

# Relationship between Plant Distribution Patterns and the Process of River Island Formation

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## ABSTRACT

We examined the distribution of trees and shrubs on 14 mid-channel islands in the Swan River, northwest Montana. We observed the general trend that plants were distributed in a linear sequence of seral stages. Pioneer successional phase plants dominated the downstream ends of islands, mid-successional vegetation dominated the middle of the islands, and late successional vegetation and the oldest trees were largely restricted to the upstream portions of the largest islands. The observed pattern was most distinct on islands farthest upstream in the river channel (i.e., smallest catchment area) and least distinct on islands farthest downstream in the catchment basin. We conclude the consistent pattern of seral organization and the influence of catchment size would be unlikely if the development of mid-channel river islands were controlled by site-specific factors influencing individual islands independently. We suggest that all islands are responding similarly to the shared influence of fluvial dynamics (i.e., timing, duration, and magnitude of rise and fall of river discharge), but smaller scale variability in plant distribution among individual islands suggests site-specific variables and/or random events modify the action of fluvial dynamics.

## INTRODUCTION

Plant assemblage organization within river-floodplain ecosystems appears to be a response to feedback loops among the timing, rate, and magnitude of the rise and fall of river discharge (e.g., fluvial dynamics), sediment particle size and nutrient concentration, and plant establishment and growth (Hupp and Osterkamp 1996, Schnitzler 1997). High levels of river-land connectivity tend to maintain a juvenile condition including unstabilized sediments, large median grain size, low nutrient and organic matter concentrations, shallow depth to ground water, and high solar irradiance levels, where only stress-tolerant plant species can flourish (Hupp and Osterkamp 1985, Bravard et al. 1986, Malanson and Butler 1990). Weakening of river-land interactions allows for site maturation, involving a typical progression of decreased soil pH and median grain size, increased soil moisture content, organic to mineral content, nutrient concentrations and depth to ground water, and a shift in plant assemblage composition and/or biomass (Amoros et al. 1986, Amoros et al. 1987). In turn, enhanced plant growth furthers site maturation by buffering the land surface from fine sediment and nutrient loss during flood inundation and by stabilizing the sediments, contributing organic matter, altering the local micro-climate, and trapping new sediments (Malanson and Butler 1990, Shankman 1991).

It has been suggested that plants serve as "functional describers" (Amoros et al. 1986) of present and historic conditions of alluvial land forms because they are "ecological integrators" of the complex mixture of site-specific edaphic, hydrologic, and climatic conditions that are present. This function has been well documented from studies of primary succession on abandoned river channels (Shankman 1991, Bornette et al. 1994), meander loop scroll bar chronosequences (Nanson and Beach 1977, Kalliola and Puhakka 1988), glacial forelands (Chapin et al. 1994), and progressions of alluvial

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surfaces organized along a gradient of high to low connectivity (i.e., gravel bar, floodplain, terrace; Hupp and Osterkamp 1985). However, limited information exists concerning plant organization on land surfaces wholly contained within active river channels or the processes responsible for observed patterns (Kollmann et al. 1999).

Abbe and Montgomery (1996) suggested that the colonization and subsequent stabilization of gravel bars by plants is one mechanism for initiation of river island formation. Both Green (1982) and Barnes (1985) found positive correlation between river island land surface elevation and plant species diversity. Barnes noted that land surface age, elevation, and the distribution and age structure for tree species were all strongly positively correlated with each other. In addition to also finding a positive correlation between elevation and plant diversity on gravel bars and islands, Malanson and Butler (1991) found sediment depth and soil organic content co-varied with surface elevation and distance from the upstream end of the deposit. To the contrary, Puhkka et al. (1992) did not find clearly delineated vegetation zonation on islands or floodplain deposits from braided or anastomosed river reaches of the Amazon River despite documenting such patterns on scroll bar deposits of meandering reaches.

In this study, we predicted that the maturation of river islands is largely controlled by fluvial dynamics and that patterns in plant distribution would correspond with the pattern of island development (Fig. 1). If the "common-to-all" force of fluvial dynamics, a force originating at the scale of the drainage basin, were the primary force controlling river island development, we would expect to find a high degree of consistency in plant distribution patterns between all islands of a river and a relatively linear organization of plants by seral stage. We tested this prediction by evaluating age and distribution patterns of trees and shrubs on alluvial islands of the Swan River, northwest Montana, USA, at three spatial scales (individual islands, river reaches, and drainage basin).

#### MATERIALS AND METHODS

The Swan River basin is located within the headwaters of the Columbia River system and drains an area of 2,070 km<sup>2</sup>. Elevation of the valley floor ranges from 1830 m near the beginning of the main channel to 1000 m where the river enters Swan Lake. The river is 64 km long, and the upper 50 km are unregulated and free of significant civil engineering works. Dominant land cover is temperate mixed coniferous forest with patches of deciduous forest (Frissell et al. 1995). The gradient of the valley floor averages 0.013 m/m (Kendy and Tresch 1996). The channel of the upper river is not deeply incised into the underlying alluvium and alternates between a single sinuous channel and an anabranching plan form (Kendy and Tresch 1996). The hydrograph of the river is dominated by a predictable peak in discharge corresponding to snow melt run-off, typically in May or June. This study was conducted in anabranching portions of the river, and we assumed floodplain and channel gradients, climatic conditions, underlying geology, and the floodplain vegetation were similar along the length of the Swan River within the study area.

The islands we studied occurred in three reaches, designated as lower, middle, and upper reaches, which drained catchment basins of 842 km<sup>2</sup>, 622 km<sup>2</sup>, and 414 km<sup>2</sup>, respectively. Fourteen islands were surveyed (Table 1), and all were islands formed via deposition of sediments within the active channel of the river.

To describe colonization patterns, islands were divided longitudinally into 10 m intervals and the downstream end of each island was designated as the first interval. Abundance and distribution data for each plant species were summarized in each interval. Tree and shrub distribution patterns were determined for species that represented >5% of the plant community when plant abundance data from all islands was combined. Each species was assigned to a seral stage according to physiological and ecological characteristics determined from a literature review of tolerance to flooding, seed size and dispersal mechanism, ability for clonal reproduction, life history traits, shade tolerance,

and nutrient requirements. Identification and nomenclature followed Lackschewitz (1991), except for the genus *Salix*, which followed Heinze (1994).

*Tree Community Distribution Pattern*

Tree distribution patterns were determined using the centered point-quarter method (Cottom and Curtis 1956) along two-three transects parallel to the long axis of the island. Twenty sample points, equally spaced, were measured on each transect line. Distance from a sample point to the selected tree was measured and the diameter at breast height (DBH). No tree was counted more than once. When no tree was present within a sample quadrant, the quadrant was recorded as vacant. If the nearest tree within a quadrant to a sample point had been previously included in the point-quarter survey, the quadrant was skipped (e.g., no value assigned). If one tree fell within two or more quadrants, it was recorded in the quadrant where the largest portion of the tree resided, and the next nearest tree was sampled in the "vacated" quadrant. Trees were assigned to one of three lifestages based on DBH; adult (DBH > 1.67 cm), sapling (DBH 0.008 – 1.67 cm), or seedling (DBH < 0.008 cm). The division between adult and sapling was based on whether a tree was large enough to allow for age determination by coring without killing

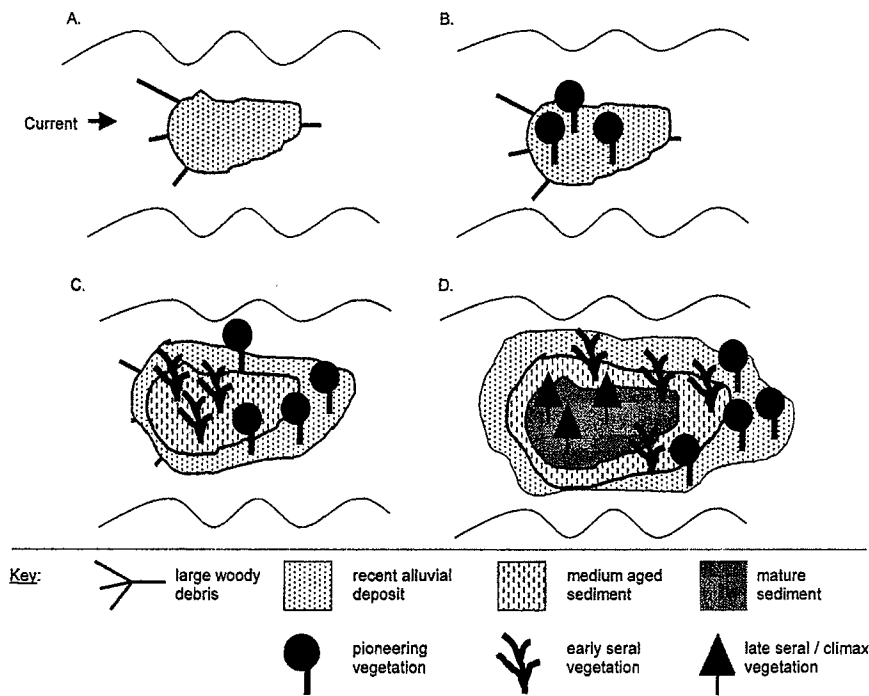


Figure 1. Hypothesized process of river island formation. A) A gravel bar forms during a high water event. Deposition of sediments frequently occurs in proximity to an accumulation of large woody debris. B) Pioneering plant species establish on the gravel bar. Developing vegetation stabilizes the deposit, limits erosion, contributes organic matter, and traps small sediment particles entrained in the current during subsequent high water events. C) Seral succession occurs on the initial gravel bar deposit. Pioneering vegetation dominates on more recently deposited sediments. D) Structure of a mature river island. Older sediments lie upstream of younger sediments and plants are distributed in a linear gradient of seral stages reflecting the gradient of sediment ages.

Table 1. Characteristics of the fourteen islands from the Swan River, Montana, USA, included in the study.

Reach and island code	Surface area (m <sup>2</sup> )	Length (m)	Width (m)	Length:Width ratio	# of Transects
Lower 1	2680	159.2	30.6	5.2	2
Lower 2	1728	69.3	34.7	2.0	3
Lower 3	603	89.0	10.7	8.3	2
Lower 4	353	44.4	11.1	4.0	2
Middle 1	966	73.8	13.7	5.4	2
Middle 2	904	49.0	30.6	1.6	2
Middle 3	2934	106.1	42.4	2.5	2
Middle 4	1950	71.5	35.8	2.0	2
Middle 5	51	19.7	3.9	5.0	2
Middle 6	232	30.2	13.7	2.2	2
Upper 1	988	63.0	24.2	2.6	2
Upper 2	404	49.2	15.4	3.2	2
Upper 3	620	70.8	12.2	5.8	2
Upper 4	7959	177.6	84.6	2.1	3

the tree. Any tree that did not reach breast height was considered a seedling. Ages of adult trees were determined by microscope counts of annual growth rings from cores collected at breast height and ages were corrected to include the number of years to reach breast height (Table 2). Procedures for collection, transport, storage, and assessment of cores followed Cole (1977) and Campell (1981).

The location of trees along the long axis of an island was determined from point-quarter data according to the following rules: For trees in sample quadrants 1 or 2 (quadrants upstream of the sample point): location (m) = distance from downstream end of island to the sample point + [(sample point to tree distance)(cosine 45°)]. For trees in sample quadrants 3 or 4 (quadrants downstream of the sample point) location (m) = distance from the downstream end of island to the sample point - [(sample point to tree distance)(cosine 45°)].

To facilitate comparisons across islands, we calculated relative abundance (RA) for tree species within each interval on each island (density, cover, and importance value are reported in Cooperman 1997). RA for each species within an interval was calculated as

$$\text{Relative Abundance} = \left[ \frac{\text{\# individuals of species A in 10 m interval Y}}{\text{total \# individuals in 10 m interval Y}} \right] \times 100$$

Standard errors were calculated based on comparisons of each species abundance within a specified distance interval from all study islands. Data summaries presented in figures 3 – 6 were smoothed using a three point moving average.

#### *Shrub Community Distribution Pattern*

Shrub communities were surveyed using the line intercept technique (McDonald 1980) along the same transect lines used for tree sampling. Shrub presence was recorded if any portion of a given shrub intersected the plane of the transect line. Data collected included species name, start and end distance along the transect line each intersected shrub occupied, and width of the shrub at its widest point. When a shrub was part of a larger clump of con-specifics and the dimensions of the individual could not be delineated (e.g., willows), the size of the entire clump was measured to reduce the chance that clones were recorded as more than one individual.

Shrubs were assigned to a 10 m interval based on the location of the midpoint of the shrub along the transect line (as previously described for trees). Abundance of shrubs

in a given interval was calculated as

$$\text{Abundance} = \left[ \frac{\text{Length of transect line occupied by species A in distance increment Y}}{\text{Total transect length available in distance increment Y}} \right] \times 100$$

This formula determines the abundance of a shrub species within a given distance increment as a function of the amount of available transect length it occupies. It is not a measure of relative abundance, but for continuity in results reporting and interpretation, this value is referred to as "relative abundance." For example, at the basin scale of analysis ( $n = 14$  islands, all greater than 10 m long), there was a total of 300 m of transect line available in the 0 – 10 m distance increment, because 12 islands had two transect lines each (24 transect intervals each 10 m long; totaling 240 m transect length) and 2 islands had 3 transect lines each (six transect intervals 10 m long; totaling 60 m transect length). If species A covered 100 m of transect line in this interval, its abundance was 30%. The procedure for calculating standard error was the same as described for trees.

### RESULTS

We sampled 1,676 quadrants and 77% ( $n = 1,284$ ) were occupied by either *Populus trichocarpa*, *Alnus tenuifolia* var. *incana*, or *Picea engelmannii*. Sixteen quadrants were occupied by "rare" tree species, and 374 quadrants were empty (Table 2). Only the three most common tree species were abundant enough for inclusion in the analysis of tree distribution patterns. Two islands in the middle reach had no trees.

Shrubs were found on all islands (Table 3), and four species were common - *Salix exigua*, *S. candida*, *S. drummondiana*, and *Cornus stolonifera*. Only 23 individuals of four other species of *Salix* or *Salix* hybrids were encountered, and these were not included in the analysis. No other species of shrub were common; however, the uncommon shrub species we identified shared many ecological and physiological attributes, so data on these species were lumped into a composite category called "rare shrubs."

Sixty-seven tree cores were collected. The average age of adult trees on these

Table 2. Trees found on the fourteen study islands, Swan River, Montana, USA.

Family Species	Common name	Number of occurrences	Years to reach breast height <sup>a</sup>
Betulaceae			
<i>Alnus tenuifolia</i> var. <i>incana</i> Nutt.	Thinleaf alder	417	4
<i>Betula papyrifera</i> Marsh.	Paper birch	1	NA
Pinaceae			
<i>Abies grandis</i> (Dougl.) Lindl.	Grand fir	1	15
<i>Abies lasiocarpa</i> (Hook.) Nutt.	Sub-alpine fir	1	15
<i>Larix occidentalis</i> Nutt.	Western larch	1	5
<i>Picea engelmannii</i> Parry ex Englem	Engelman spruce	149	10
<i>Pinus contorta</i> var. <i>latifolia</i> Emgelm.	Lodgepole pine	8	14
<i>Pinus monticola</i> Dougl.	Western white pine	2	12
<i>Pseudotsuga menziesii</i> var. <i>glauca</i> (Beissn.) Franco.	Douglas-fir	1	9
Salicaceae			
<i>Populus trichocarpa</i> Torr. & Gray	Black cottonwood	716	3

<sup>a</sup> Determined by literature review. Elapsed time from germination to reaching breast height assumes no growth suppression of juveniles. NA = not available.

islands was 16.2 yr (95% CI = 15.0 – 17.3 yrs), indicating most adult trees were established during or shortly after 1977. Three individuals of *Picea engelmannii* were significantly older than the mean (44, 95, 115 yrs). There were no consistencies in the location of these three trees, and they were considered statistical outliers and removed from further analysis (Hamilton 1990). Regression analysis of adult tree age by location provided evidence that tree age was correlated with distance from the downstream end of islands, although the relationship was weak ( $n = 64$ ,  $r^2 = 0.113$ ,  $p = 0.007$ ). Average adult tree age at the downstream ends of islands (0 – 10 m interval) was 14.0 yrs and at the upstream end of the islands (160-170 m interval) was 17.5 yrs.

Table 3. Shrubs found on the study islands, Swan River, Montana, USA.

Family <i>Species</i>	Common name	Number of occurrences
Caprifoliaceae		
<i>Lonicera ciliosa</i> (Pursh)DC.	Orange honeysuckle	2
<i>Lonicera utahensis</i> Wats.	Utah honeysuckle	8
Celastraceae		
<i>Pachistima myrsinites</i> (Pursh) Raf.	Oregon boxwood	1
Cornaceae		
<i>Cornus stolonifera</i> Michx.	Red-Osier dogwood	103
Cupressaceae		
<i>Juniperus communis</i> L.	Common juniper	7
Elaeagnaceae		
<i>Shepherdia canadensis</i> (L.) Nutt.	Buffalo-berry	1
Ericaceae		
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	Kinnikinnick	1
Grossulariaceae		
<i>Ribes setosum</i> Lindl.	Missouri gooseberry	2
<i>Ribes lacustre</i> (Pers.)Poir.	Prickly currant	1
<i>Ribes</i> spp.	Gooseberry	1
Rhamnaceae		
<i>Rhamnus alnifolia</i> L'Her.	Alder buckthorn	2
Rosaceae		
<i>Crataegus douglasii</i> Lindl.	Hawthorn	1
<i>Rosa acicularis</i> Lindl.	Prickly rose	1
<i>Rosa nutkana</i> var. <i>hispidata</i> Ferm.	Nootka rose	3
<i>Rosa</i> spp.	Rose	2
<i>Rosa woodsii</i> Lindl.	Wood's rose	10
<i>Rubus idaeus</i> L.	Red raspberry	52
Salicaceae		
<i>Salix candida</i> Fluegge	Hoary willow	141
<i>Salix drummondianna</i> Barratt	Drummond willow	118
<i>Salix exigua melanopsis</i> (Nutt.)Cronq.	Gravel bar willow	232
<i>Salix exigua</i> subsp. <i>exigua</i> var. <i>exigua</i> Nutt.	Gravel bar willow	26
<i>Salix geyeriana</i> Anderss.	Geyer willow	5
<i>Salix lasiandra</i> Benth.	Whiplash willow	2
<i>Salix lutea</i> Nutt.	Yellow willow	3
<i>Salix planifolia</i> Pursh	Planeleaf willow	1
<i>Salix</i> hybrid <sup>a</sup>	Willow hybrids	12

<sup>a</sup> *Salix* hybrids were those specimens showing distinct characteristics of two or more *Salix* species.

### Plant Distribution Patterns - Individual Island Scale

The abundance of each tree and shrub species at specified distances from the downstream end of each island was highly variable (Fig. 2). For both *Populus trichocarpa* and *Alnus tenuifolia*, standard error values frequently reached or exceeded 80%. For other species, the range of standard error values was smaller but still frequently approached or exceeded 40%. Less abundant species typically had smaller standard error ranges about their mean abundance value.

### Plant Distribution Patterns - River Reach Scale

In all three reaches, the highest abundance of *Populus trichocarpa* occurred at both ends of the islands, and the abundance of *Alnus tenuifolia* peaked 75 - 95 m from the downstream end of islands (Figure 3). Abundance of *Picea engelmannii* in the lower and upper reaches was low at the downstream ends of islands, increased from 75 m to 125 m, and reached the highest values between 115 m and the upstream end of the islands. *P. engelmannii* was largely absent from islands in the middle reach. Shrub distribution patterns between the reaches were less consistent.

The tree community on islands in upper reach was dominated by *Alnus tenuifolia* and *Picea engelmannii*. This was the only reach where the relative abundance of *Populus trichocarpa* did not exceed 50%. Abundance of *P. trichocarpa* was highest at the downstream end of the islands; abundance of *A. tenuifolia* peaked in the middle of the islands; and *P. engelmannii* had peak abundance at the upstream end of the islands. In shrub communities of upper reach islands, *Salix exigua* was the most abundant species from the downstream end of these islands to 95 m (Fig. 4). Abundance of this species was notably lower on the upstream halves of islands, despite an increased abundance at the heads of islands. *S. candida* was the most abundant shrub from 95 m to 135 m from the downstream end of these islands. From 135 m to the upstream heads of islands, *S. exigua* was the most abundant. Rare shrubs were largely absent near the downstream end of the islands, but they were found occasionally near the upstream end.

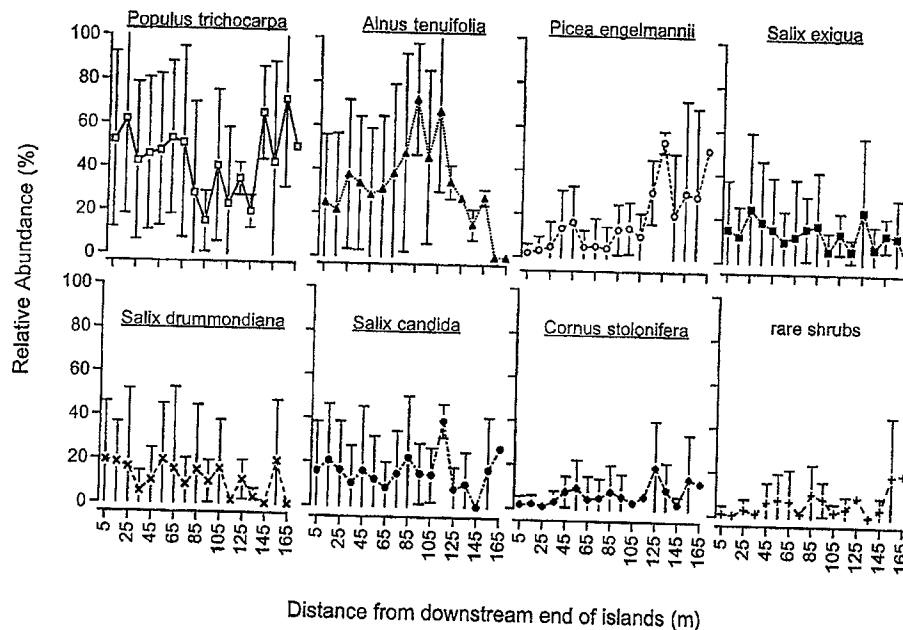


Figure 2. Distribution of trees and shrubs on study islands. Data are means  $\pm$  1 standard error.

In the middle reach, no islands were longer than 95 m. *Populus trichocarpa* was the most abundant tree on the downstream half of each island in this reach, and *Alnus tenuifolia* was the most abundant tree on the upstream halves. *Picea engelmannii* was scarce in this reach. *Salix drummondiana* was the most abundant shrub on the downstream halves of these islands. Rare shrub abundance increased with increasing distance upstream from the island tails.

The tree community of islands in the lower reach was uniformly dominated by *Populus trichocarpa*. *Alnus tenuifolia* and *Picea engelmannii* were rare in this reach. The organization of peak abundance of trees in this reach was similar to those of the middle and upper reaches, but the distribution pattern of shrubs in this reach was somewhat less distinct than in the other two reaches. There was no clear zonation between the three most abundant *Salix* species. *Cornus stolonifera* was the only common non-*Salix* shrub and its abundance increased with increasing distance upstream. There was no decrease in any other species as *C. stolonifera* increased.

*Plant Distribution Pattern - Drainage Basin Scale*

The tree community on the downstream portion of islands was dominated by *Populus trichocarpa*, the middle portions were dominated by *Alnus tenuifolia*, and regions greater than 115 m from the tail of islands were co-dominated by *Picea engelmannii* and *P. trichocarpa* (Figure 5). *P. engelmannii* was almost never found at the

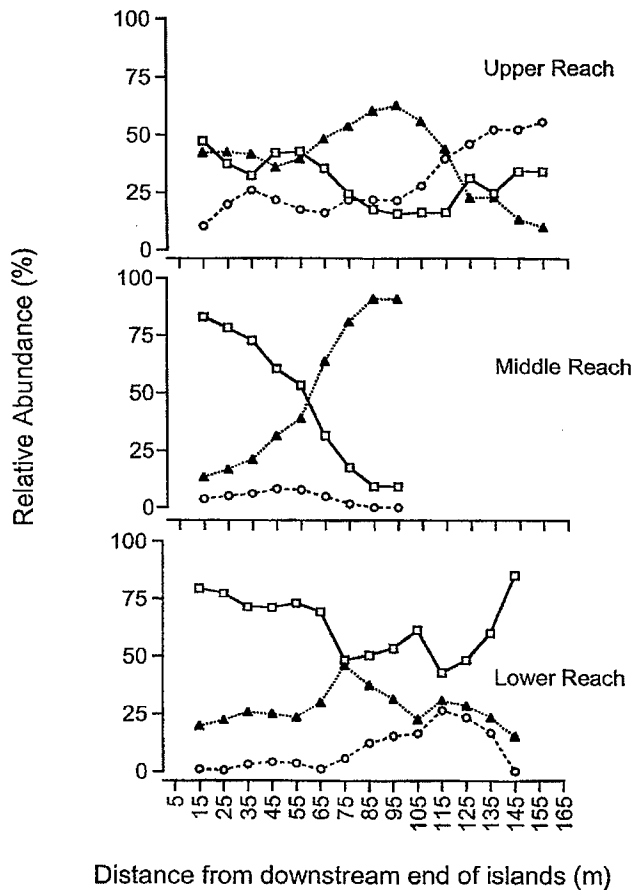


Figure 3. Distribution of trees in three reaches with different catchment areas. □ are *Populus trichocarpa*, ▲ are *Alnus tenuifolia*, ○ are *Picea engelmannii*.



downstream ends of islands. *Salix exigua* was the most abundant shrub from the downstream ends to 75 m upstream. Between 75 m and 125 m, *S. candida* replaced *S. exigua* as the most abundant shrub. *S. exigua*, *S. candida*, and rare shrubs were almost equally abundant near the upstream ends of longer islands. The pattern of *S. drummondiana* was similar to that of *S. exigua*, although peak abundance of *S. drummondiana* occurred slightly more upstream. *Cornus stolonifera* was largely absent from the downstream ends of islands, but increased to about 10% abundance from 55 m to the upstream ends of islands. Rare shrubs were most common at the upstream ends of longer islands.

#### Life Stage Analysis

Lifestages of *Picea engelmannii* and *Alnus tenuifolia* were organized in a linear fashion along the islands. *P. engelmannii* seedling abundance was highest at 105 m, saplings peaked at 135 m and adults at 155 m from the downstream ends of islands (Fig. 6). *A. tenuifolia* seedling abundance was greatest at 65 m, while sapling and adult

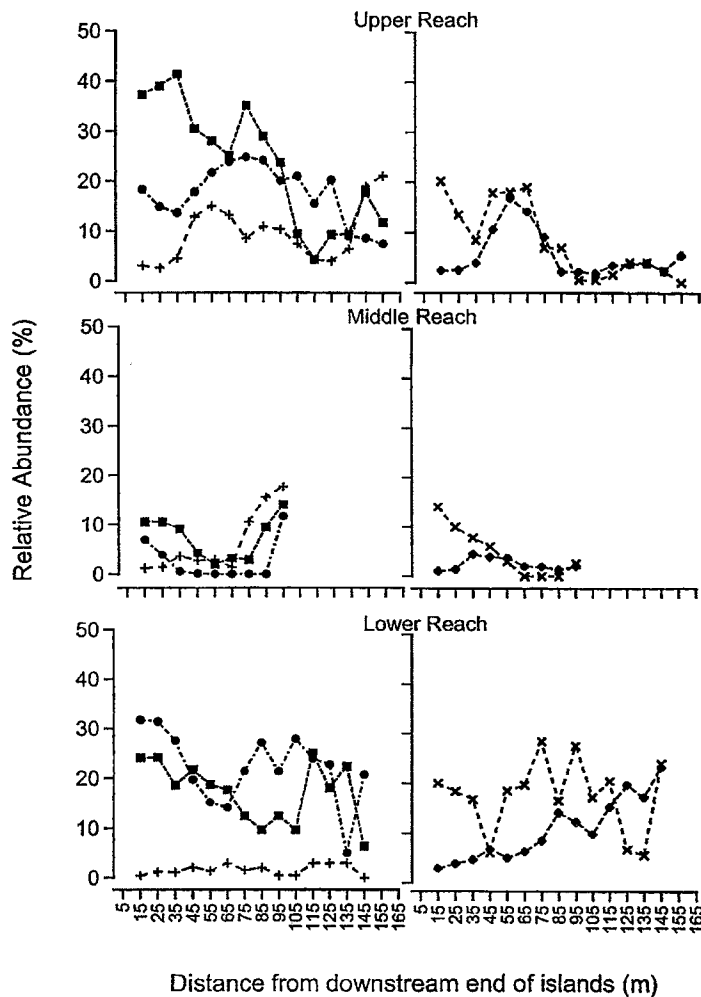


Figure 4. Distribution of shrubs in three reaches with different catchment areas. ■ are *Salix exigua*, X are *S. drummondiana*, ● are *S. candida*, ▼ are *Cornus stolonifera*, + are rare shrubs.

abundance peaked at 85 m from the downstream ends of islands. The pattern for *Populus trichocarpa* is more difficult to interpret, owing to the bi-modal occurrence of seedlings and the scarcity of adults.

A strong pattern of lifestage organization among the tree species was also evident. *P. trichocarpa* seedlings occurred predominantly between the downstream end of islands to 65 m and in a small zone at the heads of islands. *A. tenuifolia* seedlings were scarce throughout the study area but were concentrated between 45 m – 85 m. *Picea engelmannii* seedlings occurred predominantly from 75 m to 135 m. The distribution of saplings was similar, with peak abundance of *P. trichocarpa* between 5 m and 45 m, peak *A. tenuifolia* abundance between 75 m and 95 m, and the highest abundance of *P. engelmannii* between 125 m and 165 m. Adult trees also displayed this pattern, although the scarcity of adult *P. trichocarpa* makes interpreting distribution data for this species difficult.

#### DISCUSSION

Our data suggest that the colonization of gravel bars by plants and the subsequent changes in vegetation patterns as gravel bars mature into islands are controlled by a combination of basin-scale and site-specific forces in the fluvial corridor. At the basin scale, distinct patterns of tree and shrub organization (e.g., early colonizers at the downstream ends of islands, mid-seral species at intermediate distances from the downstream end of islands, later seral species at larger distances from downstream end of islands) suggest fluvial processes exert significant control over the development of river islands.

The relatively low number of tree and shrub species found on islands in the Swan River made analysis of seral organization patterns a practical method of investigation, particularly because many of the observed plant species possess a unique array of life history traits that make assignment to a distinct seral role relatively straight-forward. *Populus trichocarpa* and *Salix exigua* produce many small seeds with morphological adaptations to enhance dispersal, and the species tolerate low nutrient levels and frequent disturbance and have the ability to reproduce from adventitious roots or by resprouting from a damaged stump, all characteristics of pioneering species (Fenner 1987, Chapin et al. 1994). *P. trichocarpa* and *S. exigua* were consistently the first plants to colonize scarcely vegetated, newly exposed gravel bars in the Swan River (Cooperman, unpublished data), reinforcing their status as pioneering species in this system. These species were consistently the most abundant plants on the downstream ends of the study islands.

*Salix drummondiana* and *S. candida* also possess many characteristics typical of pioneering species, yet they were largely absent from the recently exposed gravel bars where *P. trichocarpa* and *S. exigua* were common (Cooperman, unpublished data). Peak abundance of *S. candida* was upstream of pioneering species but downstream of late seral species, and this pattern was most similar to that of *Alnus tenuifolia*, of which highest abundances consistently occurred some distance upstream from pioneering species but downstream from late seral species. The majority of research on *A. tenuifolia* suggests this tree is a seral species that enters the successional progression relatively early (e.g., Furlow 1979, Chapin et al. 1994), and our data suggest *S. candida* is fulfilling a comparable successional role. Since *S. candida* commonly occurs on soils with higher organic content (Heinze 1994) than the other willow species commonly found on islands of the Swan River, the observed distribution of this species is consistent with the prediction that areas upstream from the tails of islands would have sediments with higher organic content than areas closer to the tails.

*Picea engelmannii* is typically considered a climax species in the Rocky Mountains, although it may exist as a persistent late seral species under some conditions

(Burns and Honkala 1990). When present on islands, *P. engelmannii* typically was restricted to areas farthest away from the downstream end of islands. *Cornus stolonifera* and the various rare shrubs found on islands of the Swan River typically are shade tolerant and produce fruit, traits common of mid- to late seral species (Fenner 1987, Rydin and Borgegard 1991). In general, these shrubs were largely restricted to the upstream portions of the larger islands, supporting the premise these regions had more mature site conditions.

The resurgence of pioneering species (i.e., *Populus trichocarpa*, *Salix exigua*) at the upstream ends of the islands was unexpected. It is likely that a zone of "fluvial reset" (Amoros et al. 1987) occurred at these locations, caused by the continuous scouring of the heads of islands as they intercepted the flow of the river, resulting in edaphic and hydraulic conditions being maintained in "immature" conditions.

Additional support for the premise that plant distribution pattern would correspond with patterns of island development is that within each species, peak abundances of seedlings occurred closer to the downstream end of the islands than did the

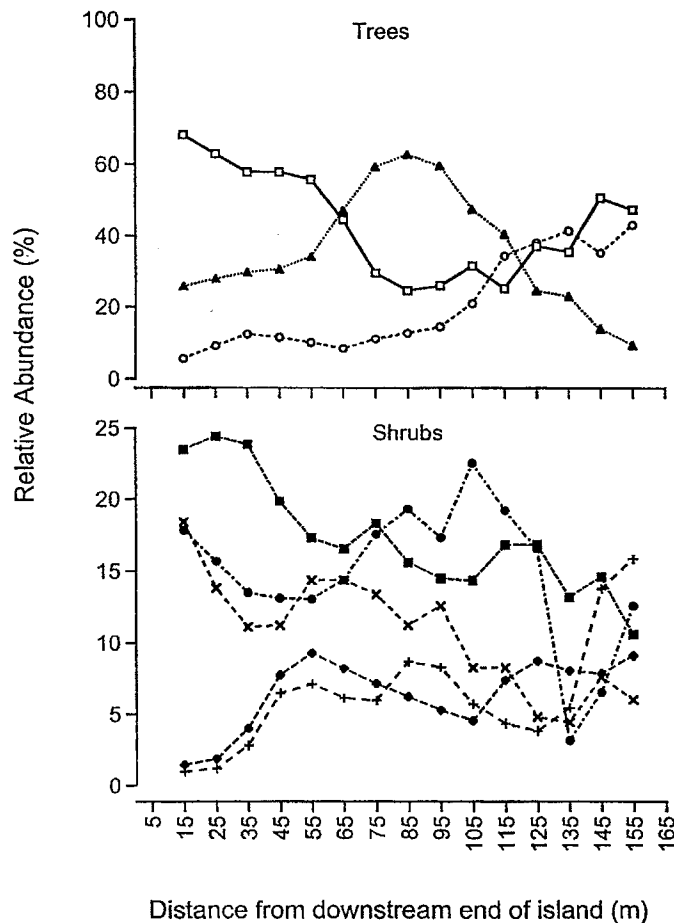


Figure 5. Distribution of trees and shrubs at the whole basin scale of analysis. □ are *Populus trichocarpa*, ▲ are *Alnus tenuifolia*, ○ are *Picea engelmannii*, ■ are *Salix exigua*, × are *S. drummondiana*, ● are *S. candida*, ▼ are *Cornus stolonifera*, + are rare shrubs.

peak abundance of saplings, which was downstream of peak abundances of adults. Also, similar lifestages of the different species were organized in a linear gradient of pioneering to late seral from downstream to upstream. These patterns suggest that a "wave of colonization" is occurring on these islands, probably following a gradient of site conditions. Barnes (1985) found a similar organization pattern in the tree assemblage of a large island in the Chippewa River, where the age structure of con-specific trees shifted from many young individuals at one end of the island to fewer, older individuals at the other end of the island, and the pattern corresponded to increased island age and surface elevation.

The finding of only a 3.5 yr. difference in the average age of trees from the upstream to downstream ends of islands suggests that at least some of the islands included in this study reached their present size within 3.5 years of initial emergence. This fails to support our hypothesis that river islands grow incrementally in response to

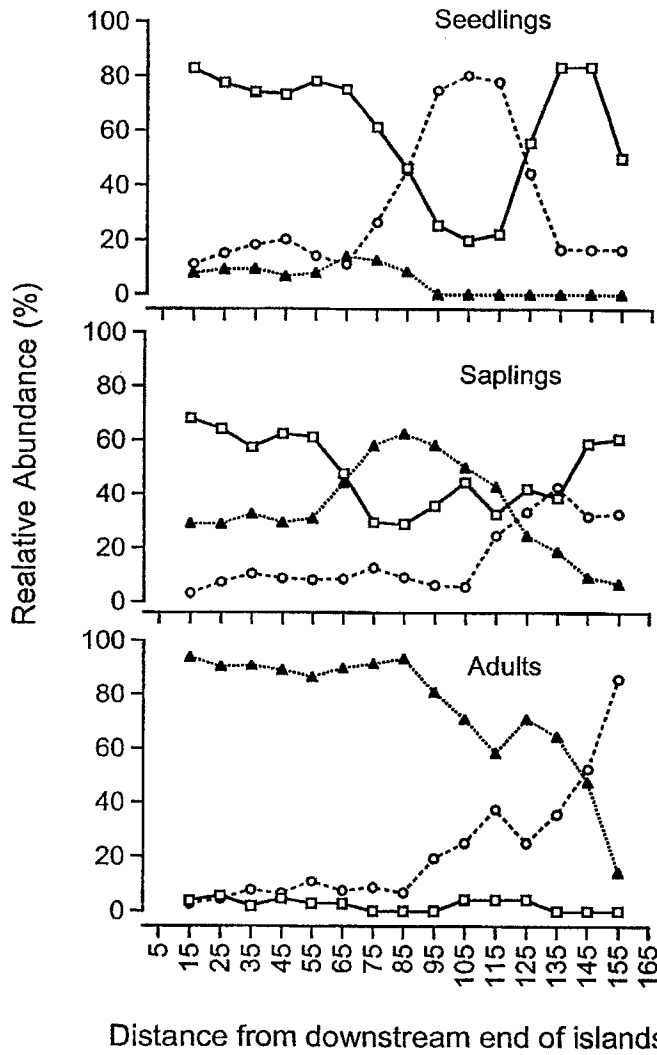


Figure 6. Distribution of trees at the whole basin scale, organized by lifestages. □ are *Populus trichocarpa*, ▲ are *Alnus tenuifolia*, ○ are *Picea engelmannii*.

the interaction between fluvial dynamics, plant establishment, and sediment recruitment. However, unusual fluvial events in the mid 1970s may be confounding our interpretation.

The record high peak discharge of the Swan River of  $252 \text{ m}^3 \text{ s}^{-1}$  occurred in 1974, and the record low peak discharge of  $95 \text{ m}^3 \text{ s}^{-1}$  occurred in 1977. Tree ages indicate 64 of the 67 aged trees established during or shortly after 1977. The presence of only three trees that germinated prior to 1974 suggests the 1974 flood scoured away much of the existing vegetation. From 1974 to 1977, it appears that trees did not successfully establish on islands within the active river channel, possibly because appropriate land surfaces were not available at the time of seed availability or because climatic conditions were not appropriate for germination or survival. During the low water year of 1977, land surfaces were exposed at the time of seed release, climatic conditions were appropriate, and a large number of trees successfully germinated and survived. Potential explanation for the inconsistent support for incremental island growth is that Swan River islands are in a recovery phase following a significant disturbance event that eliminated the pre-existing tree assemblage and insufficient time has elapsed since disturbance to allow for emergence of a greater age gradient. Baker (1990) and Friedman et al. (1995) have similarly reported the need for consilience between timing of high and low water events and appropriate climatic conditions and seed release for the successful establishment of riparian species.

By analyzing our data at three spatial scales, we were able to identify patterns that otherwise might not have been detected. At the scale of individual islands the high degree of inter-island variability in plant distribution patterns suggests that site-specific forces or random events play important roles in structuring plant community organization on any given island. Such conditions may include local channel geometry, channel and floodplain gradients, and the orientation of local accumulations of large wood. Malanson and Butler (1990) suggested that the presence of infrequently inundated over-flow channels bisecting the surface of a developing gravel bar or island could mask otherwise identifiable patterns of plant organization. Additionally, inter-island variability in plant distribution patterns may be attributable to differential recruitment and survival of plant propagules, even though the process of land surface formation is similar.

At the reach scale of analysis, distinct differences existed in the organization of the plant assemblages. Within the upper reach, all three seral community types (e.g., pioneer, early seral, late seral) were present, and there was evidence of a linear gradient of seral stages. Evidence of organization by seral stage was less distinct in the two reaches with larger catchment areas, and, as discharge increased (measured as drainage basin size), the abundance of mid- and late seral species decreased. These differences may be a function of fluvial reset, whereby river dynamics maintain islands lower in the drainage basin in an earlier successional condition relative to islands farther upstream.

When plant distribution data were pooled for comparison at the basin scale, the strongest evidence of a linear sequence of seral stages emerged, suggesting that plant establishment and survivorship are responding to a shared influence because it is unlikely that such a pattern could have developed by chance or if site-specific influences were the primary driving force of island development. Processes known or assumed to be similar to all study islands include climatic conditions, timing and composition of seed recruitment, and timing and duration of high and low discharge events. Reports from similar studies investigating plant distribution patterns on alluvial islands (e.g., Malanson and Butler 1991, Puhakka et al. 1992) typically have not reported evidence of zonation by seral stage. This may be because data were analyzed at only one spatial scale.

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#### LITERATURE CITED

- Abbe, T.B. and D.R. Montgomery. 1996. Large woody debris jams, channel hydraulics, and habitat formation in large rivers. *Regulated Rivers: Research and Management* 12: 201-221.
- Amoros, C., A.L. Roux, and J.L. Reygrobellet. 1986. A method for applied ecological studies of fluvial hydrosystems. *Regulated Rivers: Research and Management* 1: 17-36.
- Amoros, C., J. Rostan, G. Pautou, and J. Bravard. 1987. The reversible process concept applied to the environmental management of large river systems. *Environmental Management* 11: 607-617.
- Baker, W.L. 1990. Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado. *Journal of Biogeography* 17: 59-73.
- Barnes, W.J. 1985. Population dynamics of woody plants on a river island. *Canadian Journal of Botany* 63: 647-655.
- Bornette, G., C. Amoros, and D. Chessel. 1994. Effect of allogenic processes on successional rates in former river channels. *Journal of Vegetation Science* 5: 237-246.
- Bravard, J-P., C. Amoros, and G. Pautou. 1986. Impact of civil engineering works on the successions of communities in a fluvial system. A methodological and predictive approach applied to a section of the Upper Rhone River, France. *Oikos* 47: 92-111.
- Burns, R.M. and B.H. Honkala, Editors. 1990. *Silvics of North America - Hardwoods*. USDA Agricultural Handbook 654.
- Campbell, J.R.B. 1981. Field and laboratory methods for age determination of Quaking Aspen. USDA Forest Service research note INT-314.
- Chapin, F.S.I., L.R. Walker, C.L. Fastie and L.C. Sharman. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* 64: 149-175.
- Cole, D.M. 1977. Protecting and storing increment cores in plastic straws. USDA Forest Service research note INT-216.
- Cooperman, M.S. 1997. The process of mid-channel alluvial island formation as inferred from plant distribution patterns on islands of the Swan River, northwest Montana. Division of Biological Sciences, University of Montana. Missoula, Montana. 166 pgs.
- Cotton, G. and J.T. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37: 451-460.
- Fenner, M. 1987. Seed characteristics in relation to succession, in *Colonization, Succession, and Stability: the 26th Symposium of the British Ecological Society*. A.J. Gray, M.J. Crawley, and P.J. Edwards, Editors. Blackwell Scientific Publications. pgs. 103-114.
- Friedman, J.M., M.L. Scott, and W.M.J. Lewis. 1995. Restoration of riparian forest using irrigation, artificial disturbance, and natural seedfall. *Environmental Management* 19: 547-557.
- Frissell, C.A., J. Duskocil, J.T. Gangemi, and J.A. Stanford. 1995. Identifying priority areas for protection and restoration of aquatic biodiversity: A case study in the Swan River basin, Montana, USA. Flathead Lake Biological Station open file report 136-95, The University of Montana, Polson, Montana.
- Furlow, J.J. 1979. The systematics of the American species of *Alnus* (*Betulaceae*). *Rhodora* 81: 1-121.

- Green, W.N. 1982. Mid-Channel Islands: Sedimentology, physiography, and effects on channel morphology in selected streams of the Great Bend Region of the Wabash Valley. Masters thesis, Geology department, Purdue University, Indiana. 111 pgs.
- Hamilton, L.C. 1990. Modern data analysis: A first course in applied statistics. Brooks/Cole Publishing. Pacific Grove, CA.
- Heinze, D. H. 1994. Montana Willows. U.S. Bureau of Land Management, Montana State Office. Billings, Montana. 84 pgs.
- Hupp, C.R. and W.R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landform. *Ecology* 66: 670-681.
- Hupp, C.R. and W.R. Osterkamp. 1996. Riparian vegetation and fluvial geomorphic processes. *Geomorphology* 14: 277-295.
- Kalliola, R. and M. Puhakka. 1988. River dynamics and vegetation mosaicism: a case study of the River Kamajohka, northernmost Finland. *Journal of Biogeography* 15: 703-719.
- Kendy, E. and R.E. Tresch. 1996. Geographic, geologic, and hydrologic summaries of intermountain basins of the northern Rocky Mountains. USGS Water Resources Investigations report 96-4025. US Dept. of Interior, Denver, Co. pgs 179-183.
- Kollman, J., M. Vieli, P.J. Edwards, K. Tockner, and J.V. Ward. 1999. Interactions between vegetation development and island formation in the Alpine river Tagliamento. *Applied Vegetation Science* 2: 25-36.
- Lackschewitz, K. 1991. Vascular plants of west-central Montana - identification guidebook. USDA Forest Service Intermountain Research Station, Ogden, UT. 648 pgs.
- Malanson, G.P. and D.R. Butler. 1990. Woody debris, sediment, and riparian vegetation of a subalpine river, Montana, USA. *Arctic and Alpine Research* 22: 183-194.
- Malanson, G.P. and D.R. Butler. 1991. Floristic variation among gravel bar in a subalpine river, Montana, USA. *Arctic and Alpine Research* 23: 273-278.
- McDonald, L.L. 1980. Line-intercept sampling for attributes other than coverage and density. *Journal of Wildlife Management* 44: 530-533.
- Nanson, G.C. and H.B. Beach. 1977. Forest succession and sedimentation on a meandering-river floodplain, northeast British Columbia, Canada. *Journal of Biogeography* 4: 229-251.
- Puhakka, M., R. Kalliola, M. Rajasilta, and J. Salo. 1992. River types, site evolution and successional vegetation patterns in Peruvian Amazonia. *Journal of Biogeography* 19: 651-665.
- Rydin, H. and S. Borgegard. 1991. Plant characteristics over a century of primary succession on islands: Lake Hjälmaren. *Ecology* 72: 1089-1101.
- Schnitzler, A. 1997. River dynamics as a forest process: Interaction between fluvial systems and alluvial forests in large European river plains. *The Botanical Review* 63: 40-60.
- Shankman, D. 1991. Forest regeneration on abandoned meanders of a coastal plain river in western Tennessee. *Castanea* 56: 157-167.