

CHANNEL NARROWING AND VEGETATION DEVELOPMENT FOLLOWING A GREAT PLAINS FLOOD¹

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Abstract. Streams in the plains of eastern Colorado are prone to intense floods following summer thunderstorms. Here, and in other semiarid and arid regions, channel recovery after a flood may take several decades. As a result, flood history strongly influences spatial and temporal variability in bottomland vegetation. Interpretation of these patterns must be based on understanding the long-term response of bottomland morphology and vegetation to specific floods.

A major flood in 1965 on Plum Creek, a perennial sandbed stream, removed most of the bottomland vegetation and transformed the single-thread stream into a wider, braided channel. Channel narrowing began in 1973 and continues today. In 1991, we determined occurrences of 150 vascular plant species in 341 plots (0.5 m²) along a 7-km reach of Plum Creek near Louviers, Colorado. We related patterns of vegetation to elevation, litter cover, vegetative cover, sediment particle size, shade, and year of formation of the underlying surface (based on age of the excavated root flare of the oldest woody plants). Geomorphic investigation determined that Plum Creek fluvial surfaces sort into five groups by year of formation: terraces of fine sand formed before 1965; terraces of coarse sand deposited by the 1965 flood; stable bars formed by channel narrowing during periods of relatively high bed level (1973–1986); stable bars similarly formed during a recent period of low bed level (1987–1990); and the present channel bed (1991).

Canonical correspondence analysis indicates a strong influence of elevation and litter cover, and lesser effects of vegetative cover, shade, and sediment particle size. However, the sum of all canonical eigenvalues explained by these factors is less than that explained by an analysis including only the dummy variables that define the five geomorphically determined age groups. The effect of age group is significant even when all five other environmental variables are specified as covariables. Therefore, the process of postflood channel narrowing has a dominant influence on vegetation pattern. Channel narrowing at Plum Creek includes a successional process: annual and perennial plants become established on the channel bed, sediment accretes around the vegetation, and increasing litter cover, shade, and scarcity of water eliminate species that are not rhizomatous perennials. However, successional trajectories of individual surfaces are modified by flow-related fluctuations of the bed level; surfaces deposited by the 1965 flood have had distinct sediment and vegetation since their formation. Species richness is highest on surfaces dating to 1987–1990; the many species restricted to this transitory assemblage are perpetuated by flood-related fluctuations in channel width. Since the 1965 flood, seedling establishment of the dominant trees (genus *Populus*) has occurred only on low surfaces formed during channel narrowing. Thus, the flood has indirectly promoted *Populus* establishment over a 26-yr period.

Key words: bottomland vegetation; channel narrowing; Colorado; cottonwood; dendrochronology; disturbance; flood; patch dynamics; succession.

INTRODUCTION

Floods control both the physical environment and biotic community of stream and riparian ecosystems. Immediate effects of floods include widening, filling, deepening, or relocation of the channel (Baker et al.

1988); alteration of substrate particle sizes (Schumm and Lichty 1963, Osterkamp and Costa 1987); damage to riparian and aquatic vegetation (Sigafoos 1964); and addition or removal of organisms from the local community (Meffe 1984, Grimm and Fisher 1989). When geomorphic effects are minor, recovery of populations of short-lived organisms may occur within weeks (Grimm and Fisher 1989). However, when extensive geomorphic changes and long-lived organisms are in-

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involved, recovery may require decades or longer (Schumm and Lichty 1963, Hereford 1984).

In gradient analyses of bottomland vegetation, flood frequency and intensity have been shown to be important influences on vegetation zonation, both perpendicular (Bedinger 1971, Menges and Waller 1983, Osterkamp and Hupp 1984, Day et al. 1988, Shipley et al. 1991) and parallel (Hupp 1982, Nilsson 1987) to the direction of flow. One limitation of these gradient analyses is that they assume that the vegetation is in a state of quasi-equilibrium with respect to the flow regime; thus, they reveal little information about processes of vegetation change initiated by floods. Several studies have investigated the short-term effects of specific flood events on establishment and removal of woody vegetation (Everitt 1968, Yanosky 1982, Bradley and Smith 1986, Stromberg et al. 1991, Stromberg et al. 1993, Scott et al. 1996). However, the long-term influence of extreme floods on processes of bottomland vegetation change has rarely been addressed.

Although channel geometry is largely determined by high discharges in most streams, relative importance of the most extreme floods depends upon flow variability. In large watersheds in humid regions, flow variability is low, most fluvial work is done by high flows that recur once every year or two, and recovery from more extreme events is rapid (Wolman and Miller 1960). In arid regions and smaller watersheds, flow variability is higher and extreme events can cause channel changes that persist for decades or centuries (Baker 1977). Where the recovery time following events approaches the time between events, channel geometry commonly will be in a state of disequilibrium (Wolman and Gerson 1978). In this context, spatial and temporal variability in bottomland vegetation can be influenced strongly by flood history, and interpretation of these patterns must be based on understanding the long-term response of bottomland morphology and vegetation to specific floods.

Along sandbed streams in dry regions, floods can increase channel width by as much as an order of magnitude (Schumm and Lichty 1963, Burkham 1972). Increased width may persist for decades, and subsequent narrowing typically occurs as a result of vegetation establishment on the channel bed during periods of low peak flow (Schumm and Lichty 1963, Hereford 1984, Osterkamp and Costa 1987). The rate of channel narrowing is also influenced by fluctuations in bed level resulting from variation in discharge and sediment load (Friedman et al. 1996). Postflood channel narrowing is a common and widespread phenomenon (Schumm and Lichty 1963, Northrop 1965, Burkham 1972, Hereford 1984) closely related to the narrowing that can follow dam construction (Johnson 1994) or climate change (Schumm 1969). Recent work in vegetation science has emphasized nonequilibrium aspects of vegetation (Pickett and White 1985, Bravard et al. 1986, Hupp 1992, Johnson 1994). However, in spite of the impor-

tance of the physical process of postflood channel narrowing, the associated spatial and temporal patterns of vegetation have received little attention, in part because of the difficulty of following complex changes in channel form and vegetation over decades.

The present study is an analysis of the vegetation patterns along a sandbed stream 26 yr after a major flood. We hypothesized that present patterns of vegetation are related to a temporal sequence of fluvial surfaces formed during the flood and the ensuing process of channel narrowing. We dated fluvial surfaces using dendrogeomorphic techniques (Sigafoos 1964) and used direct gradient analysis (Whittaker 1967) to relate patterns of vegetation to year of surface formation, elevation, litter cover, vegetative cover, and sediment particle size. We then interpreted these relations in light of five decades of geomorphic data from the site (Matthai 1969, Osterkamp and Costa 1987), including records of discharge and bed level.

METHODS

Study site

Plum Creek, a perennial sandbed stream in the Colorado Piedmont section of the Great Plains physiographic province (Madole 1991), flows north 14 km along the base of the Rocky Mountains and then joins the South Platte River south of Denver, Colorado (Fig. 1). The study area is a 7-km reach of Plum Creek from Sedalia downstream to Louviers. The watershed at Louviers has an area of 782 km² and mean bottomland elevation of 1720 m. Mean annual precipitation in Sedalia is 445 mm (Colorado Climate Center, *unpublished data*). The median daily discharge for water years 1958–1990 was 0.38 m³/s at Louviers (United States Geological Survey, *unpublished data*). Plum Creek flows through a valley \approx 1 km wide, consisting of rarely inundated Quaternary alluvial terraces, frequently inundated alluvial deposits, and eolian deposits. The study area is privately owned and includes both grazed and ungrazed parcels.

In most years, the highest flow in Plum Creek originates from snowmelt in foothills of the Rocky Mountains, and is sustained for several weeks in April or May. Less often, the peak annual flow is a flash flood resulting from thunderstorms in the plains from mid-May through September (Friedman et al. 1996). The eastern part of the watershed drains Palmer Divide, a focus of intense precipitation (Fig. 1). On 16 June 1965, 360 mm of rain, 81% of the mean annual precipitation, fell on parts of the watershed of Plum Creek in 4 h (Matthai 1969). The resulting peak discharge in the study reach was 4360 m³/s, and the valley floor was inundated for 2.5 h (Matthai 1969).

Geomorphic investigations at Plum Creek have been ongoing since the flood (Matthai 1969, Osterkamp and Costa 1987, Friedman 1993). Before 1965, Plum Creek was a single-channel stream with steep, wooded banks,

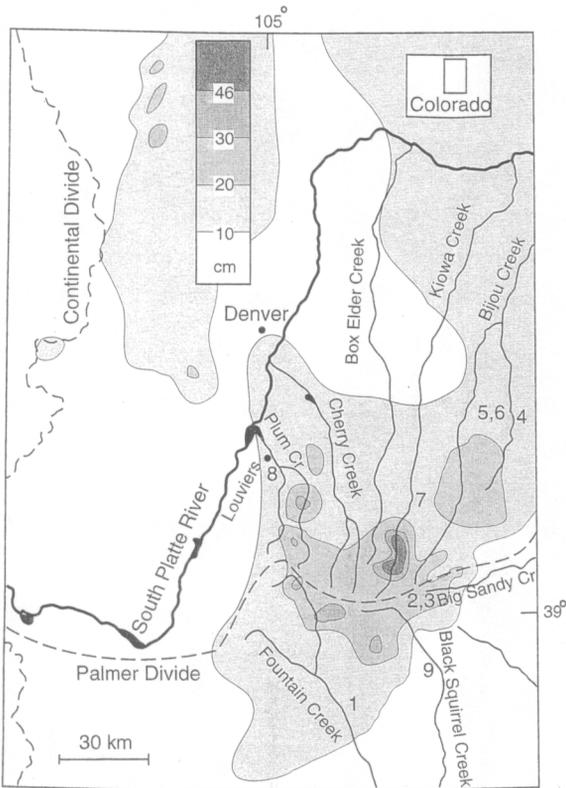


FIG. 1. Major streams draining the Palmer Divide, Colorado. Shading indicates maximum precipitation in a 24-h period (modified from Hansen et al. 1978). Numbers indicate the location of floods listed in Table 5.

mean width of 26 m, gradient (elevation change/stream length) of 0.0053, and sinuosity (length of stream/length of valley) of 1.22 (Osterkamp and Costa 1987). The flood sheared off or uprooted half of the trees on the bottomland and transformed the stream into a wider, straighter, and steeper braided channel. Many bends in the former channel were filled with deposits of coarse sand up to several metres deep. The decrease in ve-

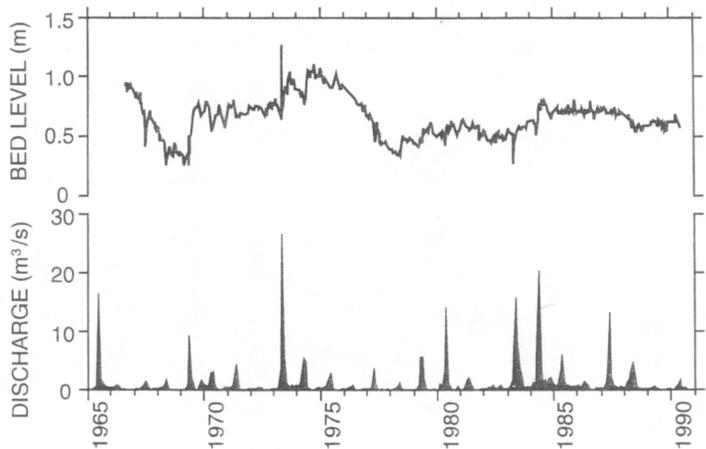
etative cover reduced bank stability, promoting continued widening during the relatively minor high flows of 1969 and 1973. By 1973, mean channel width had increased to 116 m, gradient had increased to 0.0064, and sinuosity had decreased to 1.01 (Osterkamp and Costa 1987). After 1973, 9 yr of relatively low peak flows allowed vegetation establishment on the channel bed, and sustained channel narrowing began.

Channel narrowing has been facilitated by flow-related variation in channel-bed level (Fig. 2; Friedman et al. 1996). Sediment enters Plum Creek only during high discharge, when the stream is able to erode laterally into adjacent terraces and its ephemeral tributaries are flowing (Osterkamp and Costa 1987). As a result, bed level rises during high flow. During a subsequent period of low flow dominated by groundwater discharge, a narrower channel may be incised. Relatively high portions of former channel bed are then stable enough for colonization by vegetation (Friedman et al. 1996). At the inception of this study in 1991, postflood channel narrowing was not yet complete. Vegetation had stabilized portions of the channel bed in the preceding 4 yr, and Plum Creek was still wider and straighter than it had been before the 1965 flood. Most of the study reach was still braided, although some channel branches had become stabilized by vegetation and associated accumulations of cohesive fine sediment.

Field methods

In 1991, we located eight cross sections to provide a representative sample of geomorphic conditions at Plum Creek. The cross sections ranged in length from 150 to 208 m, encompassing the entire width that has been inundated since 1965 plus ≈ 80 m of terrace. We established 341 circular plots (0.5 m²) along the cross sections. This plot size was large enough to provide a representative sample of herbs and shrubs, and small enough to be relatively uniform in elevation and age of surface. Plots were 3 m apart except on terraces,

FIG. 2. Bed level and mean monthly discharge at the U.S. Geological Survey gaging station on Plum Creek near Louviers, Colorado. Bed level is relative to the arbitrary datum of the gaging station. (Redrawn after Friedman et al. 1996.)



where the interval was increased to 9 m to decrease the spatial dependence of adjacent plots resulting from the influence of large trees. Between 8 July and 21 August 1991, we determined the presence or absence of all vascular plant species in all the plots and counted all stems of woody species. Voucher specimens have been deposited at the University of Colorado Herbarium in Boulder, Colorado. Nomenclature follows the Great Plains Flora Association (1986), except that we used the name *Salix × rubens* Schrank instead of *S. fragilis* for crack willow (Shafroth et al. 1994).

Using a plot frame, we determined the proportion of the ground surface covered by litter and the proportion of the ground surface covered by living vegetation below a height of 1.65 m. We characterized the dominant surface sediment as either clay-silt or sand-gravel (>0.063 mm), and characterized overstory shade as open, partial shade, or full shade. Using a rod and level, we determined the elevation of each plot relative to the water surface at the cross section on the afternoon of 16 April 1991. To calculate the proportion of perennials in each plot (Shipley et al. 1991), we assigned values of 1, 0.5, and 0, respectively, to all occurrences of perennials, biennials, and annuals (Great Plains Flora Association 1986). These numbers were summed and divided by the total occurrences in the plot. In the same way, we calculated the proportion of native species (Weber and Wittman 1992) in each plot.

The bottomland at Plum Creek consists of a set of discrete, relatively flat, fluvial surfaces generally separated by breaks in elevation. In 1992, we determined the year of formation of the fluvial surface containing each plot by aging the oldest woody plants in or near the plot on the basis of winter bud scars, rings in a core taken within 30 cm of the ground (Phipps 1985), or rings at the point of germination, as determined by the position of the excavated root flare (Sigafos 1964). We used the most accurate method, sectioning at the root flare, for 63 of the 129 woody plants examined. Almost all cored or sectioned plants were members of the Salicaceae, a family with diffuse-porous wood. We defined the year of formation of a surface as the establishment year of the oldest woody plant occupying it, and verified these years using historical ground-level and stereo aerial photography. All surfaces other than terraces and the channel bed supported woody vegetation. Because many of the terraces did not, we used stereo aerial photographs (1:6000) to divide terrace surfaces into two groups: those formed during the 1965 flood and those formed before the 1965 flood. Terraces dating to 1965 were formed by deposition of coarse sand and gravel in bends of the channel cut off by the flood.

Because plots of 0.5 m² were not large enough to measure tree abundance, we carried out a separate survey of those species capable of exceeding 10 cm in diameter. In autumn 1992, we recorded diameter at 1.2 m of all trees in belt transects 30 m wide and centered

on the cross sections. We then calculated basal area and density of each species by year of formation of the underlying surface.

Ordination

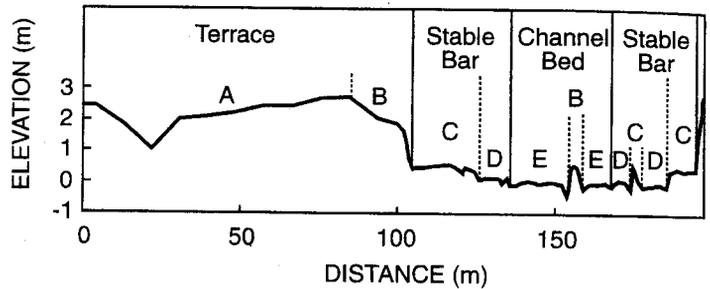
We explored the relationship between vegetation and environmental variables using canonical correspondence analysis (CCA; ter Braak 1987–1992) and detrended correspondence analysis (DCA). CCA and DCA are particularly effective where the vegetation is distributed along a gradient that is longer than the range of occurrence of individual species (ter Braak 1987–1992, Peet et al. 1988). Seedlings of *Salix*, *Populus*, and *Prunus* could be identified only to genus. In the ordinations, therefore, we lumped by genus all occurrences of seedlings and adults in these three genera. This was done to avoid circular reasoning: the use of age-related pseudospecies to demonstrate a relationship between vegetation and year of formation of a surface. Because surfaces of different ages are not all part of the same successional sequence, surface age was represented not as a continuous variable but as a set of five age classes indicated by the geomorphic investigations: pre-1965, 1965, 1973–1986, 1987–1990, and 1991. Some of the dummy variables defining these age classes were strongly correlated with other environmental variables; therefore, to avoid multicollinearity in CCA, we carried out two separate ordinations. In the first ordination, the independent variables were the four dummy variables that define the five age groups; in the second ordination, the independent variables were the other five environmental factors. We used forward selection of environmental variables to test whether or not each added variable made a significant contribution to the sum of all canonical eigenvalues. Significance was determined by permutation tests, using the eight cross sections as blocks and distance along the cross section as an additional covariable. Permutations were generated in the software CANOCO (version 3.1), using an algorithm that preserves the autocorrelation structure of the data (ter Braak and Wiertz 1994). To test the significance of vegetation patterns associated with the five age groups, we carried out an additional permutation test that added all other environmental variables as covariables.

RESULTS

Bottomland morphology

The cross sections included from 10 to 47 m of channel bed (dating to 1991), an undulating, unvegetated or sparsely vegetated surface of recently reworked channel sediment (Fig. 3). Channel sediment at Plum Creek is a poorly sorted mixture dominated by gravel and sand (Osterkamp and Costa 1987). In most years, the channel bed is completely inundated for a few weeks in the spring. During the rest of the growing season, this surface is only partly inundated by the

FIG. 3. Sample cross section of Plum Creek near Louviers, Colorado, facing downstream. Elevation is relative to the water surface on 16 April 1991. The letters indicate surfaces formed in different years: A, pre-1965; B, 1965; C, 1973–1986; D, 1987–1990; and E, 1991.



shifting anabranches of Plum Creek. The channel bed ranges in elevation from -0.20 to 0.14 m relative to the water surface on 16 April 1991 (Table 1, Fig. 4).

Adjacent to the channel bed are sparsely to densely vegetated stable bars, which have been deposited since the onset of postflood narrowing, and now occupy from 43 to 104 m of the cross section (Fig. 3). These surfaces consist of channel sediment covered by several layers of well-sorted overbank sediment ranging from silt to sand. Stable bars can be separated into two groups by year of formation and elevation. Surfaces dating to 1987–1990 are former portions of the channel bed stabilized during a recent period of low flow (Fig. 4). These surfaces are at or slightly above the 1991 bed level (Table 1, Fig. 4). In most years, surfaces dating to 1987–1990 are inundated for a few days in the spring. Surfaces dating to 1973–1986 are relict portions of the channel bed from periods when the bed was higher than in 1991 (Figs. 2 and 4; Friedman et al. 1996). These surfaces average 44 cm above the channel bed (Fig. 4, Table 1), and generally have not been inundated since June 1987. Beyond the stable bars is a steep slope up to a terrace averaging 2.42 m above the channel bed (Table 1, Fig. 3). Terraces formed by the flood of 1965 are similar in elevation to those formed before the flood (Fig. 4, Table 1). Terraces have not been inundated since the flood of 1965.

Vegetation

Table 2 describes 150 vascular plant species that occurred in at least one plot. Most species are typical of

bottomlands at low elevation in Colorado, but several foothills and montane species are also present (Friedman 1993). Many of the plants at Plum Creek are ruderal species with wide distributions. Thirty-six percent of the species are exotics, many of which were already common in the region by 1905, ≈ 50 yr after settlement (Young 1907, Friedman 1993).

The first axis of the CCA ordination (eigenvalue = 0.65; Fig. 5) is strongly correlated with elevation (canonical coefficient = 0.98; Table 3). The second axis (eigenvalue = 0.35) is associated with decreasing litter cover (canonical coefficient = -0.80) and, to a lesser extent, with decreasing vegetative cover, increasing soil particle size, and decreasing shade (Fig. 5, Table 3). The third axis (eigenvalue = 0.19) is most strongly associated with vegetative cover (canonical coefficient = -0.85 ; Table 3). Forward selection of environmental variables demonstrated that all five of these environmental variables make a significant contribution to the sum of all canonical eigenvalues ($P < 0.02$). The highest values of plots on CCA axis 2 are at opposite ends of the elevation gradient; coarse sediment, low litter, and vegetative cover occur both at low elevations on the channel bed and at high elevations on terraces deposited by the 1965 flood (Fig. 5, Table 1).

Although CCA shows a strong relation between species composition and elevation, litter, vegetative cover, shade, and sediment particle size (Fig. 5, Table 3), the sum of all canonical eigenvalues explained by these factors (1.33) is less than that explained by an ordination including only the four dummy variables that

TABLE 1. Summary data for plots at Plum Creek by year of surface formation. Where an estimate of variation is given, data are means ± 1 SE. Elevation is relative to the water surface on 16 April 1991. Occurrence of sand or gravel is expressed as the percentage of plots having a surface sediment dominated by particles at least as coarse as sand.

	Year of formation				
	1991	1987–1990	1973–1986	1965	Pre-1965
Fluvial surface	channel bed	stable bar	stable bar	terrace	terrace
Mean relative elevation (m)	-0.02 ± 0.01	0.11 ± 0.02	0.42 ± 0.02	2.45 ± 0.15	2.40 ± 0.07
Mean litter cover (%)	0.7 ± 0.4	13 ± 2	76 ± 2	37 ± 5	69 ± 4
Mean vegetative cover (%)	3 ± 1	60 ± 3	49 ± 2	33 ± 3	57 ± 3
Occurrence of sand or gravel (% of plots)	97	31	41	93	74
Mean percentage of full shade	7	8	30	30	36
Mean number of species per plot	3.3 ± 0.4	18.0 ± 0.7	10.2 ± 0.3	5.4 ± 0.4	5.0 ± 0.3
Mean percentage of native species	56 ± 3	51 ± 2	60 ± 1	71 ± 4	22 ± 3
Mean percentage of perennial species	76 ± 4	71 ± 2	91 ± 1	75 ± 4	63 ± 4
Number of plots	71	65	120	28	57

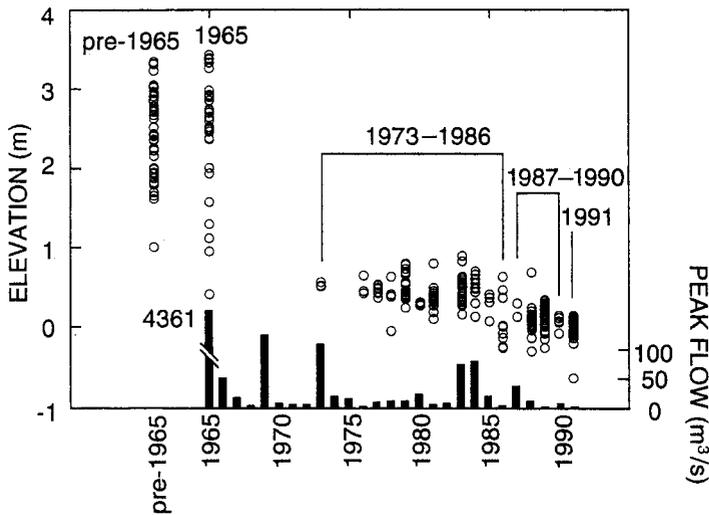


FIG. 4. Relative elevation of plots along Plum Creek, Colorado, vs. year of formation of the underlying surface, as determined by ring counts of the oldest woody vegetation. Bars are peak instantaneous annual discharge. Elevations are relative to the water surface on 16 April 1991.

define the five geomorphically determined age groups (1.49; Table 3). A permutation test that preserves the autocorrelation structure of the data indicates that the effect of the age groups is significant ($P = 0.001$) even when effects of the five other environmental variables and the eight cross sections are removed from the data. However, it is still possible that local spatial autocorrelation, at a scale >3 m but smaller than a whole transect, contributes to the signal attributed to age group. Plots in the five age groups form visually distinct clusters when age is added passively to the ordination of vegetation against the other environmental variables (Fig. 5). The same distinct groups are evident when DCA is used to ordinate plots on the basis of species occurrence alone (ordination not shown). Most species are essentially restricted to a single age group or to two adjacent groups (Table 2). These data indicate that the process of postflood channel narrowing has a dominant influence on vegetation pattern.

All plots dating to 1991 occurred on the channel bed, and had low litter and vegetative cover (Table 1). Nineteen of these plots were unvegetated because of recent disturbance by flowing water, and could not be included in the ordinations. Unvegetated plots occurred only on the channel bed. Plots dating to 1991 had few species (Table 1). The taxa with $>10\%$ frequency of occurrence were seedlings of cottonwood and willow, two annual graminoids (*Cyperus aristatus* and *Eragrostis pectinacea*), an annual herb (*Polygonum persicaria*), and a perennial herb apparently capable of flowering in its 1st yr (*Veronica anagallis-aquatica*; Table 2).

Surfaces dating to 1987–1990 (young stable bars) were, on average, only 13 cm higher than the channel bed (Fig. 4, Table 1). The substrate consisted of channel sediment, which was usually covered by a few centimetres of silt or clay. Litter cover was low, but vegetative cover was much greater than on the channel bed (Table 1). The vegetation in this group was distinct from that in plots dating to 1991. Plots dating to 1987–

1990 had the highest species richness of all groups (Table 1). Forty-eight species, as well as seedlings of cottonwood and willow, had a frequency of occurrence $>10\%$ on this surface. These species were a mixture of annuals, biennials, and both rhizomatous and caespitose perennials (Table 2).

Plots on surfaces dating to 1973–1986 (old stable bars) averaged 31 cm higher than plots dating to 1987–1990, and had higher litter cover, lower vegetative cover, higher proportion of perennials, and fewer species (Table 1). Of the 23 species with a frequency of occurrence $>10\%$ in these plots, 19 were perennials and 15 were rhizomatous (Table 2). The 17 most frequently occurring species in this group were also common on plots dating to 1987–1990.

Plots dating to 1965 were on terraces formed when the flood cut off bends in the channel and filled them with coarse sand. Surfaces dating to 1965 were essentially treeless (Table 4), and had low litter cover, low vegetative cover, and few species per plot (Table 1). The dominants were mostly native taprooted or caespitose species (Table 2). Plots dating to before 1965 were on surfaces dominated by medium sand and finer sediment, with a considerable amount of organic matter near the surface (Scott 1963). Plots dating to before 1965 had more trees, higher cover of litter and vegetation, and a greater proportion of exotic and rhizomatous species than did plots dating to 1965 (Tables 1 and 4).

The abundance and elevation of surfaces formed in different years can be explained by the records of bed level and discharge (Figs. 2 and 4). No plots are on surfaces formed from 1966 to 1972, because the two highest flows since 1965 (1969 and 1973) reworked all developing stable bars (Fig. 4). As a result of the 1973 high flow, bed level peaked in 1975 (Fig. 2); subsequent incision of a narrower channel made available portions of the former bed for establishment of vegetation (Fig. 4). The high flows of 1983 and 1984 deposited sediment

on pre-existing surfaces and formed new surfaces for colonization. Low flows since 1987 have allowed establishment of vegetation at low elevations on the present channel bed. Thus, the difference in vegetation between surfaces dating to 1987–1990 and those dating to 1973–1986 is determined by the sequence of high and low flows since 1965.

The dominant trees on surfaces formed before 1965 were *Populus deltoides* ssp. *monilifera* and *P. × acuminata*, a hybrid between *P. deltoides* and *P. angustifolia*. The largest trees, those stems that survived the flood of 1965, were mostly *P. × acuminata*. *P. angustifolia* was uncommon on surfaces dating to before 1965, but abundant on surfaces dating to 1973–1986. *Salix amygdaloides*, which dominates some other bottomlands in the Colorado Piedmont, was dominant at Plum Creek only on slopes separating terraces from younger, lower surfaces (Table 4). The relatively low values for all species on plots dating to 1987–1991 result from the fact that most trees on these surfaces were too short to be tallied.

Populus and *Salix* seedlings were restricted to the moist, open surfaces dating to 1991 and 1987–1990 (Table 2). Older, higher surfaces were apparently too dry for establishment of such seedlings, which were absent even where shade, litter cover, and vegetative cover were low (Table 2). Abundant saplings and small trees on surfaces dating to 1973–1986 indicate that these surfaces had formerly been moist enough for seedling establishment. On the other hand, surfaces dating to 1965 were essentially treeless (Table 4), and surfaces dating to before 1965 had few small individuals (Fig. 6), suggesting little or no reproduction by seed on terraces since 1965. Present forest on surfaces dating to before 1965 is limited to areas that were already forested before the flood (Friedman 1993); most of the smaller stems occur in groups of two to six attached near the ground. Therefore, postflood reproduction on surfaces dating to before 1965 appears to have been limited to root sprouts and stump sprouts from trees sheared off by the flood.

DISCUSSION

Channel narrowing as succession

Some of the vegetation pattern on the channel bed and stable bars at Plum Creek (Fig. 5) can be explained by a successional model combining processes of vegetation development and channel narrowing. The sequence begins with establishment of willows, cottonwoods, and a few fast-growing herbs on an exposed portion of the channel bed during several years of low flow (Schumm and Lichty 1963, Hereford 1984, Williams and Wolman 1984, Johnson 1994). If the surface is not reworked by streamflow, additional species become established on the new stable bar, including taprooted, caespitose, and rhizomatous perennials. As roots and shoots enlarge, the surface becomes more

resistant to erosion (Smith 1976) and more efficient at trapping sediment (Burkham 1972, Osterkamp and Costa 1987). Deposition of fine sediment raises the elevation of the surface and decreases the frequency of disturbance. The increase in litter and shade and the decrease in water availability result in decreased seedling establishment and increased competition for light and moisture; these factors eliminate species that are not rhizomatous perennials (Menges and Waller 1983, Shipley et al. 1991, Tilman 1993). The peak in species richness on surfaces of intermediate age (1987–1990) is evident, in terms of both the number of species per plot (Table 1) and the total number of species with a frequency of occurrence >10% on each surface (Table 2). An analogous pattern occurs in some old-field successions (Brown and Southwood 1987).

The vegetation on surfaces dating to 1973–1986 evidently developed from that on surfaces like those dating to 1987–1990 through interspecific competition and a decline in seedling establishment. The dominant species in plots dating to 1973–1986 are almost all rhizomatous perennials, and are a subset of the dominants on plots dating to 1987–1990 (Tables 1 and 2). Tall rhizomatous species dominate fertile, infrequently disturbed sites along streams in Wisconsin (Menges and Waller 1983) and along the Ottawa River in Ontario and Quebec (Day et al. 1988). At least four factors contribute to this trend at Plum Creek. First, litter cover increases from plots dating to 1987–1990 to plots dating to 1973–1986 (Table 1). This is both because litter accumulates over time and because litter at higher elevations is less likely to be removed by flowing water or buried by sediment. Bell and Sipp (1975) reported a similar increase in litter with elevation in an Illinois bottomland. Litter can decrease seedling establishment by preventing seeds from reaching the sediment, by shading or physically obstructing those seedlings that do germinate, or by changing light quality (Facelli and Pickett 1991). Second, the higher surfaces are farther from the water table (J. M. Friedman, *unpublished data*) and, therefore, more subject to water shortage. Third, the development of shade from woody species (Table 1) reduces establishment opportunities for shade-intolerant species. Fourth, higher surfaces are inundated less frequently and, therefore, receive fewer water-borne seeds.

The importance of litter, moisture, and competing vegetation in limiting seedling establishment has been demonstrated experimentally along another bottomland in eastern Colorado (Friedman et al. 1995). On sites similar to Plum Creek surfaces dating to 1973–1986, no cottonwood seedlings were established unless the sod and litter were removed or supplemental water was applied. Applying both treatments greatly increased cottonwood establishment, but addition of seed had little effect. On an Alaska floodplain, removal of litter had a similar effect on establishment of seedlings of the Salicaceae (Walker et al. 1986).

TABLE 2. Life history information and frequency of occurrence (percentage of plots) by year of surface formation for vascular plants at Plum Creek. All species with frequency of occurrence >10% in at least one year group are shown. For each species, the maximum frequency of occurrence is highlighted in boldface type. P, perennial; B, biennial; A, annual; R, rhizomatous; C, caespitose; T, taprooted; N, native; E, exotic.

Species	Family	Longevity	Growth form	Native or exotic	Frequency of occurrence (%)					Total occurrences
					1991	1987-1990	1973-1986	1965	Pre-1965	
<i>Veronica anagallis-aquatica</i>	Scrophulariaceae	P	R	E	52	29	3	0	0	60
<i>Eragrostis pectinacea</i>	Poaceae	A	C	E	23	2	0	0	0	17
<i>Agrostis stolonifera</i>	Poaceae	P	R	E	6	89	86	7	2	168
<i>Juncus articulatus</i>	Juncaceae	P	R	E	4	75	7	0	0	60
<i>Populus</i> sp. seedling	Salicaceae	P	T	N	63	69	3	0	0	94
<i>Juncus bufonius</i>	Juncaceae	A	C	N	8	58	0	0	0	44
<i>Juncus dudleyi</i>	Juncaceae	P	C	N	4	58	34	0	0	82
<i>Trifolium repens</i>	Fabaceae	P	T	E	3	57	9	0	0	50
<i>Bidens frondosa</i>	Asteraceae	A	C	E	1	52	3	0	0	38
<i>Lycopus americanus</i>	Lamiaceae	P	R	N	1	49	29	4	0	69
<i>Salix</i> sp. seedling	Salicaceae	P	CR		34	48	6	0	0	62
<i>Agalinis tenuifolia</i>	Scrophulariaceae	A	C	N	0	48	6	0	0	38
<i>Eleocharis macrostachya</i>	Cyperaceae	P	R	N	6	42	6	0	0	38
<i>Salix lutea</i>	Salicaceae	P	C	N	0	42	33	0	0	67
<i>Polygonum persicaria</i> and <i>P. lapathifolia</i>	Polygonaceae	A	T	E	20	40	1	0	0	41
<i>Populus deltoides</i> ssp. <i>monilifera</i>	Salicaceae	P	T	N	1	40	11	0	2	41
<i>Lactuca serriola</i>	Asteraceae	AB	C	E	0	38	4	0	2	31
<i>Potentilla norvegica</i>	Rosaceae	AB	T	E	3	38	5	0	0	33
<i>Cyperus aristatus</i>	Cyperaceae	A	C	N	30	35	1	0	0	45
<i>Medicago lupulina</i>	Fabaceae	AP	T	E	0	31	24	0	4	51
<i>Melilotus alba</i> and <i>M. of-</i> <i>ficinalis</i>	Fabaceae	AB	C	E	1	31	23	4	4	52
<i>Juncus nodosus</i>	Juncaceae	P	R	N	0	31	3	0	0	23
<i>Phalaris arundinacea</i>	Poaceae	P	R	E	7	31	26	0	0	56
<i>Bidens cernua</i>	Asteraceae	A	C	E	6	29	0	0	0	23
<i>Plantago major</i>	Plantaginaceae	P	C	E	7	28	4	0	0	28
<i>Sphenopholis obtusata</i>	Poaceae	AP	C	N	0	26	6	0	0	24
<i>Epilobium ciliatum</i> ssp. <i>glandulosum</i>	Onagraceae	P	C	N	3	25	3	0	0	21
<i>Alopecurus aequalis</i>	Poaceae	P	R	N	3	25	0	0	0	18
<i>Bromus japonicus</i>	Poaceae	A	C	E	1	25	6	4	4	27
<i>Conyza canadensis</i>	Asteraceae	A	C	E	0	22	6	4	4	24
<i>Salix</i> × <i>rubens</i> and <i>S.</i> <i>alba</i> var. <i>vitellina</i>	Salicaceae	P	C	E	1	20	3	0	0	18
<i>Gnaphalium chilense</i>	Asteraceae	AB	C	E	0	18	2	0	0	14
<i>Hordeum jubatum</i>	Poaceae	P	C	N	0	18	2	0	0	14
<i>Artemisia biennis</i>	Asteraceae	AB	C	E	0	17	0	0	0	11
<i>Rorippa palustris</i> ssp. <i>gla-</i> <i>bra</i>	Brassicaceae	A	T	N	0	17	0	0	0	11
<i>Trifolium hybridum</i>	Fabaceae	P	T	E	0	17	3	0	0	14
<i>Echinochloa crusgalli</i>	Poaceae	A	C	E	3	14	0	0	0	11
<i>Scirpus validus</i>	Cyperaceae	P	R	N	0	12	0	0	0	8
<i>Juncus torreyi</i>	Juncaceae	P	R	N	0	12	0	0	0	8
<i>Oenothera villosa</i> ssp. <i>strigosa</i>	Onagraceae	B	T	N	0	12	8	0	0	17
<i>Leersia oryzoides</i>	Poaceae	P	R	E	4	12	1	0	0	12
<i>Trifolium fragiferum</i>	Fabaceae	P	T	E	0	11	0	0	0	7
<i>Juncus ensifolius</i> var. <i>montanus</i>	Juncaceae	P	R	N	0	11	1	0	0	8
<i>Muhlenbergia asperifolia</i>	Poaceae	P	R	N	0	11	0	0	0	7
<i>Panicum capillare</i>	Poaceae	A	C	E	0	11	0	0	0	7
<i>Poa pratensis</i>	Poaceae	P	R	E	3	32	73	25	32	135
<i>Salix exigua</i>	Salicaceae	P	R	N	6	35	73	4	4	117
<i>Carex emoryi</i> and <i>C. lanu-</i> <i>ginosa</i>	Cyperaceae	P	R	N	7	25	64	11	4	103
<i>Aster hesperius</i>	Asteraceae	P	R	N	1	34	45	4	2	79
<i>Juncus balticus</i> var. <i>mon-</i> <i>tanus</i>	Juncaceae	P	R	N	0	17	42	11	2	65
<i>Equisetum arvense</i>	Equisetaceae	P	R	N	3	17	31	4	5	54
<i>Taraxacum officinale</i>	Asteraceae	P	T	E	0	22	22	0	7	44
<i>Poa compressa</i>	Poaceae	P	R	N	1	18	22	0	2	40
<i>Solidago canadensis</i> var. <i>scabra</i>	Asteraceae	P	R	N	0	18	20	7	0	38

TABLE 2. Continued.

Species	Family	Longevity	Growth form	Native or exotic	Frequency of occurrence (%)					Total occurrences
					1991	1987-1990	1973-1986	1965	Pre-1965	
<i>Equisetum laevigatum</i>	Equisetaceae	P	R	N	0	0	19	7	0	25
<i>Cirsium</i> sp.	Asteraceae	BP			1	5	16	4	4	26
<i>Festuca arundinacea</i>	Poaceae	P	CR	E	0	5	11	0	0	16
<i>Sporobolus cryptandrus</i>	Poaceae	P	C	N	0	0	5	79	21	40
<i>Chrysopsis villosa</i>	Asteraceae	P	T	N	0	0	9	54	7	30
<i>Artemisia campestris</i> ssp. <i>caudata</i>	Asteraceae	B	T	N	0	2	3	43	2	18
<i>Ambrosia psilostachya</i>	Asteraceae	P	R	N	0	14	27	39	7	56
<i>Bromus inermis</i> ssp. <i>inermis</i>	Poaceae	P	R	E	0	2	8	14	9	19
<i>Salsola collina</i>	Chenopodiaceae	A	C	E	0	0	0	14	2	5
<i>Onosmodium molle</i> var. <i>occidentale</i>	Boraginaceae	P	C	N	0	0	0	14	0	4
<i>Gilia pinnatifida</i>	Polemoniaceae	BP	T	N	0	0	1	14	0	5
<i>Talinum parviflorum</i>	Portulacaceae	P	C	N	0	0	0	11	4	5
<i>Festuca octoflora</i>	Poaceae	A	C	N	0	0	0	11	0	3
<i>Penstemon glaber</i> var. <i>alpinus</i>	Scrophulariaceae	P	T	N	0	0	0	11	0	3
<i>Berteroa incana</i>	Brassicaceae	A	C	E	0	6	7	14	63	52
<i>Centaurea diffusa</i>	Asteraceae	AB	T	E	0	3	13	21	42	48
<i>Bromus tectorum</i>	Poaceae	A	C	E	0	3	1	14	42	31
<i>Agropyron intermedium</i>	Poaceae	P	R	E	0	0	0	21	44	31
<i>Agropyron</i> sp.	Poaceae	P	R		0	2	17	4	26	37
<i>Symphoricarpos occidentalis</i>	Caprifoliaceae	P	R	N	0	0	3	4	21	16
<i>Cynoglossum officinale</i>	Boraginaceae	B	T	E	0	0	0	4	18	11
<i>Convolvulus arvensis</i>	Convolvulaceae	P	R	E	0	0	1	0	14	9
<i>Prunus virginiana</i>	Rosaceae	P	R	N	0	0	0	0	14	8
<i>Conium maculatum</i>	Apiaceae	B	T	E	0	0	0	0	11	6

Nonsuccessional processes

The successional interpretation of vegetation pattern assumes that all surfaces began at the elevation of the present channel bed and reached their present elevation as a result of accretion. This assumption is correct for

surfaces dating to 1987-1990 (Table 1). Woody plants excavated from these surfaces were established at the elevation of the present channel bed (Friedman et al., 1996). However, surfaces dating to 1973-1986 are relicts of the channel bed from a time when bed level was

FIG. 5. Canonical Correspondence Analysis ordination of plots along Plum Creek, Colorado. Axis 1 is horizontal and Axis 2 is vertical. Arrows point in the direction of increasing elevation, litter cover, vegetative cover, sediment particle size, and shade. Plots are coded by the year of formation of the underlying surface. (Year of formation was not included as an independent variable in this ordination.) Eigenvalues and canonical coefficients are given in Table 3.

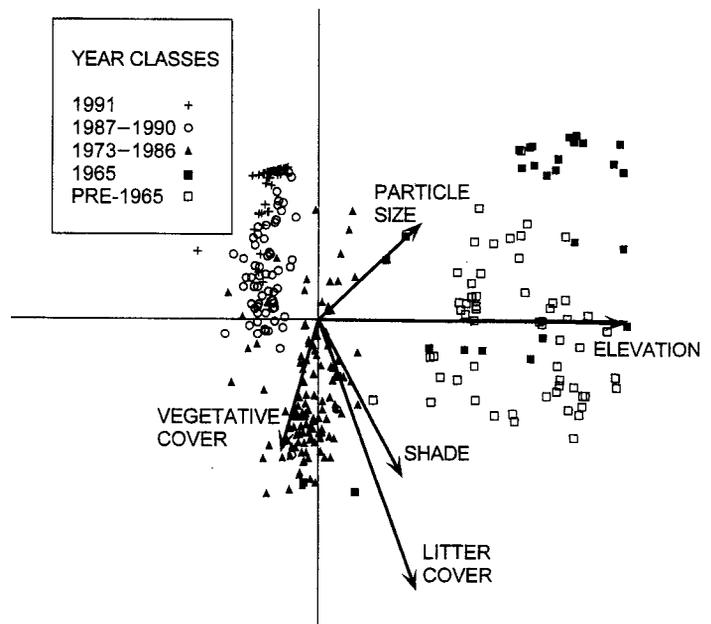


TABLE 3. Eigenvalues, canonical coefficients (approximate *t* ratios in absolute value in parentheses), and interset correlations for two canonical correspondence analyses of Plum Creek species occurrence data. Explanatory variables are environmental data in analysis A (Fig. 5) and temporal data (dummy variables) in analysis B. Sum of all canonical eigenvalues is 1.33 for analysis A and 1.49 for analysis B.

Variable	Axis			
	1	2	3	4
Analysis A				
Eigenvalue	0.65	0.35	0.19	0.09
Canonical coefficient				
Relative elevation	0.98 (46.0)	0.24 (6.7)	-0.32 (7.1)	-0.07 (0.8)
Litter cover	0.04 (2.0)	-0.80 (20.7)	0.52 (10.8)	-0.67 (7.0)
Vegetative cover	-0.07 (3.3)	-0.33 (9.3)	-0.85 (19.1)	0.00 (0.1)
Shade	-0.02 (0.8)	-0.26 (6.8)	-0.04 (0.8)	1.12 (11.9)
Particle size	0.03 (1.4)	0.11 (2.9)	0.21 (4.4)	-0.06 (0.6)
Interset correlation				
Relative elevation	0.94	-0.01	-0.07	0.01
Litter cover	0.30	-0.75	0.26	-0.11
Vegetative cover	-0.11	-0.37	-0.70	-0.08
Shade	0.26	-0.44	0.17	0.45
Particle size	0.32	0.27	0.32	0.04
Analysis B				
Eigenvalue	0.62	0.33	0.32	0.22
Canonical coefficient				
1991	-0.88 (32.0)	0.15 (3.6)	0.64 (12.6)	0.68 (14.2)
1987-1990	-1.43 (38.2)	0.82 (14.6)	0.44 (6.4)	-0.43 (6.6)
1973-1986	-1.12 (29.8)	1.32 (23.2)	-0.07 (1.0)	0.36 (5.5)
1965	-0.01 (0.3)	0.91 (23.5)	0.80 (16.8)	-0.04 (0.9)
Interset correlation				
1991	-0.27	-0.36	0.41	0.58
1987-1990	-0.48	-0.18	0.16	-0.67
1973-1986	0.00	0.51	-0.53	0.40
1965	0.49	0.43	0.56	-0.06
Pre-1965†	0.69	-0.55	-0.17	-0.04

† Variable added passively to analysis.

higher than at present (Fig. 2). Woody plants excavated from these surfaces were established at a mean of 28 cm above the present channel bed (Friedman et al. 1996). Surfaces dating to 1965 have been ≈ 2 m above the channel bed since their formation (Table 1, Fig. 2).

Because moisture availability limits establishment of many bottomland plants, the vegetation occurring on newly exposed sites should depend upon their elevation. Species restricted to sites dating to 1987-1990 might never occur on surfaces that began at a higher elevation; colonization by cottonwoods and willows would be slower, and could be delayed until the occurrence of a year with evenly distributed summer rains. Plum Creek reached its highest postflood bed level in early 1975, following the high discharge caused by snowmelt in 1973. Stereo aerial photographs taken at a scale of 1:6000 in November 1976 show a large area of unvegetated bars ≥ 0.3 m above the bed. Establishment of woody vegetation did not begin on most of these surfaces until 1979 (Fig. 4). On the highest of these surfaces, willow is scarce but cottonwood is common, probably because willow seedlings are more sensitive than cottonwoods to low-moisture stress (Hosner and Minckler 1963, Friedman et al. 1995). The coarse-textured terrace surfaces deposited by the 1965 flood have been high above the channel since their formation.

These surfaces are essentially treeless (Table 4); cottonwood seedlings occur in some years (W. R. Osterkamp, *unpublished observation*), but none have survived. Thus, the vegetation of these surfaces has never passed through stages equivalent to the vegetation of surfaces dating to 1973-1991.

Surfaces dating to 1965 are similar in elevation to surfaces antedating 1965. However, the 1965 surfaces have lower litter and vegetative cover and a much higher proportion of native species (Table 1), for two reasons. The first reason is depositional history. The 1965 substrate, which was formed all at once at high flow, is a deep deposit of relatively coarse sand (Osterkamp and Costa 1987); the episodically deposited surfaces dating to before 1965 include layers of finer particles (Scott 1963). The sparse cover of litter and vegetation on surfaces dating to 1965 is probably a result of low levels of moisture (and possibly nutrients) that began soon after these surfaces were formed. The importance of species with involute leaves (*Sporobolus cryptandrus*), thick, leathery leaves (*Chrysopsis villosa*, *Artemisia campestris* ssp. *caudata*, and *Ambrosia psilostachya*), or a taproot (*Chrysopsis villosa*, *Artemisia campestris*, and *Gilia pinnatifida*) is further evidence of surface-water shortage (Table 2). Thus, the sudden formation and xeric conditions on surfaces dating to

TABLE 4. Basal area (m²/ha) and stem density (stems/ha) of trees taller than 1.24 m, grouped by year of formation of the underlying surface at Plum Creek, Colorado. Species are listed in order of decreasing maximum basal area.

Species	Measure	Year of formation					
		1991	1987-1990	1973-1986	Slope†	1965	Pre-1965
<i>Populus × acuminata</i>	basal area	0.00	0.00	0.04	0.62	0.00	10.08
	stem density	0.00	1.89	51.76	63.93	0.00	44.54
<i>Populus deltoides</i> ssp. <i>monilifera</i>	basal area	0.00	0.04	1.40	7.13	0.08	6.97
	stem density	0.00	129.57	540.71	414.98	8.42	95.49
<i>Salix amygdaloides</i>	basal area	0.00	0.12	0.14	5.36	0.00	0.26
	stem density	0.00	44.67	150.70	597.94	0.00	18.79
<i>Salix × rubens</i>	basal area	0.00	0.19	1.04	0.99	0.00	0.26
	stem density	0.00	413.17	415.88	340.10	0.00	5.57
<i>Populus angustifolia</i>	basal area	0.00	0.00	0.36	0.60	0.00	0.94
	stem density	0.00	52.54	420.08	127.63	0.00	16.70
<i>Prunus virginiana</i>	basal area	0.00	0.00	0.00	0.00	0.00	0.24
	stem density	0.00	0.00	0.00	47.35	0.00	338.51
<i>Quercus gambelii</i>	basal area	0.00	0.00	0.00	0.23	0.00	0.01
	stem density	0.00	0.00	0.00	10.93	0.00	3.48
<i>Alnus incana</i> ssp. <i>rugosa</i>	basal area	0.00	0.00	0.18	0.00	0.00	0.00
	stem density	0.00	0.00	310.27	15.43	0.00	0.00
<i>Crataegus</i> sp.	basal area	0.00	0.00	0.00	0.13	0.00	0.03
	stem density	0.00	0.00	0.95	143.17	0.00	29.46
<i>Elaeagnus angustifolia</i>	basal area	0.00	0.00	0.07	0.00	0.00	0.00
	stem density	0.00	10.57	32.40	4.15	0.00	0.00
<i>Acer negundo</i>	basal area	0.00	0.00	0.00	0.00	0.00	0.06
	stem density	0.00	0.00	0.00	0.00	0.00	4.64
<i>Prunus americana</i>	basal area	0.00	0.00	0.00	0.00	0.00	0.00
	stem density	0.00	0.00	0.00	4.76	0.00	0.00
<i>Tamarix ramosissima</i>	basal area	0.00	0.00	0.00	0.00	0.00	0.00
	stem density	0.00	0.00	0.85	0.00	0.00	0.00
<i>Ulmus pumila</i>	basal area	0.00	0.00	0.00	0.00	0.00	0.00
	stem density	0.00	0.00	0.85	0.00	0.00	0.00
Length‡ (m)		226	176	350	36	198	479

† The steep slope between stable bars and adjacent terraces.
‡ The total distance occupied by a year group, summed over all cross sections.

1965 have favored establishment of a native assemblage, even though adjacent older terraces are dominated by exotics. This assemblage is likely to occur on similar extensive, deep deposits of sand that have been produced by extreme floods elsewhere in eastern Colorado (Follansbee and Spiegel 1937, McKee et al. 1967). The second factor is human disturbance history. Many surfaces of Post-Piney Creek alluvium were planted with *Agropyron intermedium* before the 1965 flood (G. Sutton, *personal communication*), and the flood did not remove this exotic grass. Surfaces formed by the flood of 1965 have not been planted with exotics. Thus, the two types of surface are not different stages in a successional sequence; they differ in vegetation because they were formed in different depositional environments and because they have been differentially affected by human disturbance.

Environmental gradients

The strong influence of elevation on the riparian vegetation at Plum Creek is consistent with results of several other studies of riparian vegetation (Wistendahl 1958, Menges and Waller 1983, Hupp and Osterkamp 1985, Day et al. 1988, Glavac et al. 1992). Factors

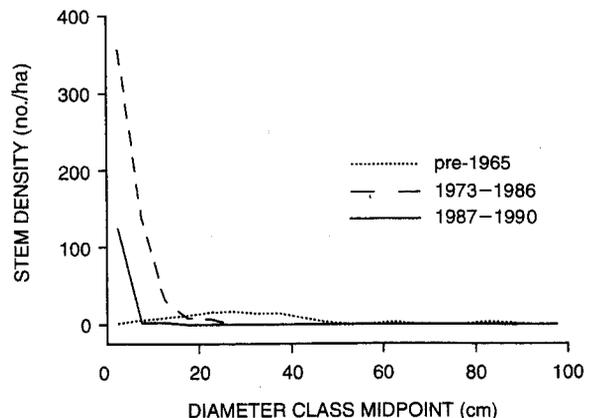


FIG. 6. Stem density of *Populus deltoides* by size class (diameter at 1.24 m) for surfaces at Plum Creek, Colorado, formed before 1965, between 1973 and 1986, and between 1987 and 1990. Surfaces formed in 1965 are excluded because they are essentially treeless (Table 4).

responsible for the strong effect of elevation include moisture availability (Friedman et al. 1995), flood disturbance (Menges and Waller 1983, Hupp and Osterkamp 1985), seed dispersal by water (Schneider and Sharitz 1988), and possibly nutrient availability and duration of anoxia (Wharton et al. 1982). Because age and elevation are strongly correlated, their effects are partially confounded. However, there are distinct age-related differences in vegetation that are independent of elevation, e.g., on surfaces dating to 1987–1990 compared with those dating to 1991, or surfaces dating to 1965 vs. those predating 1965 (Figs. 4 and 5). Furthermore, the sum of all canonical eigenvalues explained by elevation, litter, vegetative cover, shade, and sediment particle size is less than that explained by an ordination that includes only the four dummy variables defining the five geomorphically determined age groups. Finally, a permutation test indicates that the effect of the age groups is significant even after the effects of the five other environmental variables and the eight cross sections are removed. Therefore, the age-related variation cannot be interpreted as a spurious relationship resulting from the correlation between age and elevation.

Silt and clay influence vegetation by complexing with organic matter and by retaining moisture and nutrients. For example, Robertson et al. (1978) and Menges (1983) found that where the sediment is finer, bottomland plant species occur at higher elevations. At Plum Creek, fine particles are most abundant in surfaces of moderate elevation (1973–1990, Table 1), where they occur as layers of variable thickness and depth below the surface. This variability probably influences the vegetation, but is not captured by characterization of surface particle size. For example, the xeric nature of the vegetation on surfaces dating to 1965, relative to those dating to before 1965, results in part from the absence of subsurface layers of silt and clay. Several authors have detected an effect of surface particle size on vegetation patterns in bottomlands; however, surface particle size is not well correlated with elevation, and its effect is weaker than that of the complex of variables associated with elevation (Patten 1968, Robertson et al. 1978, Osterkamp and Hupp 1984, Harris 1987). Therefore, the effect of particle size on vegetation can be important, but the relation between particle size and elevation or year of formation is complex, and a description of particle size at the surface ignores the influence of subsurface layers.

Where stream gradient is low, duration of inundation is long, and fine sediment and organic matter are abundant, anoxia may influence vegetation zonation more than any other environmental factor (Wharton et al. 1982). However, along Plum Creek and many other streams in relatively dry regions, gradients are relatively steep, surfaces above the channel bed are annually inundated for weeks at most, and fine sediment

and organic matter are scarce. As a result, surface water is well oxygenated, water moves quickly through the sediment, and oxygen demand of the substrate is low. Therefore, anoxia is probably infrequent (Auble et al. 1994). Excavations on the Plum Creek bottomland rarely expose anoxic sediment, and plants tolerant of anoxic conditions, such as *Typha*, *Sagittaria*, and *Scirpus*, are uncommon.

Along streams low in nutrients, bottomland nutrient concentrations can increase with elevation above the streambed (Johnson et al. 1976, Walker and Chapin 1986, Day et al. 1988), because older and less frequently inundated surfaces often have more fine sediment and organic matter (Boggs and Weaver 1994), and offer better support for nitrogen-fixing species (Walker and Chapin 1986). However, like most plains streams in eastern Colorado, Plum Creek is rich in nutrients (mean phosphorus concentration ≈ 0.1 mg/L; Advanced Sciences, *unpublished reports*). Therefore, nutrient limitation is unlikely to be an important control of plant distribution on low surfaces irrigated by stream water. Because many terrace surfaces are coarse in texture, well drained, and low in organic matter (Table 1), nutrient availability may actually decrease toward high elevations along Plum Creek and similar streams.

Implications for future work

In order to understand and predict changing patterns of bottomland vegetation, we need to be able to relate vegetation to the fluvial processes that form and maintain the underlying surfaces. Osterkamp and Hupp (1984) and Harris (1987) have demonstrated strong relations between vegetation and distinct fluvial surfaces that are a quasi-equilibrium reflection of inundation frequency and intensity. A similar relation between vegetation and fluvial surfaces was found in the present study. However, these surfaces are not in equilibrium with the flow regime; they are transitional features produced by the ongoing process of channel narrowing following a flood. This study is part of an emerging focus on the importance of non-equilibrium fluvial processes to bottomland vegetation. Other recent studies have investigated the long-term relationship between channel change and vegetation following dam construction and channel straightening (Bravard et al. 1986, Hupp 1992, Johnson 1994).

The process of channel narrowing provides a context for predicting future changes in the vegetation along Plum Creek and other narrowing sandbed streams. In the absence of future floods, the channel should narrow until the flow is competent to keep the bed clear of new vegetation. As stable bars accrete, their vegetation should become more similar to that on terraces, and the area of the assemblage now represented by surfaces dating to 1987–1990 should decrease. Because the disturbed moist sites necessary for cottonwood seedling establishment are absent, the mean age of stands on the bottomland will increase and their mean density

TABLE 5. Major floods originating on the Palmer Divide in eastern Colorado. The locations of these floods are indicated by label number on Fig. 1. Data are from Matthai (1969) and Snipes et al. (1974).

Label	Location	Date	Watershed (km ²)	Discharge (m ³ /s)	Unit discharge (m ³ ·s ⁻¹ ·km ⁻²)
1	Jimmy Camp Creek near Fountain	17 Jun 1965	141	3511	25.0
2	Big Sandy Creek near Calhan	17 Jun 1965	127	1719	13.5
3	Big Sandy Creek near Calhan	5 Aug 1954	127	1263	10.0
4	East Bijou Creek near Deer Trail	17 Jun 1965	782	7759	9.9
5	Middle Bijou Creek near Deer Trail	17 Jun 1965	492	4106	8.3
6	Middle Bijou Creek near Deer Trail	30 May 1935	492	4067	8.3
7	Kiowa Creek north of Kiowa	30 May 1935	492	3115	6.3
8	Plum Creek near Louviers	16 Jun 1965	782	4361	5.6
9	Black Squirrel Creek near Ellicott	17 Jun 1965	914	3993	4.4

will decline. Vegetation on terraces dating to 1965 should remain distinct from that on older terraces because of their distinct sediment profiles. As channel narrowing slows, other processes, including meandering, will become relatively more important (Schumm and Lichty 1963).

At the landscape scale, the occurrence of channel narrowing is proportional to its duration, which varies greatly across watersheds. The lower the flow between floods, the longer time necessary for the fluvial work that brings about channel recovery (Wolman and Gerson 1978). Because flow variability is greatest in arid regions and small watersheds, flood effects last longest in these situations. In humid regions, recovery typically occurs over months or years (Costa 1974). In semiarid and arid regions, recovery time can be decades to centuries, and may exceed the time between floods (Baker 1977, Wolman and Gerson 1978). Both the immediate effects of extreme floods and the subsequent recovery time can be increased by a shortage of the fine sediments (silt and clay) necessary for bank cohesion. Therefore, floods can be expected to have especially important long-term effects on bottomland morphology along small sandbed channels in the western Great Plains and in dry regions worldwide.

Many other streams draining the Palmer Divide have had cloudburst floods similar in discharge and unit discharge to the Plum Creek flood once or twice during this century (Table 5, Fig. 1). Similar floods have occurred in streams draining the Raton Divide along the Colorado–New Mexico border (Snipes et al. 1974) and elsewhere in the western Great Plains (Follansbee and Spiegel 1937). The spatial and temporal pattern of channel widening and narrowing at Plum Creek also has been observed following floods along other eastern Colorado streams, including Bijou and Kiowa Creeks (J. M. Friedman, *unpublished data*), and along many other streams in the western Great Plains (Schumm and Lichty 1963, Northrop 1965) and southwestern United States (Burkham 1972, Hereford 1984). Therefore, the non-equilibrium patterns of vegetation observed at Plum Creek should be shared by many other flood-prone sandbed channels in the region. When dams re-

duce peak flows and bed sediment load along formerly braided channels, the result is typically channel narrowing by establishment of vegetation on the bed (Williams and Wolman 1984, Johnson 1994). As with post-flood narrowing, the channel change is a response, mediated by vegetation, to disequilibrium between channel width and stream power. The vegetation patterns observed in the present study should be similar to those present during dam-induced narrowing.

Establishment of cottonwood 1–3 yr following a flood has been reported elsewhere (Bradley and Smith 1986, Baker 1990, Stromberg et al. 1991, Scott et al. 1996). However, the present study shows that a flood can promote forest regeneration for decades by initiating a long-term process of channel change. Since 1965, seedling establishment has been restricted to portions of the channel bed abandoned during years of low peak flow, as part of the ongoing process of postflood channel narrowing. Thus, cottonwood establishment is related to low flow at the time scale of years, but to high flow at the time scale of decades. Such complexity in the relationship between tree establishment and flow regime has hampered management attempts to use streamflow to promote or retard tree establishment (Johnson 1994, Scott et al. 1996). Therefore, successful management of riparian forest must be based on understanding of the important local, long-term geomorphic processes.

This study demonstrates the importance of flow variability and fluctuations in channel width for maintaining landscape biodiversity. Many bottomland plants in the western Great Plains, including seedlings of cottonwood, are restricted to transient surfaces formed during channel narrowing (Table 2). Because synchronous floods have occurred in several streams in the region, most notably in 1935 and 1965 (Table 5, Matthai 1969), regional surveys of biodiversity or status of cottonwood forest must take flood history into account. Stream alterations, such as channel stabilization, that decrease fluctuations in width could lead to a failure in cottonwood recruitment and a decline in species richness (Bravard et al. 1986, Friedman et al. 1995). Finally, changes in the frequency of extreme floods, as

have occurred during the Holocene (Ely 1993), would bring about regional changes in bottomland morphology and biodiversity.

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