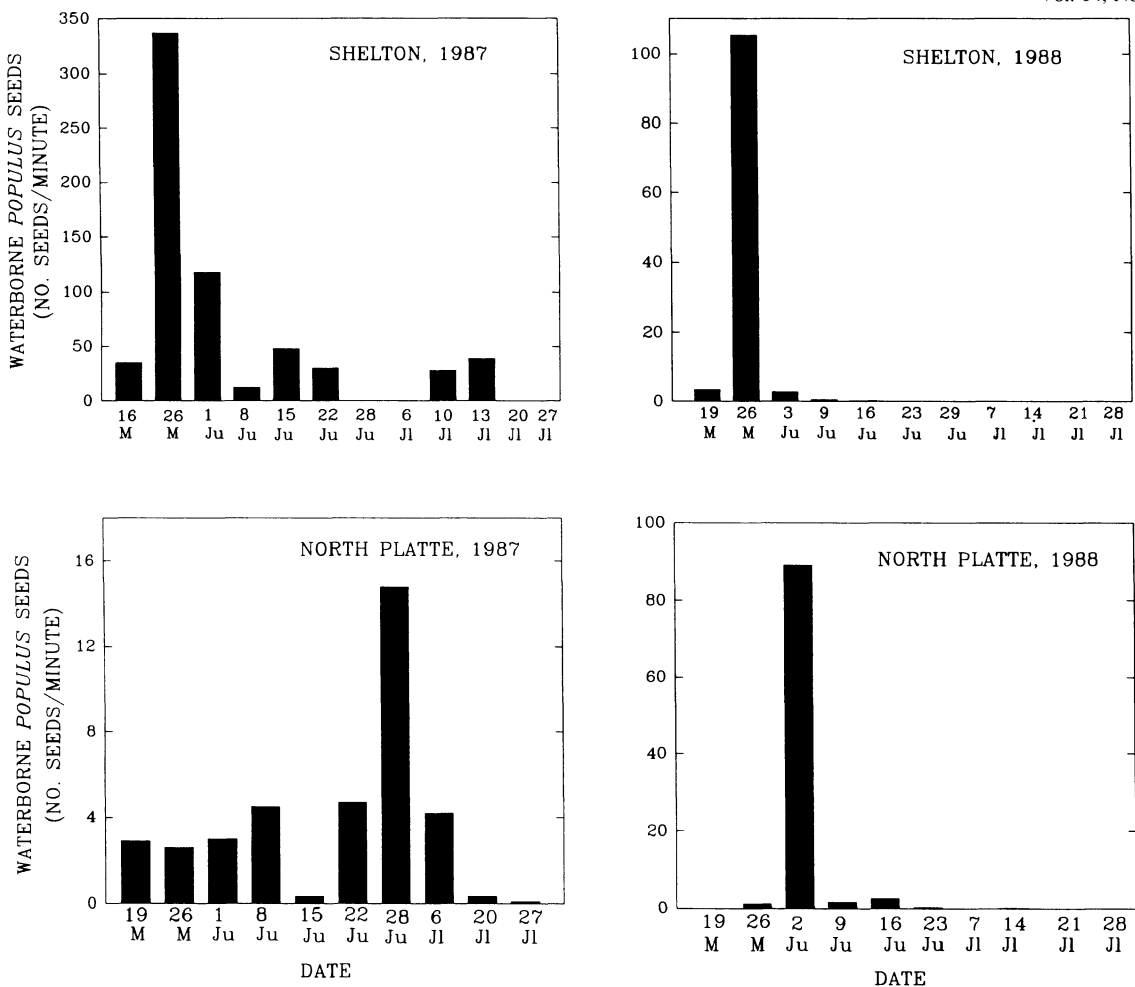


FIG. 23. Rate of waterborne *Populus* seeds (number of seeds trapped per minute) at Shelton and North Platte, Nebraska, field sites in May–June 1987 and 1988. Scales of vertical and horizontal axes differ among graphs.

June and remained low and sporadic through mid-July (Fig. 23). No seeds were netted at North Platte after 14 July.

The lower waterborne capture rates in 1988 may have been the result of lower seed production combined with lower June flows. Mean June flow at Kearney was $\approx 100 \text{ m}^3/\text{s}$ in 1987 and $40 \text{ m}^3/\text{s}$ in 1988. Lower flows would have delivered fewer seeds per unit of time to the sampling net, and a smaller water-filled channel with numerous sandbars would have more effectively stranded seeds.

Seed germinability.—Seed germinability for trapped seeds was very high: 85.0% for *Populus* and 82.8% for *Salix* summed across all lots and years. There was no strong trend of declining germinability of newly dispersed seeds during the dispersal season. Germinability of *Populus* was 89% during the first half and 78% during the second half of the dispersal season (summed across sites and sample years), while *Salix* germinability was 83% and 83%, respectively. Variation observed in the germinability of water-dispersed *Populus* seeds prob-

ably was caused by the mixing of seeds with different release dates during rises in river stage. Once dispersed, seeds of the Salicaceae lose germinability after several weeks (Currier 1982). Thus, *Populus* and *Salix* recruitment potential remains high, despite short seed viability, as long as seeds are being released from trees. However, the short viability and strong seed dispersal peak in late May–early June combine to concentrate actual recruitment in June except when flows are unfavorable.

Tree seedling demography.—1. *Seedling recruitment.*—Recruitment of *Populus* and *Salix* varied markedly among years, and much of the variation was explained by flows during the germination period. The most extensive recruitment occurred in 1987 and 1988 during low flow. Flow during the early part of the 1987 seed dispersal period was unfavorable for recruitment because sandbars colonized later by seedlings were covered by flowing water (Fig. 24). Flow dropped sharply in mid-June, which allowed recruitment on the newly

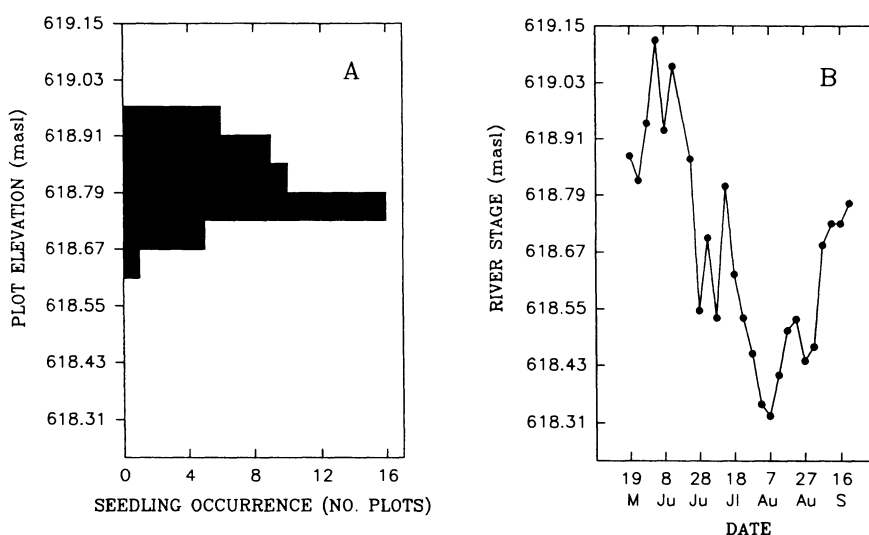


FIG. 24. Elevation distribution of 1st-yr *Populus* and *Salix* seedlings (A) in relation to river stage (B) in spring and summer 1987 at Shelton, Nebraska. Stage data (elevation above mean sea level) were from a Stevens portable gage located in the study area.

exposed sandbars. Sandbars at middle- and high-elevation positions in the riverbed were exposed for ≈ 20 d.

This mid-June recruitment was sampled in two episodes. The first was a small set of plots ("pre-flood") established in late June, before a small flood in early July (Fig. 24). The second was a larger sample in mid-July after the flood ("early germinants"). A third set of sample plots was established in mid-July for 1- to 2-d-old seedlings that had germinated at the end of the seed dispersal period ("late germinants"). The elevation range over which seedlings occurred at the end of the germination period was 0.4 m (Fig. 24).

June flow was markedly lower in 1988 than in 1987 and exposed a larger portion of the active channel. Field observations in July indicated that as much as half of the riverbed had been colonized by *Populus* and *Salix* seedlings. 1988 seedlings occurred over a slightly greater elevational range (0.5 vs. 0.4 m) and occupied lower riverbed positions than 1987 seedlings.

In contrast to 1987 and 1988, 1986 was a year of extremely low seedling survival. June flows were low enough ($17.5 \text{ m}^3/\text{s}$) to expose much of the active channel and to allow considerable recruitment; but the subsequent high peak flow of $183.2 \text{ m}^3/\text{s}$ on 19 June probably eroded most germinants (Fig. 21). Flows then remained high until early July, thus preventing germination in the active channel until after most seeds had been dispersed or had lost viability.

2. *General seedling mortality patterns.*—Interval-specific seedling mortality rates ranged widely at both sites during the 4 yr of observations, from 4 to 98% at Shelton and from 16 to 90% at Odessa (Fig. 25; Table 3). At Shelton, extremely high initial values were followed by a trough of low mortality. The highest mortality rates occurred during the winter (identified by

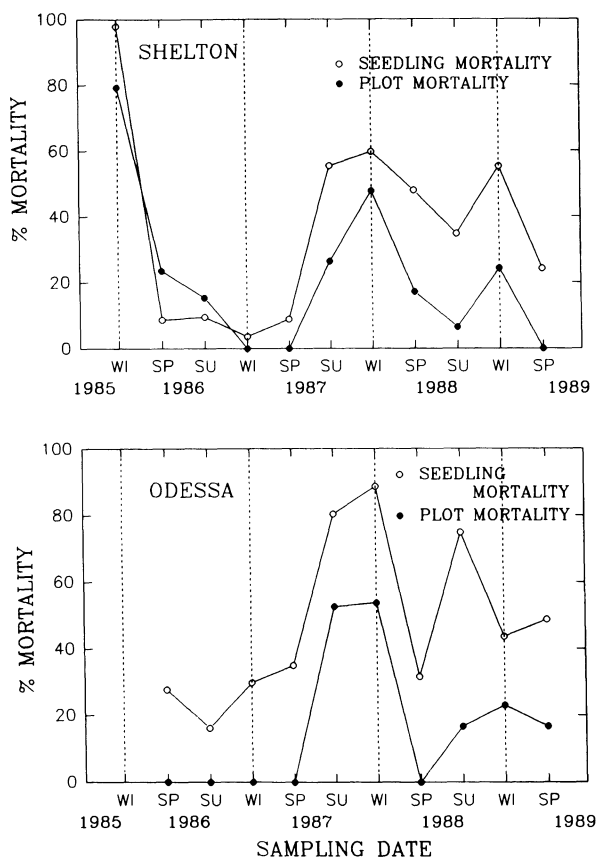


FIG. 25. Proportional seedling mortality (percentage of individuals present at the start of the period that died during that interval) and plot mortality (percentage of plots that lost all seedlings during that interval) by sampling date (WI = winter; SP = spring; SU = summer). See Table 3 for exact sampling dates. Dotted vertical lines identify the mortality rates during winter.

vertical dashed lines in Fig. 25). Seasonal mortality patterns were similar for Odessa, except that mortality rate was more variable during 1988. Plot mortality rates closely tracked seedling mortality rates at both sites (Fig. 25).

3. *Spring–summer mortality.*—MAXFLOW was the single environmental variable most strongly correlated with seedling mortality in both spring and summer (Table 9). The relationship was negative, suggesting that higher flows reduced mortality. Higher seedling mortality was most strongly associated with periods of low flow and low rainfall.

The best two-variable model for spring included MAXFLOW and MAXEL (Table 9). Elevation correlated positively with seedling mortality, indicating an effect of depth to water table, with higher plots experiencing higher mortality.

Three other two-variable models also were statistically significant (Table 9). These models all had MAXFLOW flow as the strongest variable. Secondary variables (MFLOW90, MXFLOW90, and MPPT) were climate related. MFLOW90 and MXFLOW90 were negatively correlated with seedling mortality, suggesting that low flow during periods of high air temperature led to higher mortality. MPPT was also negatively correlated, indicating that climatic drought contributed to higher seedling mortality.

Field evidence supported the statistical correlations and provided additional insight into mortality mechanisms. The three groups of 1987 seedlings each experienced different survival rates between June and September (Fig. 26). The early germinants had the highest survival, with approximately $\frac{1}{3}$ of the seedlings still alive by September. Some early germinants (mon-

itored in the pre-flood plots) were all eroded by the early July flood (day 55, Fig. 24; Fig. 26); however, the plot network was not extensive enough to include all conditions. Many early germinants survived the flood either by occurring on high sandbars or on silty, less friable substrates in small channels.

A severe climatic drought in July and August combined with a low water table (i.e., low river flows) caused high seedling mortality. Virtually all of the late germinants were killed (Fig. 26); only ≈ 12 of some 500 seedlings counted in July had survived by September. The early germinants had higher survival during the drought (Fig. 26). Survival depended primarily on their elevation in the riverbed (i.e., distance from the water table). Plot mortality increased directly with plot elevation (Fig. 27).

The 1987 summer drought was severe by most standards, but by no means unusual for the Platte River valley. During July and August 1987 there were 16 consecutive days without significant rain (trace or less at the Kearney weather station). Mean maximum daily temperature for those days was 35.5°C. Flow reached a minimum of 8.8 m³/s on 4 August (USGS gage data—Kearney). Since 1905 17 summers (≈ 1 in 5) were of comparable or greater severity (10 consecutive days or more without rain and mean maximum daily temperature for rain-free period of $\geq 35^\circ\text{C}$). Minimum flows for the nine droughty summers since 1939 were all lower (from 0 to 4 m³/s) than in 1987, except for 1942 which had minimum flows of 13.2 m³/s.

The 1988 cohort was established just before another severe climatic drought, this time in June. Seedling mortality was strongly correlated with plot elevation. The relationship was stronger than the mortality–ele-

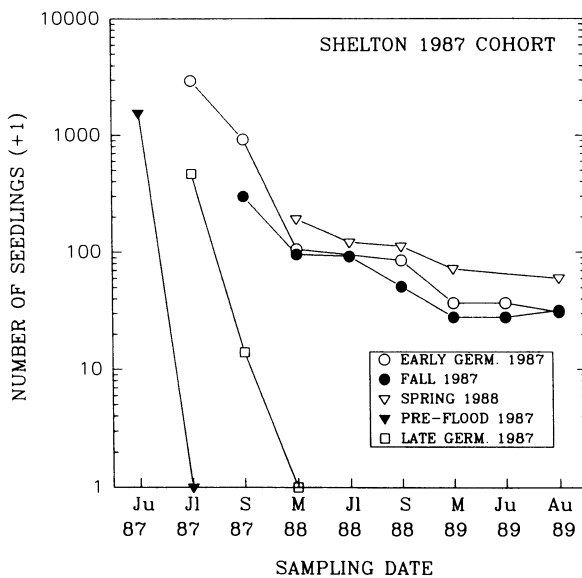


FIG. 26. Survivorship of 1987 *Populus* and *Salix* cohorts for plots installed in summer 1987 (early, pre-flood, and late), fall 1987 and spring 1988. See Table 3 for exact sampling dates.

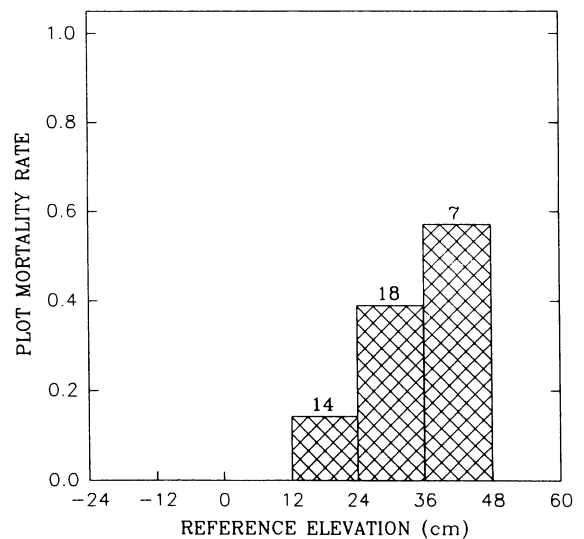


FIG. 27. Elevation-specific plot mortality rates between July and September 1987 at Shelton, Nebraska, for germination year seedlings. Number of plots is shown above bar. Elevations are relative to river stage on 17 November 1985.

TABLE 9. Correlations and regression models relating environmental variables to proportional mortality of seedlings, by season. Only correlations with a coefficient (Pearson's r) of 0.80 or greater are shown. Only regression models in which both variables are significant at .10 are shown.*

Winter ($n = 4$)				
Single-variable models	Pearson's r	P		
ICE	0.96	.04		
MINEL	-0.85	.15		
COLD	0.82	.18		
MEANEL	-0.82	.18		
Two-variable models	Slope	P	R^2 (%)	P (model)
MAXFLOW2	0.0003	.06	99.7	0.05
MEANEL	-0.9446	.04		
Spring ($n = 4$)				
Single-variable models	Pearson's r	P		
MAXFLOW	-0.97	.03		
MXFLOW90	-0.88	.12		
MIFLOW90	-0.87	.13		
MFLOW90	-0.86	.14		
MPPT90	0.86	.14		
DROUGHT	0.85	.15		
MINFLOW	-0.85	.15		
RAINO	0.82	.18		
Two-variable models	Slope	P	R^2 (%)	P (model)
MAXFLOW	-0.0001	.01	99.99	0.01
MAXEL	0.2293	.03		
MAXFLOW	-0.0001	.01	99.97	0.02
MPPT	0.6835	.04		
MAXFLOW	-0.00008	.03	99.94	0.02
MXFLOW90	-0.00003	.06		
MAXFLOW	-0.00008	.04	99.91	0.03
MFLOW90	-0.00003	.08		
Summer ($n = 3$)				
Single-variable models	Pearson's r	P		
MAXFLOW	-0.998	.04		
MPPT	-0.987	.10		
MAXEL	-0.956	.19		

* See Appendix for identification of variables.

vation patterns during the late summer drought in 1987. During the June drought, all the seedlings in >80% of the plots in the 0.25–0.35 m elevation class died; only 12% died in the 0.0–0.12 m elevation class. The results clearly showed the much greater vulnerability to mortality of young seedlings on high sandbars during drought periods. Survivorship patterns were similar between Shelton and Odessa sites (Figs. 26 and 28).

4. *Winter seedling mortality.*—Proportional mortality during the winter was most strongly and positively correlated with ICE (Table 9). ICE increased as winter temperatures decreased and as flows increased. The index score for winter 1985–1986 was 36, near the decadal average. The highest score was 63 for the winter of 1984–1985 and the lowest was 8 for 1982–1983.

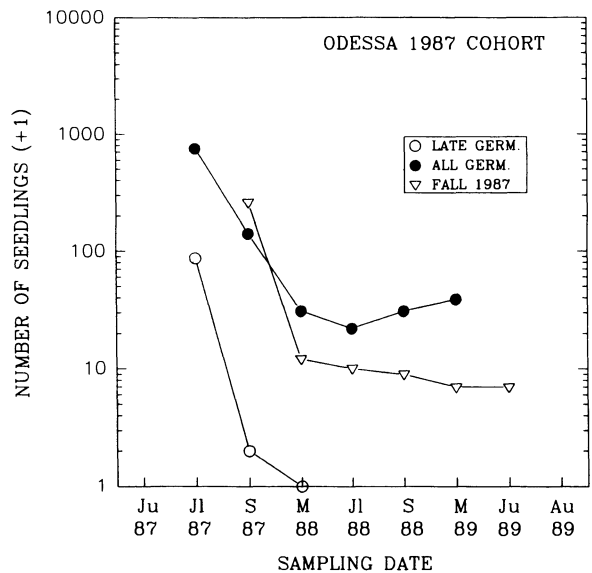


FIG. 28. Survivorship of 1987 *Populus* and *Salix* cohort at Odessa, Nebraska. Includes summer-installed plots with late-germinating seedlings, all seedlings and plots installed in fall 1987. See Table 3 for exact sampling dates.

Three other variables had moderately high, but statistically insignificant, correlations with winter mortality (Table 9).

The lowest winter mortality rate (Fig. 25) occurred in 1986–1987 during the warmest winter in the series. Mean December minimum temperatures at Kearney were -11.9° , -6.3° , -7.0° , and -7.3°C for 1985–1986, 1986–1987, 1987–1988, and 1988–1989, respectively (NOAA data).

The best two-variable model included a measure of maximum flow and weighted mean plot elevation, indicating that higher mortality occurred on lower sandbars and during winters of higher river stage (Table 9). Two other two-variable models exhibited high values of R^2 , but the small sample size ($n = 4$) made it difficult to obtain statistically significant results.

Field evidence supported ice and river stage as important winter seedling-mortality factors. Observers found that the river on 18 December 1985 was mostly ice covered; many sample plots were covered by as much as 0.2 m of ice. In late December and early January the ice began to melt and break up. By late January river ice was virtually absent. Moving cake ice and channel degradation in ice-capped channels were the forces that killed seedlings.

All sample plots in 1985–1986 at Shelton were covered by water and/or ice at some time during the winter (Fig. 29). River stage during field sampling on 18 November just covered the lowest plots. At the peak of winter stage (early January), the highest plot was covered by ≈ 0.2 m of ice and/or water, while the lowest plots were covered by ≈ 0.6 m (Fig. 29).

Winter 1986 conditions devastated the 1985 seed-

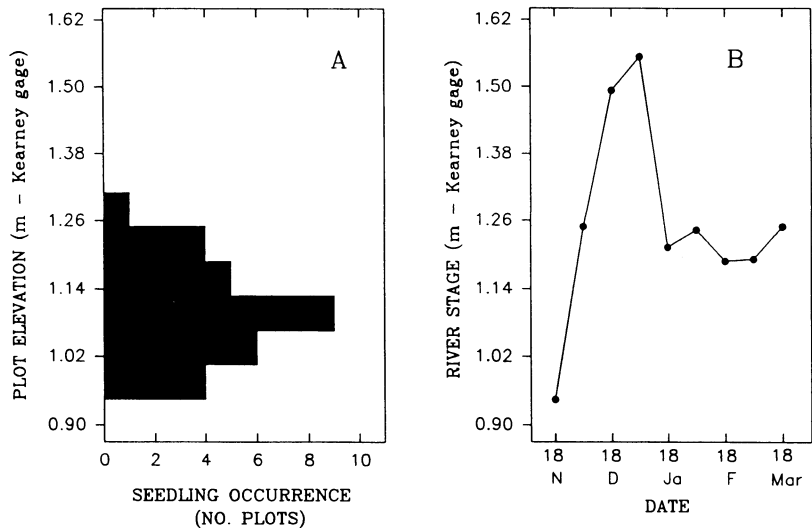


FIG. 29. Platte River stage height (B) in relation to plot elevation (A) in winter 1985–1986 at Shelton, Nebraska. Plots were established in November 1985.

ling cohort at Shelton (Fig. 25). Only 60 of the initial 3000 first-year seedlings (2%) remained alive by the May 1986 remeasurement. During this remeasurement, two new sets of sample plots of surviving 1985 cohort seedlings were installed: one of silt-covered seedlings that had been abraded by sediment and ice, and a second that included unabraded seedlings at the downstream end of the study reach and that had survived the 1986 winter atop relatively high sandbars. The frequency distribution of these plots was strongly skewed toward the high-elevation classes, since most seedlings on lower sandbars had been eroded.

By the next May remeasurement (1987) all the abraded seedlings had died, as had the 60 or so monitored seedlings that had survived the 1986 winter (Fig. 30). Thus, of the 3500 or so seedlings initially counted (fall 1985 + abraded spring 1986), none survived 1–1.5 yr later. All 1985 cohort seedlings abraded during the 1985 winter at Odessa also died by fall 1986. The few remaining seedlings (unabraded) of the 1985 cohort on high bars sampled in May 1986, however, had high subsequent survival (Fig. 30). All elevation classes

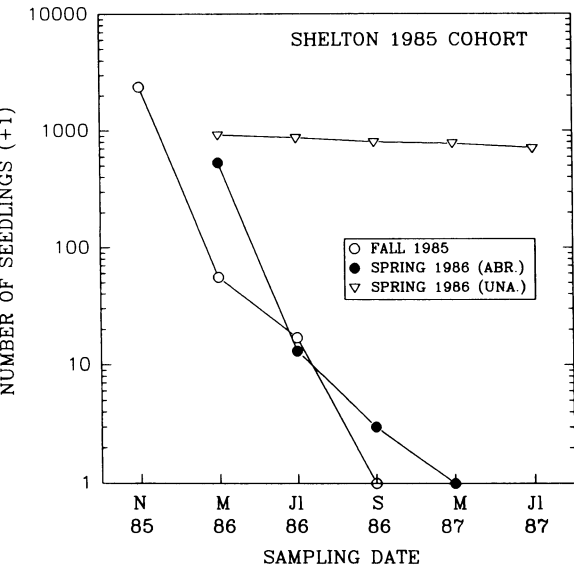


FIG. 30. Survivorship of 1985 cottonwood and willow cohort for plots installed in fall 1985 and spring 1986 (abraded seedlings and unabraded seedlings). See Table 3 for exact sampling dates.

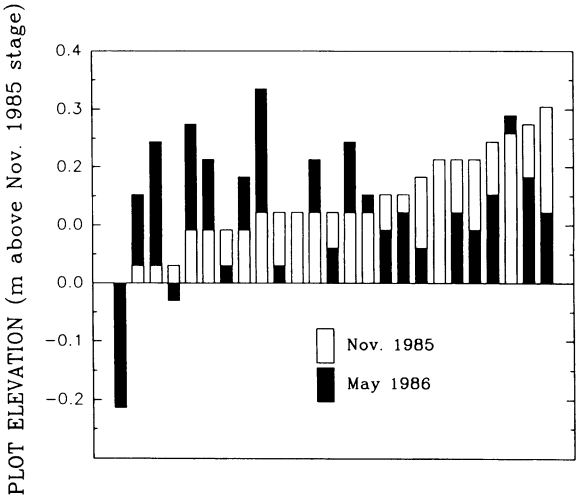


FIG. 31. Change in plot elevation between November 1985 and May 1986 caused by a combination of flowing ice and water. The elevation of 25 of the 29 sample plots in fall 1985 (elevation of the other four could not be reconstructed) is shown by the height of the white bars. The post-winter elevation measured in May 1986 is shown by the height of the black bars. The difference between the two bar heights (i.e., the amount of black in the graph) is a general measure of the amount of channel sediment redistribution.

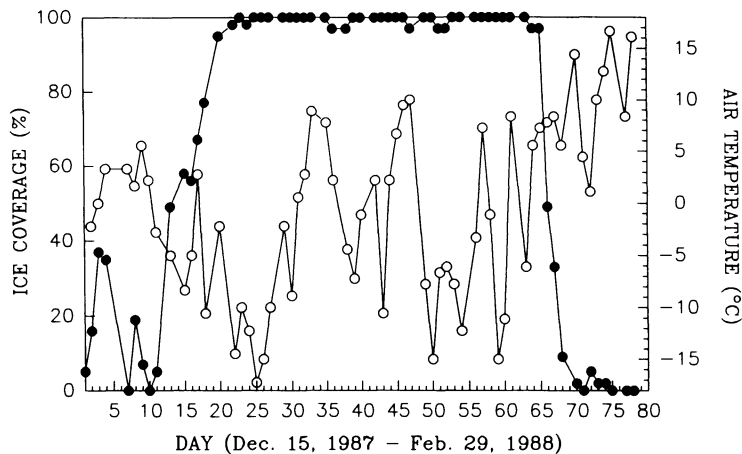


FIG. 32. Ice coverage and afternoon (1400–1600) air temperature at the Kearney Bridge during winter 1987–1988. See *Methods: Tree seedling demography: Field methods—tree seedlings* for methods of estimation of ice coverage.

experienced high rates of plot mortality during winter 1986.

Winter conditions caused extensive restructuring of the riverbed. Many plots were aggraded by >0.2 m, while others were comparably degraded (Fig. 31). The greatest change in elevation occurred at the elevation extremes; lowest plots were aggraded the most while highest plots were degraded the most. The high rate of seedling mortality was matched by the high degree of riverbed restructuring, indicated by the proportion of black in Fig. 31.

Subsequent winters (1988, 1989) provided additional information on ice formation, ice disappearance, and the general influence of winter conditions on seedling mortality. To illustrate, ice coverage below the Kearney Bridge varied below 50% until early January 1988 when it rose sharply to 100% (Fig. 32). The ice cover formed following ≈ 1 wk of air temperatures that ranged from -15°C to slightly above freezing. Ice coverage remained high until dropping precipitously to near zero during 17–20 February when air temperatures consistently stayed above 5°C .

Ice of thicknesses up to 0.2 m covered most 1987 sample plots. During ice-out many of the plot markers were severely bent. Seedlings were apparently killed by both scouring and by being lifted frozen in ice from sandbars. Field observations in March 1988 of the elevation of water-transported debris along channels indicated that localized ice jams occurred in both study reaches and raised stage by as much as 0.6 m.

Seedling mortality during winter 1987–1988 was very high, particularly at Odessa where it reached 90% (Fig. 25), but it did not reach the extreme values seen during winter 1986.

Seedling numbers in fall 1987 approached a normal distribution over a 60-cm elevation range (Fig. 33). Plot mortality during the following winter was strongly elevation-dependent; mortality rate for the plots in the

higher elevation intervals ranged from 14 to 33% while mortality for plots in the lowest elevation intervals ranged from 60 to 100% (Fig. 33). The winter inverse relationship between elevation and mortality was opposite the spring–summer pattern.

Seedling mortality during the subsequent winter of 1988–1989 was among the lowest of the four winter measurements (Fig. 25). This occurred despite ice cover comparable to 1988 when mortality was higher. The difference may have resulted from lower base flows at the time of ice formation and prior to ice breakup. Elevational patterns of mortality, however, were similar to those of the winter of 1987–1988.

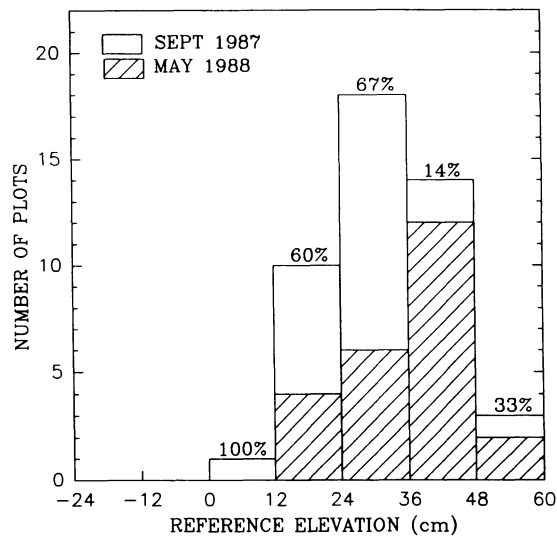


FIG. 33. Elevation distribution of all plots present in September 1987 and those that survived to May 1988 at Shelton, Nebraska. Elevations are relative to river stage on 17 November 1985. Plot mortality (%) is shown above bars.

TABLE 10. Average rate of plot mortality per sampling interval for 1987 and 1988 cohorts by channel size.

	Channel width		
	Small (<25 m)	Medium (25–50 m)	Large (>50 m)
Avg. loss rate (percentage of starting no. of plots/sampling interval)	6.0	9.8	80.0
Range among cohorts	0.0–11.0	0.0–23.0	40.0–100.0
Sample size (no. of plots)	28	41	17

Mortality vs. channel width.—Survival rate of tree seedlings varied among channel sizes at Shelton. Plot loss rates for small and medium channels were low and statistically indistinguishable ($P > .05$; Table 10). The loss rate for large channels, however, was dramatically higher (80%) and significantly different from the other two rates ($P < .01$). Very few plots survived more than one sample interval in wide channels.

Too few sites were sampled at Odessa to perform a comparable channel width and plot mortality analysis. Only two small sites with seedlings could be found in wide channels at Odessa during 1987 and 1988. The scarcity of available sites for monitoring reflected the very low propensity for seedling recruitment and woodland expansion in wide channels even during periods of low flow.

DISCUSSION

Pre-development baseline environment

The General Land Office (GLO) survey notes indicated the following for the Platte River in Nebraska: islands and woodland were more extensive than indicated on the plat maps; woodland occurred both on banks and on islands; trees on main banks declined upstream and westward from Fort Kearny (although exacerbated by cutting); small, wooded, in-channel islands were ubiquitous; woodlands were dominated numerically by cottonwood and willow; and tree population size structure was relatively balanced.

Reconstruction of the pre-development woody vegetation of the Platte River was complicated by several factors, including (1) the start of the GLO survey after the woody vegetation already had been impacted by the military, settlers, and pioneers migrating westward through the Platte River Valley; (2) general exclusion from the survey of the small, but numerous, riverine islands; and (3) inconsistency of survey methods and detail provided by the surveyors, which led to geographic gaps in descriptions of instream ecological conditions.

Currier et al. (1985) portrayed the undeveloped Platte River as being dominated by sandbars and water and generally devoid of permanent woody vegetation. They interpreted plat maps, historical accounts, and old photographs to indicate that the Platte was a rather fea-

tureless river, and riverine islands were simply “elevations of earth” prevented from becoming permanently vegetated by the high spring flows. This interpretation is sharply at odds with the direct evidence in the survey notes. One explanation may be that early photographs taken near bridges (Williams 1978) were not representative of the Platte River throughout its length since cutting would have been greatest near population centers, which were closely associated with bridges.

The ability of woodland to inhabit the Platte River, despite what must have been a rigorous and highly variable environment, suggests that even minor modification of the river's water resources could have initiated subsequent woodland expansion and channel narrowing. This differs from the view that human modification of the river was so massive that it quickly changed it from virtually inhospitable to trees to one that was highly favorable (e.g., Currier et al. 1985). A less extreme and probably more accurate view is that the balance between woodland extent and active channel area was quite dynamic, changing during climatic cycles, and sensitive even to small but persistent changes in flow.

Causes of woodland expansion

Woodland was a natural part of the Platte River ecosystem prior to water development; however, it expanded rapidly following flow decreases caused by the storage and diversion of water for agriculture. Evidence presented here that woodland expansion was caused by flow alteration includes statistical correlations between historic narrowing rates and environmental factors; the observation that expansion cascaded downstream over time, closely tracking the temporal pattern of water development; and field observations of flow effects on tree seedling dynamics in the modern river. Non-flow-related historical factors also may have contributed initially. For example, during early settlement woodland expansion may have been favored by the cessation of prairie fires (Currier 1982). The introduction of exotic tree species such as *Elaeagnus angustifolia* may have contributed to more recent woodland expansion, primarily in temporary and seasonal palustrine wetlands along the Platte River, but also as a later successional species on riverine islands (Knopf and Scott 1990).

The single, most significant result of the historical analysis relating changes on aerial photographs to flow showed that woodland expansion rate was more sensitive to flow in certain seasons. Results indicated that low June flows in the developed river, caused by upstream storage and diversion of water for agriculture, have allowed extensive plant recruitment and a build-up of tree populations in the formerly active channels of the Platte River and its two major tributaries.

Life histories.—Life history characteristics of *Populus* and *Salix* help explain the strong relationship be-

tween June flows and woodland expansion rate and their overall success as pioneer species on floodplains. Relevant characteristics include a relatively short seed dispersal period and short seed viability; rapid germination; rapid root and height growth enabling tolerance to flooding, drought, and sedimentation; tolerance to low soil fertility and soil submergence; and the ability to reproduce vegetatively, particularly after physical damage.

The relationship between June flow and recruitment is tied to the relatively short seed-dispersal period (spanning ≈ 2 mo with peak dispersal late May to early June) and short seed viability (several weeks; Moss 1938, Noble 1979, Currier 1982, Fenner et al. 1984), which concentrate significant seedling recruitment within the early part of the growing season.

Germination and early seedling establishment depend on seed dispersal coinciding with receding water levels. Optimal conditions for establishment include moist mineral soil located just above the water table, a condition best met on exposed sandbars or banks in the active river channel (Moss 1938, Wistendahl 1958, Lindsey et al. 1961, Wilson 1970, Johnson et al. 1976, Irvine and West 1979, Noble 1979, Sedgwick and Knopf 1989, Rood and Mahoney 1990). Although *Populus* germination can occur under water in laboratory conditions (Kapustka 1972), standing or flowing water in the riverbed appears to prohibit successful establishment. Disruption of the natural timing between seed dispersal and receding flows by dams has reduced *Populus* establishment in some southwestern U.S. rivers (Fenner et al. 1985).

Initial survival depends on the soil remaining continually moist for at least the 1st wk after germination, due to the initially slow growth into the soil of the primary root and time for development of collet hairs (Moss 1938, Noble 1979). Prior to the development of the radicle, a zone of collet hairs arises at the base of the hypocotyl (Noble 1979). These are anatomically distinct from root hairs and attach quickly to sand particles, providing both anchorage and absorption.

Populus and *Salix* possess adaptations to enhance survival after germination from drought or submergence, particularly their rapid shoot and root growth rates. Rapid root growth enables plants to maintain water balance during a declining river stage. Fenner et al. (1984) found in Arizona that *Populus fremontii* roots grew an average of 6 mm/d following a receding water table. Most seedlings could tap groundwater at depths of 72 cm by the end of the summer, and could potentially reach 162 cm. Rapid root growth also improves anchorage during floods; however, the most important adaptations to flooding are rapid shoot growth to survive at least moderate sedimentation (Krasny et al. 1988) and flexible root physiology, which allows for alcoholic fermentation in submerged roots (Keeley 1979).

Since the texture of newly deposited sandbars is often

relatively coarse (sand-size particles), rapid height growth may depend on subsequent, more fertile deposits of finer texture from floods. Rapid shoot growth may increase survival by elevating leaves from hot soil surfaces during drought (thereby reducing tissue water loss) or reducing the chance of complete burial by sediment during floods. *Populus* and *Salix* are well adapted to partial burial because active root primordia occur in young stem tissue, allowing rapid exploitation of new layers of sediment (Walker et al. 1986, Krasny et al. 1988).

Hydrogeomorphic processes interact with colonizing vegetation to alter the sandbar environment and to increase both the survival and growth of early successional species and the colonization potential of later successional species. The presence of plants increases the surface roughness of sandbars and facilitates sedimentation during small floods (Hupp 1992). This process benefits those colonists adapted to sedimentation by raising the sandbar with nutrient-rich silt, leading to increased fertility and a reduced hydroperiod. On higher sandbars, reduced disturbance from flooding enables accumulation of detritus, which further improves the soil environment for later successional species and restricts germination of early successional species. In this way colonizing vegetation and geomorphic processes facilitate succession on floodplains by modifying the highly dynamic low-riverbed environment, suited to early species, into relatively stable surfaces favorable for recruitment of later species, which in the Platte River include *Fraxinus pennsylvanica*, *Acer negundo*, *Ulmus* spp., *Juniperus* spp., and *Catalpa speciosa*.

Environmental factors.—The demographic data demonstrated the close relationships among flow, life history characteristics, and the potential for woodland expansion. To illustrate, June flows largely determined the proportion of the active channel available for colonization and the early survivorship of young recruitment. High flows, which completely covered the unvegetated riverbed, generally precluded seedling recruitment and/or eroded young germinants, while low flows provided ample substrate for colonization and higher survival of young germinants. Substrate exposure at other seasons would not have affected recruitment, only survivorship.

The demographic study in the modern river corroborated the statistical significance of June flow in the historic analysis. For example, high flows in June (e.g., 1986) were found to prohibit seedling recruitment in the active channel, while low flows in June (e.g., 1988) allowed extensive recruitment. The pattern of flow, as well as the mean flow, is also important. The ascending flows during June 1986 that caused erosion and burial of seedlings established earlier in the month resulted in higher seedling mortality than would have occurred with a steady flow of the same magnitude. In contrast, descending flows through the month would allow mid- to late-June germinants to survive the period without

the disturbances associated with inundation. Thus, mean June flow and peak flow (magnitude and timing) during the germination period largely determined both the areal extent of seedling populations at the close of the germination period each year and the long-term pattern of woodland expansion. Mean June flow and peak flow were themselves strongly correlated, and therefore it was difficult to determine their proportional effect on woodland expansion.

During time intervals with relatively stable channel widths (e.g., 1969–1978), mean June flow was high enough that elevated colonization in a year with low flows was counterbalanced by increased mortality and reduced germination in high-flow years. Approximately half of the years during 1969–1978 had mean June flows in the 75–85 m³/s range. Field observations indicated that flows of this magnitude covered most of the active channel and therefore strongly limited germination of tree seeds. Moreover, in four of five occurrences, a year of low June flow with high colonization potential was followed by a year with at least moderate potential for erosion of young seedlings.

The historic statistical analysis further identified several secondary factors weakly correlated with woodland expansion rate. These factors included weather (late summer drought, ice) and erosive flows at times other than during the seed germination/seedling recruitment period. None of these was highly significantly correlated with historic woodland expansion rate; however, detection of a statistical relationship may have been more difficult since these factors operate episodically (up to several occurrences per decade), while June flows may have significantly affected demographic parameters each year. Statistical detection of the effect of episodic factors was difficult because woodland expansion rates only could have been averaged between photograph intervals; too few photographs were available to single out the effects of specific events or factors (e.g., erosion by a single ice event) in the historic analysis.

The statistical models based on demographic field data indicated that other flow and climate factors may affect tree seedling survivorship. The predominant mortality factor was ice, and its degree of influence was strongly affected by several environmental factors, including (1) cold winter temperatures needed to form thick cake ice, (2) relatively high winter flows (70–85 m³/s) which caused ice formation higher in the riverbed and more ice-scouring, and (3) the elevational distribution of seedlings in the riverbed. Highest seedling survival should be expected during relatively warm, low-flow winters and when most seedlings were growing on high sandbars. The lowest survival should occur during relatively cold, high-flow winters and when most seedlings are in low riverbed positions.

Mortality by ice may have greatly increased as channels have narrowed. Woodland could not have expanded in the past at the high rates observed had ice

been as strong a mortality factor as measured in the modern river. Greater ice action with time probably was caused by increasing water depth in the river as active channels have narrowed. Early in this century when active channels were wide and flows greatly reduced from pre-development levels, scouring by ice was restricted in most years to the proportionally small, water-covered portion of the channel. In the modern and much narrower river, ice reaches and scours much or sometimes all of the riverbed under comparable flows. Also, ice jams now may be more likely to form due to shorter distances between vegetated banks. Shelf ice and woody vegetation (including the now numerous beaver-felled trees extending into adjacent channels) lining the channels of the modern river may more effectively trap ice, thereby raising stage (without increasing volume of flow) and contributing to increased scouring of the bed, especially on higher sandbars, which are the most likely to become permanently vegetated. High base flows in winter, which cause ice formation at higher elevations in the riverbed and contribute to local ice jams, appear to be necessary before ice can cause widespread seedling mortality.

Drought was another significant mortality factor in the modern river. The statistical models suggested strong relationships during the growing season between seedling mortality and moisture supply factors such as precipitation and flow. For example, maximum flow was negatively and the most strongly correlated of the environmental variables to seedling mortality in both spring and summer. The highest seedling mortality occurred during periods of low flow, extremely high air temperatures, and no rainfall. A lower water table would increase mortality during climatic drought by depriving seedlings of soil water. The coarse-textured soils of sandbars, which contained no clay-sized and a very small silt-sized fraction, made tree seedlings particularly susceptible to drought mortality. Lower flows may also have increased surface soil and leaf temperatures, leading to greater moisture stress for seedlings. Drought can be so severe as to kill older, better established seedlings, such as occurred in 1988 during a drought in June. Early drought was more severe for older seedlings because it occurred at the time of most rapid growth for vernaly adapted floodplain trees (Reily and Johnson 1982).

The negative correlations between mortality and flow indicated that low flow, which deprived seedlings of moisture, was a stronger mortality factor than was submergence, erosion, or sedimentation caused by high flow. High flows of the magnitude experienced during the study actually contributed to seedling survival. The 1985–1989 period, however, did not include large peak events such as those of 500–750 m³/s which occurred in the late 1970s and early 1980s and which probably would have resulted in higher seedling mortality.

While summertime peaks of 125–225 m³/s were effective in scouring new germinants, these peaks do not

occur every year, or sometimes occur before the end of the seed germination period. Thus, seedlings often survive their first year on higher bars (if they escape ice scouring) and become more resistant to erosion because of their larger size, larger root system, and occupation of higher bars. Summertime peak flows experienced in this study were generally ineffective in removing previous-year or older seedlings.

The effectiveness of summertime peaks in eroding tree seedlings is further diminished by the protective effects of often taller and denser plants growing with them, particularly annual plants such as cocklebur (*Xanthium strumarium* L.), barnyard grass [*Echinochloa crusgalli* (L.) Beauv.], nut-sedge (*Cyperus odoratus* L.), and lovegrass [*Eragrostis pectinacea* (Michx.) Nees]. Though these herbaceous plants can compete with tree seedlings for moisture in some situations, they may also increase survivorship by reducing erosion and by encouraging sedimentation during small floods.

In contrast to ice, which often completely removed seedlings from extensive areas of the riverbed, at least a few seedlings in most plots survived summer drought. Drought acted more to thin than eliminate seedlings from large areas. The density of drought survivors often would have been adequate to form a woodland eventually, especially for *Salix*, which reproduced vegetatively by age two and could have rapidly made up for occasional thinning losses from drought. Thus ice was considerably more effective as a factor in slowing woodland expansion than was drought.

This is borne out by the historic photograph analysis. Had drought been a strong mortality factor, woodland expansion rates during drought periods such as the 1930s and 1950s should have been low. The observation that rates were highest during droughts (i.e., a negative correlation between mortality and late summer flow) supports the conclusion that increased mortality during droughts, as was indicated by the demographic data, did not offset the increased recruitment caused by greater exposure of the riverbed.

It would be incorrect, however, to use results from the post-1938 period to reject the broader hypothesis that low-flow or no-flow periods in late summer in the pre-development river restricted woody plant establishment. The modern river with subsurface irrigation return may not experience flows as low as may have occurred in late summer prior to settlement.

The General Land Office Survey notes, however, do not support extremely droughty riverbed conditions, and therefore high seedling mortality, in late summer under pre-development conditions. For example, of nearly 100 references by surveyors to flow conditions in the Platte, South Platte, and North Platte rivers (including 13 yr [July–October] between 1858 and 1881 from Grand Island west to the Nebraska state line), none refers to a dry riverbed, and only several references were made to a “nearly dry” riverbed. The large majority of entries indicated that the river was flowing

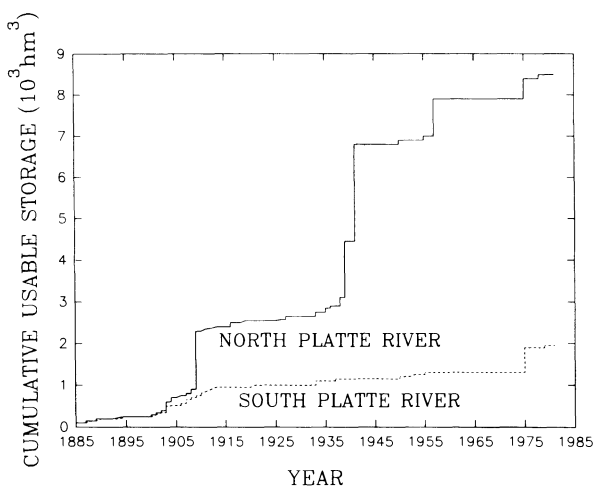


FIG. 34. Comparison of cumulative usable reservoir storage in North Platte (—) and South Platte (---) basins (after Bentall 1975).

with shallow water (often 3–7 dm deep) and a swift current.

Few natural ecosystems exhibit an environment as variable as floodplains. The floodplain experiences the same suite of disturbances incurred by upland vegetation (e.g., fire, windthrow, disease, browsing) plus those associated with rivers (e.g., erosion, sedimentation, submergence). Fluvial processes contribute considerable stochasticity to demographic processes. For example, alternating drought and severe rainstorms in a single year (1987) combined temporally to strongly determine overall recruitment success and 1st-yr seedling survival. Seedling survival also differed markedly depending on whether germination occurred early or late in the relatively short seed dispersal/recruitment period. Moreover, a different environmental factor predominated each year of the field study—ice in one year, summer drought in another—and high flows during the seed germination period in another. However, despite marked variation in environment and in plant response over hours, days, and weeks, vegetation dynamics over years or decades correlated very strongly with average flow.

Steady state

Channel width.—The post-development trend of monotonic decreases in channel width and increases in woodland area in the Platte River ceased following the last major episode of channel narrowing in the 1960s. Since that time, comparatively small and mostly nonsignificant changes have taken place. This suggests that flow utilization has stabilized, thus allowing time for woodland and channel area to stabilize. The rate of increase in reservoir storage capacity has dramatically slowed since the major dam-building period on the North Platte River between 1910 and 1941 (Fig.

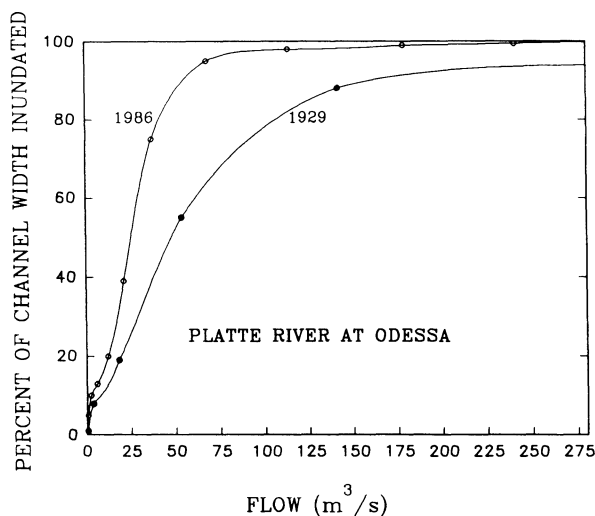


FIG. 35. Proportion of active channel at Odessa, Nebraska, covered by a given amount of flowing water in 1929 and in 1986 (R. Simons, unpublished data).

34). No new mainstem dams have been built on the Platte and North Platte rivers since 1956, although several have been proposed.

Recent patterns of change, characterized by both small increases and decreases in channel area (depending on the time period and reach) fit the classic, narrowly oscillating pattern expected for rivers in dynamic equilibrium or steady state. Numerous authors have used these terms and others to refer to rivers that have reached a relatively stable condition of self-regulation (Strahler 1952, Wolman 1955, Hack 1960, Morisawa 1968). The steady state is achieved and maintained by mutual interaction of channel characteristics such as gradient, cross-sectional form, roughness, and channel pattern (Morisawa 1968).

Other authors differentiate between steady state and equilibrium on the basis of time scale. Richards (1982), following Schumm (1975), uses steady state to denote medium-term responses (10–>100 yr) of streams to environment. At steady state, width will vary some, but the slope of a best-fit line through the data is near 0, implying no directional change at this time scale. In the short term, width can vary; for example, when there is temporary widening caused by bank collapse during and after peak flows. This may be counterbalanced by slower depositional processes, especially in asymmetrical sections on active meanders, where the outer bank retreat is balanced by deposition on the inner bank (Richards 1982).

In the long term (time scales of >1000 yr), these random variations occur about a progressive trend in mean width caused by climatic change, tectonic influence, or long-term changes in valley gradient reflecting the long, slow process of landscape degradation (Richards 1982). This slower acting, but directional, trend

may be characterized as dynamic equilibrium because the stream continually adjusts to maintain equilibrium with its environment.

The channel dynamics described in this paper fit with Richards' medium time-scale and steady-state terminology rather than with dynamic equilibrium. In the near term, channel and woodland area appear to be in a steady state; however, the long-term future of Platte River channels is uncertain because of the possibility of flow changes caused by climate change (Schneider 1989, Waggoner 1990, Poiani and Johnson 1991), natural climatic cycles (Helley and LaMarch 1973), or additional water development (Knopf et al. 1988).

The general decline in the rate of woodland expansion since the 1930s was the product primarily of reduced tree seedling establishment caused by changing channel hydraulics as channels narrowed. To illustrate, the proportion of the active channel width covered by a given flow has dramatically changed as active channel widths have declined. For example, a flow of 28 m³/s at Odessa in 1929 covered ≈30% of the active channel, while in 1986 the same flow covered 60% of the active channel (Fig. 35). A flow of ≈85 m³/s in 1986, which was close to the mean June flow estimated to arrest further woodland expansion, covered 98% of the active channel width in 1986, but only 70% in 1929 (Fig. 35).

The advance of woodland into the channel has stopped because recruitment has become restricted to a smaller and smaller area of the active channel. The higher flows per unit of active channel width have simultaneously increased mortality of tree seedlings, both shortly after germination and during winter as ice conveyance has increased.

The factors that maintained the wide, active channels and scattered woodland present in the pre-development Platte River cannot be known with certainty. The present study, however, suggests that several factors were important, including the known high June flows, which would have restricted seedling recruitment, and ice, which would have reduced survivorship of tree seedlings. Water development altered the high-flow and ice-disturbance regime that probably regulated the pre-development balance in woodland and channel area allowing woodland to replace extensive areas of active channel. As flow and channel width have come more into balance, perhaps as a microcosm of the pre-development balance, the disturbance regime associated with colonization and primary succession to woodland has returned.

As was probably the case in the pre-development Platte River, the existing balance is dynamic and responsive to wet and dry climate periods. For example, when flows in 1983 at Odessa exceeded 700 m³/s, permanent vegetation in some reaches was eroded and channels widened. Mean June flows have dropped dramatically during 1988–1992 due to climatic drought in the Great Plains, and there was evidence of increased recruitment and higher survivorship of tree seedlings.

This has led to the establishment of relatively permanent vegetation in portions of the channel that were unvegetated in 1985–1988. These observations of small increases in permanent vegetation under low flows and small decreases under high flows match those expected under steady-state conditions.

Geomorphic type.—The geographic variation among river systems in the response of vegetation to flow alterations has many possible causes, including geomorphic type, presence of exotic species, type and magnitude of water resource development, grazing intensity, agricultural activity, and others. Among these, geomorphic type appears to be a major explanatory factor, illustrated by the opposite responses of dammed meandering and braided rivers. On meandering rivers, particularly in northern latitudes where aggressive, exotic species such as *Tamarix* are not present, successful recruitment of *Populus* and *Salix* is associated with peak-flow events and active river meandering. The age of origin of certain forests often dates to specific flood events (Everitt 1968, Bradley and Smith 1986, Foster et al. 1986, Baker 1990, Howe and Knopf 1991, Stromberg et al. 1991). On meandering rivers, flood peaks must both erode established communities on the outside of river curves and produce high-elevation point bars through sedimentation on the inside of river curves to enable recruitment to survive subsequent minor floods. Decreases in peak floods caused by dams (Williams and Wolman 1984) reduce meandering rate (and hence reduce colonizeable area for *Populus* and *Salix*) and point bar elevation.

In sharp contrast, successful recruitment and expansion of *Populus* and *Salix* in braided rivers are not positively associated with peak-flow events but with periods of low flow. The findings on the Platte River clearly showed that flow reductions (either natural reductions during droughts or unnatural reductions due to diversion) increased both recruitment and survivorship of *Populus* and *Salix* seedlings.

The differences in response relate to differences in riverbed cross section between the two geomorphic types. Braided streams are relatively wide and shallow. Large increases in flow translate into large increases in the width of the wetted channel and into small increases in average depth. Thus, the proportion of the active channel exposed and available for plant colonization is variable and highly sensitive to small flow changes in the low-flow range. Much of the riverbed of braided streams is suitable for plant colonization under low flows.

In contrast, meandering rivers are considerably deeper and narrower, except at flood stage, when they may overtop the normal banks and spread onto the adjacent floodplain. Except at flood stage, large changes in flow translate into large changes in depth and small changes in wetted width. Most permanent vegetation is located on the floodplain outside the channel (except for in-stream islands), since the large vertical rise in

river stage during floods allows little successful in-channel plant establishment.

The geomorphic types also differ in responsiveness to altered flow. Detectability of the effects of flow changes in the forest vegetation along meandering rivers is difficult over the short term because recruitment is naturally episodic (several- to 10-yr intervals between suitable peak flow events), and the decline of *Populus-Salix* forests established prior to the flow change is slow since they are not actually replaced by later successional species for nearly a century (Johnson et al. 1976). In contrast, the effect of reduced flows in braided rivers soon would be evident by the expansion of early successional woodland into active channels, as occurred historically in the Platte River.

Variation in stream geomorphology (including intermediates between meandering and braided systems), biota (presence of aggressive exotic species), and in the type, timing, and magnitude of flow alteration, makes prediction of the behavior of a given stream system to alteration difficult. The complex intertwining of current and historic factors affecting vegetation along rivers confuses cause and effect. For example, Rood and Mahoney (1990) cite the combination of dynamic riparian ecosystems and agricultural and urban development in making it difficult to pinpoint the onset of changes or verification of the causal link between dams and downstream forest decline. The recent increase in riparian research, especially in long-term studies and monitoring (Bradley and Smith 1986, Osterkamp and Costa 1987, Streng et al. 1989) and in experimental approaches (Walker and Chapin 1986, Walker et al. 1986, Schneider and Sharitz 1988, Stromberg and Patten 1990) offers promise that cause and effect can be disentangled and that generalizations can be made to assist in management prescriptions.

Management

Although Platte River channels have stabilized in width in recent decades, temporary narrowing will occur during droughts. More permanent narrowing could result if climate changed or exploitation of streamflow and groundwater increased. Further channel narrowing may not benefit certain rare or uncommon migratory birds that utilize wide, active channels (e.g., Whooping Crane, Piping Plover, Least Tern; FWS 1981).

The findings of this study may prove useful should flow management be attempted to minimize future woodland expansion. Several options are available: (1) prohibit recruitment in the active channel by augmenting June flows to maintain a several-year average of at least 75–85 m³/s below the J-2 Return (Table 1, Fig. 5) and 30–40 m³/s above the Return; and increase seedling mortality by (2) raising winter flows to increase ice scouring, (3) increasing spring peak erosive flows to remove seedlings, or (4) reducing late-summer flows to increase seedling desiccation. While these are river-wide management options, others have proposed and

have implemented local solutions to the narrowing problem by clearing woodland from banks and islands (Currier and Stubbendieck 1985).

Effectiveness of options 2 and 4 would depend on climate; one of the four winters between 1986 and 1989 was too warm to form thick cake ice, and two of the four summers were either too wet or cool to cause high mortality even during very low flows. Option 4 is probably the least effective of all, given the need for climatic drought and the observation that desiccation mortality, when it does occur, primarily thins seedling ranks rather than removes large areas of seedlings from the riverbed. Option 2 would be effective in most years, especially if flow increases from reservoirs could be timed to co-occur with cake ice formation and with ice breakup. The statistical results showed that only small increases in flow would cause large increases in seedling mortality in winter.

Options 1 and 3 would require large flow releases from storage during dry years to be effective. Option 3 would require flows of at least 170–225 m³/s for several days to remove or bury 1st-yr seedlings. Removal of older seedlings would require considerably higher flows, and established woodland could only be removed on islands and banks by floods of large magnitude, comparable to those of 700 m³/s or so that occurred in 1983.

Option 1 is perhaps the best, since prohibiting recruitment obviates the need to use options 2–4. However, during drought years, large amounts of stored water would be required to prohibit recruitment. Less water would be required if oscillating flow patterns proved effective in removing young germinants.

The most effective management may be to combine options, based on knowledge of recruitment success and seedling survivorship from a permanent plot sampling network similar to the one used in this or in other studies (McBride and Strahan 1984, Streng et al. 1989, Stromberg et al. 1991). Population monitoring could determine, first, whether flow management was needed and, second, which option would use water most efficiently. For example, under high natural flows, probably no flow augmentation would be required. During droughts, increased recruitment and survival may be removed most efficiently by augmenting winter flows (option 2) and reserving the options requiring higher flows (options 1 and 3) for periods following warm winters when ice management would be ineffective.

Experimentation would be required for successful management of Platte River channels. The degree to which flows can be controlled and timed to coincide with critical events such as ice formation and breakup are currently unknown. Also, the exact response of both the biota and the physical environment to prescribed flows is poorly known. For example, field observations indicated highly variable response of the physical environment to summer peaks of comparable magnitude. In one instance most channels within a given reach

were degraded in one year, while in another year, they were aggraded. The prospects for tree colonization in each case were markedly different, since the sandbars differed dramatically in elevation and hydroperiod. Why sedimentation patterns should differ markedly between years with comparable peaks and timing is not clear, but it does point out that our knowledge of the relationships among flow, sediment transport, and vegetation dynamics is incomplete. Development of successful management prescriptions through experimentation will require special cooperation between the operators of dams and ecologists monitoring vegetation.

The extensive, middle-aged, *Populus*–*Salix* woodland that currently exists in the Platte River will decline in the future because of replacement by later-successional species, reduced tree regeneration in recent decades, and inability of the river to provide new sandbar habitat by eroding older woodland. Any potential for expansion in the future, even if only temporary, may be precluded by flow management and clearing. *Populus* and *Salix* do not successfully regenerate under forest conditions (Johnson et al. 1976), hence the woodlands they now dominate will become dominated by later-successional species currently regenerating in the forest understory (probably *Fraxinus pennsylvanica* in the humid portions of the Platte Valley and *Elaeagnus angustifolia*, *Juniperus virginiana*, and shrubs in the semi-arid portions) (Currier 1982, Sedgwick and Knopf 1989, Knopf and Scott 1990).

The replacement woodlands may not support the high avian diversity of mid-successional *Populus*–*Salix* woodland, primarily because the later-successional tree species provide fewer nesting cavities (Hibbard 1972, Bottorff 1974, Knopf 1986). Other animals also reach maximum population sizes in *Populus*–*Salix* woodland (Hibbard 1972, Fitzgerald 1978).

Because *Populus* woodland ceased expansion into the South Platte River in Colorado much before it did in the Platte River, it has already shown substantial decline. Ironically, *Populus* is now being planted along the South Platte River in Colorado to maintain habitat for woodland fauna (Snyder and Miller 1991), while it is being cleared along the Platte River in Nebraska to widen channels for aquatic avifauna.

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APPENDIX

Environmental variables used in correlation/regression analysis of *Populus* and *Salix* demographic data.

Variables for winter			
ICE:	A composite variable of air temperatures and flow (see <i>Methods: Statistical analysis of channel/woodland change rates: Independent variables: ICE index</i>)	MEDFLOD:	Median daily mean flow for 1 December–1 March
ICEB1:	Similar to ICE index, but based on days when the minimum temperature did not exceed -12°C (10°F)	DAYS32:	Total number of days on which the daily maximum temperature did not exceed 0°C (32°F)
ICEB2:	Same as ICEB1, but based only on 1 December–1 March	INT32:	Number of consecutive days (or days separated by ≤ 3 d above 0°C) on which maximum temperature was $\leq 0^{\circ}\text{C}$
ICEC1:	Similar to ICEB1, but based on flow at the times of probable ice formation	MTMAX:	Mean daily maximum temperature for 15 November–15 March
ICEC2:	Same as ICEC1, but based only on 1 December–1 March	DAYS10:	Total number of days with minimum temperatures $\leq -12^{\circ}\text{C}$ (10°F)
ICEFLO1:	Maximum daily mean flow during intervals of at least two consecutive days with minimum temperatures $\leq -12^{\circ}\text{C}$, for 1 December–1 March	DAYS10A:	Total number of days with minimum temperatures $\leq -12^{\circ}\text{C}$, for the interval 1 December–1 March
ICEFLO2:	Same as ICEFLO1, but for entire winter sampling period	COLD:	Longest interval of consecutive days with minimum temperatures of $\leq -12^{\circ}\text{C}$
MAXFLOW1:	Maximum daily mean flow for 15 December–15 March	COLDA:	Longest interval of consecutive days with minimum temperatures of $\leq -12^{\circ}\text{C}$ for 1 December–1 March
MAXFLOW2:	Maximum daily mean flow for 1 December–1 March	MMXTDEM:	Mean daily maximum temperature for 1 December–1 March
MFLODEM:	Mean daily mean flow from 1 December–1 March	MMITDEM:	Mean daily minimum temperature for 1 December–1 March
MEDFLOW:	Median daily mean flow for entire winter sampling period		
Variables for spring and summer			
RAIN0:	% of days with no precipitation ($<.025$ cm) during sampling period	MAXFLOW:	Maximum daily mean flow during the sampling period
DROUGHT:	Longest interval of consecutive days with no precipitation	MEDFLOW:	Median daily mean flow during the sampling period
MPPT:	Mean daily precipitation (total precipitation/no. of days in period)	MINFLOW:	Minimum daily mean flow during the sampling period
MPPT90:	Mean daily precipitation on days when the maximum temperature exceeded 32°C (90°F)	MXFLOW90:	Maximum daily mean flow of days on which the maximum temperature exceeded 32°C
DRYTEMP:	Mean maximum daily temperature during longest drought (interval with no precipitation)	MIFLOW90:	Minimum daily mean flow of days on which the maximum temperature exceeded 32°C
DAYS90:	% of days with maximum temperatures $> 32^{\circ}\text{C}$ during sampling period	FLOW1%:	% of the period that daily mean flows were $21.2\text{ m}^3/\text{s}$ or less
MTMAX:	Mean daily maximum temperature during sampling period	DFLOW1:	Number of days with daily mean flows of $21.2\text{ m}^3/\text{s}$ or less during the period
MTFLOW1:	Mean daily maximum temperature on days when daily mean flow was $\leq 21.2\text{ m}^3/\text{s}$ (750 cfs [ft^3/s])		
Elevation variables			
MEANEL:	Mean seedling elevation (mean plot elevation weighted by seedling number)	MEDEL:	Median plot elevation
MNEL:	Mean plot elevation	MINEL:	Minimum plot elevation
MAXEL:	Maximum plot elevation	Q1EL:	The lower quartile of plot elevations
		Q3EL:	The upper quartile of plot elevations