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## THE ROLE OF LIFE HISTORY PROCESSES IN PRIMARY SUCCESSION ON AN ALASKAN FLOODPLAIN<sup>1</sup>

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**Abstract.** The pattern of primary succession on the floodplain of the Tanana River in interior Alaska resulted largely from interactions between stochastic events and life history traits of the dominant species. Seed rain by willow (*Salix alaxensis*), alder (*Alnus tenuifolia*), poplar (*Populus balsamifera*), and spruce (*Picea glauca*) varied substantially among years but was highest in the successional stage dominated by that species. Some seeds of each species arrived in all stages, and seedlings of all species were initially present in early successional sites. The copious, wind-dispersed seeds and rapid seedling growth rates of willow and poplar resulted in their abundant establishment on early successional vegetated-silt bars. Heavier alder and spruce seeds were less widely distributed, yet rapid growth rates of alder resulted in dense alder thickets within 20 yr of silt bar formation. We found no evidence of buried seed of the four study species. Sown seeds of willow, alder, and poplar established only in early successional vegetated-silt and willow sites. Spruce established in these same sites and in alder sites. Spruce was the only species that naturally colonized mid and late successional sites. Removal of the litter and forest floor enabled all species to germinate in all sites. Flooding resulted in substantial mortality of seedlings in early successional sites. A combination of short life span, herbivory by hares, and shade intolerance eliminated willow from mid-successional alder-dominated sites. Thereafter differences in longevity explained successional change from alder to poplar to spruce. Facilitative interactions among species did not appear essential to explain changes in species composition in this primary successional sequence.

**Key words:** *Alaska; boreal; facilitation; floodplain; germination; herbivory; life history traits; seed bank; seed rain; succession.*

### INTRODUCTION

Several authors (Drury and Nisbet 1973, Connell and Slatyer 1977, Dean and Hurd 1980) have questioned the classical explanation of succession (Clements 1936, Odum 1969), i.e., that early successional species facilitate the establishment and growth of later successional species. Support is accumulating for successional models that rely on competitive inhibition (rather than facilitation) of later successional species by early colonizers (Niering and Goodwin 1974, Harcombe 1977, van Hulst 1979) or on life history traits such as arrival time, growth rates, and longevity patterns (Glenn-Lewin 1980, Noble and Slatyer 1980, Hibbs 1983) to explain successional change.

However, the view that competitive inhibition is more important than facilitation may reflect an em-

phasis upon the study of secondary succession (cf. Collins and Quinn 1982, Parrish and Bazzaz 1982, Runkle 1982). Studies of terrestrial primary succession are few (cf. Crocker and Major 1955, Olson 1958, Viereck 1966, 1970, Reiners et al. 1971, Van Cleve et al. 1980, Walker et al. 1981), and frequently conclude (but less frequently test) that facilitative interactions drive successional changes in these systems. Few studies to date have investigated the importance of life history processes in determining primary successional changes.

Colonization of floodplains may be influenced by such life history traits as the reproductive habits of potential colonizers. For example, the timing of seed dispersal (Sigafos 1964, Nechaev 1967) must coincide with receding water levels to provide moist microsites for germination and establishment of some species. Alternatively, vegetative reproduction of poplar (Wilson 1970), willow (Bliss and Cantlon 1957), and other species (Dahlskog 1966) may influence rates and patterns of establishment in a primary floodplain succession. Plant growth rates (Nechaev 1967, Nanson and Beach 1977) and life spans (Nanson and Beach 1977) may also interact with sedimentation in determining successional development on floodplains.

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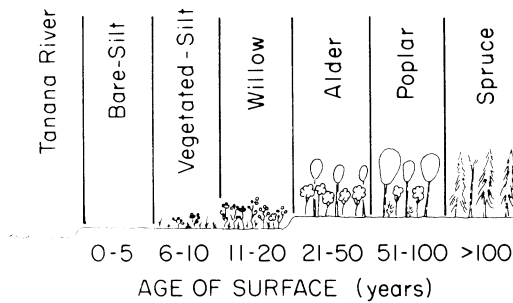


FIG. 1. Primary successional stages on the Tanana River floodplain in interior Alaska (modified from Viereck 1970).

The present study was undertaken to examine the degree to which life history traits (seed rain, seedling establishment, and longevity) direct a primary successional sequence on an Alaskan floodplain. We conclude that these life history traits and stochastic events are sufficient to explain patterns of species arrival and change through this primary successional sequence, and that neither facilitative nor competitive interactions among species need be assumed.

## METHODS

### Study area

The study area was located on a 10-km section of the glacially fed Tanana River adjacent to the Bonanza Creek Experimental Forest (64°40' N, 148°15' W), ≈32 km southwest of Fairbanks, in interior Alaska. The climate of the area is strongly continental, with large annual temperature variation (−50° to +35°, mean −3.5°C). The average annual precipitation is 286 mm, 30% of which falls as snow.

The successional sequence on the Tanana River floodplain (Fig. 1) begins with silt deposition on the inside of river meanders. Gradual aggradation of these bars due to additional silt deposition and forest litter accumulation results in terraces, which increase in elevation with distance from the river channel (Viereck 1970). *Equisetum* spp. and *Salix* spp. colonize immediately. However, frequent flooding of the lowest silt bars often delays successful establishment. Within 5 yr, seedlings of sandbar willow (*Salix interior* Rowlee), feltleaf willow (*S. alaxensis* [Anderss.] Cov.), and balsam poplar (*Populus balsamifera* L.) are abundant (nomenclature follows Viereck and Little 1972). Thinleaf alder (*Alnus tenuifolia* Nutt.) and white spruce (*Picea glauca* [Moench] Voss) seedlings are often present but less abundant. Dense feltleaf willow stands form on wetter soils. Thinleaf alder thickets predominate from ≈20–50 yr, with balsam poplar as a significant component of the canopy. White spruce seedlings are sometimes abundant in alder thickets. Stands of poplar with a white spruce and alder understory commonly predominate from ≈50–100 yr after initial colonization, after which these stands gradually become dom-

inated by white spruce (Viereck 1970, Van Cleve et al. 1980). Measurement of stand ages is discussed below.

Five replicate study sites were chosen in each of five successional stages. This permitted us to distinguish true differences among successional stages from the natural variation present among sites in a given successional stage. These stages were named for the dominant species and were chosen to include, where possible, seedlings of each of the four species studied (feltleaf willow: *Salix alaxensis*, alder: *Alnus tenuifolia*, poplar: *Populus balsamifera*, spruce: *Picea glauca*). The vegetation characteristics used in selecting these sites were: (1) vegetated-silt stage: plants <0.6 m tall, <50% bare soil; (2) willow stage: plants 0.6–1.2 m tall, >50% *Salix alaxensis* cover; (3) alder stage: more alder than poplar stems, >1 spruce seedling/m<sup>2</sup>; (4) poplar stage: a poplar canopy, more poplar than alder stems, >1 spruce seedling/m<sup>2</sup> and spruce seedlings <1 m tall; (5) spruce stage: a spruce canopy and >1 spruce seedling/m<sup>2</sup>. Spruce stands with standing dead poplar and poplar stands with dead alder stems were chosen to ensure that a true chronosequence was being studied.

### Seed rain

Seed rain was measured over 2 yr in willow, alder, poplar, and spruce stages. Rectangular plastic trays (35 × 26 × 8 cm) with a surface area of 0.09 m<sup>2</sup> were kept filled with water to collect willow and poplar seeds. Four or five of these trays were placed on the ground in each of 15 sites (three sites in each successional stage described above) from 21 May to 21 July 1982, and from 13 May to 19 July 1983, encompassing >95% of the seed dispersal periods for willow and poplar. All seeds of feltleaf willow and balsam poplar were counted and removed every 2–4 d.

Four square traps (50 × 50 × 10 cm; 0.25 m<sup>2</sup>), with a screen bottom and muslin liner, were located on the ground in each of the same 15 sites to collect alder and spruce seed. These trays were checked weekly from 27 August to 24 September 1982, and from 13 May to 16 June 1983, and they were also examined 18 September 1983 and 25 May 1984, encompassing >95% of the seed dispersal period for alder and spruce. Autumn and spring counts of alder and spruce seed were combined to give annual seed crops. Subsamples of spring-collected seed were tested for viability on wet filter paper in Petri dishes at 20° under continuous light. Germination was defined as 1 mm hypocotyl extension from the seed. Seed rain was calculated for each study species from the sum of seed collected in each tray over the course of each year.

The buried seed pool was examined in one vegetated-silt site and one poplar site in September 1984 by randomly locating 15 6.4 cm diameter cores per site. Cores included all litter and forest floor and the upper 3 cm of mineral soil. Cores were spread <1 cm thick on plastic in a greenhouse and covered with another layer of plastic to minimize evaporation. Photoperiod

was maintained at 20 h, and temperature ranged from 15°–30°. Soils were watered daily for 5 wk, and all seedlings that emerged were identified and counted.

#### Sowing experiment

At each of four sites per successional stage, four 1-m<sup>2</sup> quadrats were randomly chosen and cleared of leaf litter and organic soil to provide a mineral soil seedbed (treated plots). Three additional control quadrats were chosen at each site and left untreated. In the alder, poplar, and spruce stages the treatment involved removing between 10–200 mm of litter and forest floor (O1, O2 layers). In the willow and vegetated-silt stages, the material removed from the surface included a 5–10 mm thick salt crust of calcium sulfate and calcium carbonate. The salt crust was removed to test the hypothesis that it may inhibit seedling establishment on the floodplain (Van Cleve et al. 1980).

Seeds of each species were collected, cleaned, and sown onto one 0.2 × 0.3 m subplot within each 1-m<sup>2</sup> quadrat at densities indicated in Table 1. Sowing rates were based on estimates of field germination (willow 1%, poplar 5%, alder and spruce 10% of viable seed) and survivorship (50%) obtained from previous studies (Zasada et al. 1983, J. C. Zasada, *personal observation*). Sowing density of willow was reduced by 50% after the first sowing due to unexpectedly high germination.

Poplar and willow seeds were collected at the time seed dispersal began just prior to the first and third sowing. Seeds were stored at –10° between the first and second sowings. Spruce and alder seeds were collected in early September. With the exception of the first sowing of spruce, seeds were sown during the period of maximum seed dispersal for each species. Seeds for the first sowing of spruce were stratified at 5° for 30 d prior to sowing in order to simulate overwintering. Treated seedbeds were kept litter-free following sowing.

Seedlings were counted weekly on each subplot. Seedlings counted on adjacent unseeded plots were subtracted from the counts to allow for seedlings from natural seed rain. When the density of seedlings was > 300 per subplot, seedlings in three randomly selected subsamples of 0.06 m<sup>2</sup> were counted. The maximum number of seedlings counted on any one date during the first summer after sowing was used as a measure of germination. Maximum seedling densities and 1st- and 2nd-yr survivors were counted for each species/stage/treatment combination and were expressed as the percentage of viable seed sown. Seedbeds with no survivors were included in the calculations.

#### Transects

Densities of natural seedlings and saplings were measured along 14 2 m wide transects chosen at regular (0.8-km) intervals along the main river channel to provide unbiased estimates of natural seedling densities. These transects extended at least 50 m inland, perpen-

TABLE 1. Dates and densities at which seeds of each study species were sown in experimental plots.

Species	Sowing period	Seed density (viable seed/m <sup>2</sup> )
Willow		
First sowing	8–10 Jun 1982	48 000
Second sowing	17–18 Jun 1982	24 000
Third sowing	1–8 Jun 1983	24 000
Alder		
First sowing	22 Sep 1982	3 500
Poplar		
First sowing	9–12 Jul 1982	13 800
Second sowing	17 Jul 1982	13 800
Third sowing	28 Jun 1983	13 800
Spruce		
First sowing	24–27 May 1982	10 100
Second sowing	9–10 Sep 1982	10 100

dicular to the river course, and ended either in a mature spruce community or at a maximum distance of 300 m. Eight 1 × 5 m quadrats were sampled along each transect at randomly chosen intervals in each of the five successional stages. A bare-silt (time zero) stage and a transition stage from willow to alder were also included. Height, age, density, and presence or absence of herbivory by hare (*Lepus americanus*) and moose (*Alces alces*) were measured for each of the four study species for individuals < 2 m tall and < 50 mm dbh. Seedlings were aged from annual height increments between winter bud scars or by ring counts. The density of standing dead stems was also recorded. Elevation of each successional stage above the river was measured at each site on 18 September 1983 when the river gauge heights at Fairbanks and Nenana were, respectively, 130 and 104 m above mean sea level (R. L. Burrows, *personal communication*).

#### Longevity

The maximum age of each species was estimated in each successional stage. Growth rings were counted on 3–10 of the largest individuals at each of the five primary study sites in each successional stage. Ages of stems were determined with an increment borer at a height of 30 cm, except in the vegetated-silt and willow stages, where age was estimated from annual height increments between winter bud scars. The age of each site was assumed equal to the age of the oldest individual at that site. For vegetated-silt, willow, and alder sites these ages were confirmed (± 5 yr) by examination of aerial photographs of the study area taken between 1948 and 1978. In one alder site and one poplar site all alder and poplar stems were sampled in a 12 × 12 m area to determine the age distribution of all individuals present.

TABLE 2. Total seed rain in five successional stages in 1982 and 1983,  $n = 12$ . Number of viable seeds per square metre is in parentheses (for alder and spruce only) based on 24.4% viability for alder and 40.4% for spruce. Willow and poplar seeds were assumed to be 100% viable. Values in each row followed by the same letter are not significantly different ( $P > .05$ ).

Species	Year	Successional stage				
		Vegetated-silt	Willow	Alder	Poplar	Spruce
Total seeds per square metre ( $\bar{X} \pm SE$ )						
Willow	1982	19 $\pm$ 5 a	231 $\pm$ 47 b	127 $\pm$ 43 abc	17 $\pm$ 8 ac	<1 cd
	1983	52 $\pm$ 13 ab	131 $\pm$ 27 b	8 $\pm$ 3 a	8 $\pm$ 3 a	18 $\pm$ 4 a
Alder	1982	0 $\pm$ 0 (0 $\pm$ 0) a	5 $\pm$ 2 (2 $\pm$ 1) b	2234 $\pm$ 309 (1173 $\pm$ 162) c	251 $\pm$ 64 (132 $\pm$ 33) d	7 $\pm$ 2 (4 $\pm$ 1) b
	1983	1 $\pm$ 1 <1 a	4 $\pm$ 2 (1 $\pm$ 0.4) a	3055 $\pm$ 359 (745 $\pm$ 87) b	345 $\pm$ 116 (84 $\pm$ 28) c	37 $\pm$ 11 (9 $\pm$ 3) a
Poplar	1982	127 $\pm$ 16 a	129 $\pm$ 12 a	359 $\pm$ 95 a	1757 $\pm$ 269 b	272 $\pm$ 63 a
	1983	91 $\pm$ 20 a	102 $\pm$ 13 a	500 $\pm$ 183 a	3107 $\pm$ 211 b	285 $\pm$ 84 a
Spruce	1982	6 $\pm$ 2 (2 $\pm$ 1) a	8 $\pm$ 2 (3 $\pm$ 1) a	6 $\pm$ 2 (2 $\pm$ 1) a	15 $\pm$ 3 (6 $\pm$ 1) a	178 $\pm$ 25 (72 $\pm$ 10) b
	1983	<1 (<1) a	0 $\pm$ 0 (0 $\pm$ 0) a	0 $\pm$ 0 (0 $\pm$ 0) a	0 $\pm$ 0 (0 $\pm$ 0) a	41 $\pm$ 16 (17 $\pm$ 6) b

### Statistical analysis

Statistical analyses included *t* tests for comparisons of means (Zar 1974) and one-way analysis of variance to determine stage effects (BMDP 7D, Dixon 1981); comparisons of individual stages were made by pairwise *t* tests with Bonferroni probabilities for multiple comparisons. This method is conservative, tending to reject differences. All percentages were treated with arcsine transformation. Significance was determined at the 5% level.

## RESULTS

### Seed rain

Seed rain by alder, poplar, and spruce was highest ( $P < .05$ ) in the successional stage dominated by that species (Table 2). Input of willow seeds was highest in the willow and alder stages in 1982 and highest in the vegetated-silt and willow stages in 1983. Poplar produced the most viable seeds during this study, followed by alder, willow, and spruce. Viable seeds of each species were found in all successional stages for at least one of the two years.

The quantity of seed arriving at a particular site did not always correlate with the quantity of seed produced in the stand where the species dominated. For example, the density of willow seeds in the vegetated-silt stage was greater in the year of lower willow seed production, while in the alder stage, the density of willow seeds was greater during the year of higher seed production (Table 2). These variable seed densities suggest that

stochastic factors such as wind velocity and direction may be as important as seed production in determining seed rain at a given site. Seed mass also influenced dispersal. Light, wind-dispersed willow and poplar seeds were found in greater abundance in successional stands dominated by other species than were the heavy alder and spruce seeds. Seed dispersal of willow and poplar occurred in June and July, respectively (Fig. 2). This short, intense period of seed dispersal during the growing season is characteristic for summer-dispersing Salicaceae. Thus, willow and poplar seeds reach seedbeds at times when immediate germination and growth are possible. Dispersal of alder and spruce seed occurs primarily in the dormant season (Fig. 2) when the seeds become covered with varying amounts of snow. Conditions for germination are not present until the following spring.

We found no viable buried seed in cores from the vegetated-silt site. Only one herbaceous dicot seedling germinated from cores in the poplar site (providing a density estimate of 21 seedlings/m<sup>2</sup>). In contrast, upland sites yielded estimates of 375–650 seedlings/m<sup>2</sup> with the same techniques (F. S. Chapin, III, *personal observation*).

### Seedling survivorship

Germination of summer-dispersing willow and poplar was observed within 3 d after seeds were sown (Fig. 3). In contrast, germination of the fall/winter seed dispersers (alder and spruce) began in spring as soon as conditions were favorable for germination. Alder seed-

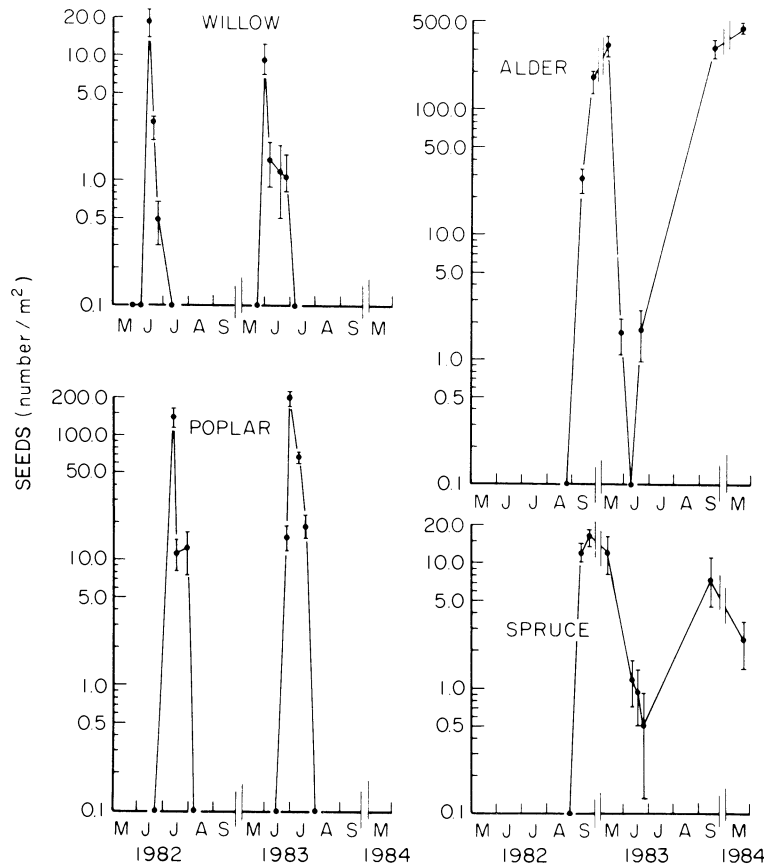


FIG. 2. Seasonal pattern of seed rain of willow, alder, poplar, and spruce from successional stages dominated by these species, in 1982, 1983, and 1984, mean  $\pm$  SE,  $n = 12$  seed traps. Note log scale.

lings appeared at least 1 wk prior to willow seed dispersal, and spruce germination, whether from spring- or fall-sown seeds, began at about the time of willow seed dispersal. For a given species, germination began at about the same time in all stages, except for alder and spruce, which began to germinate later in the spruce stage than in preceding stages. Maximum density of summer dispersers (willow and poplar) occurred within 1 wk of sowing, whereas the fall/winter dispersers reached maximum density as much as 2 wk after appearance of the first seedlings. Maximum seedling density generally differed dramatically among sowing dates for each species (Table 3), indicating that the timing of dispersal (Fig. 2) with respect to seedbed conditions was highly critical for successful germination and early survival.

Willow, alder, and poplar germinated on untreated seedbeds only in the early successional vegetated-silt and willow sites (Table 3). Spruce also germinated in these early successional sites and in alder sites but was much less successful on the litter and forest floor of the poplar or spruce sites.

Removal of the salt crust (forest floor) had no con-

sistent effect on germination of any species in the vegetated-silt or willow sites (Table 3). However, removal of the litter and forest floor in the later successional stages usually increased maximum seedling density at least 5–10 fold, indicating that the litter plus forest floor strongly inhibited germination and/or initial establishment in these later successional stages.

Willow seedling density declined markedly ( $P < .05$ ) during the first summer on both treated and untreated seedbeds in the vegetated-silt and willow stages (Fig. 3) and on treated seedbeds in the alder and poplar stages (Walker 1985); there were no willow germinants on untreated seed beds in the alder and poplar stages (Table 3). Inundation and silt deposition from summer floods (Fig. 3) were in part responsible for high willow seedling mortality. Consequently, despite higher germination on early than on late successional seedbeds, densities of willow seedlings were similar among all stages by the end of the first summer. In contrast to willow, seedling density of alder, poplar, and spruce showed no significant ( $P > .05$ ) decline through the first growing season in either treated or untreated seedbeds (Fig. 3). Spruce was the only species that

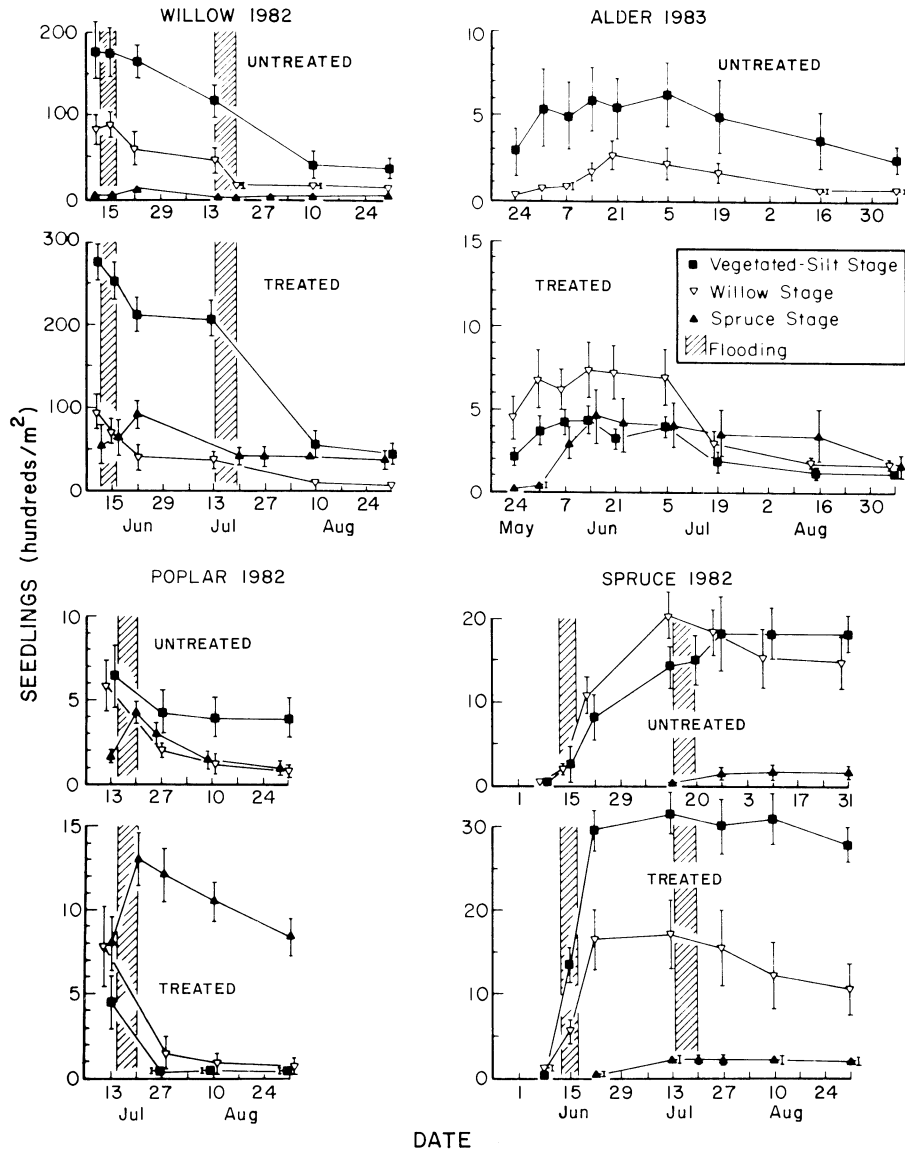


FIG. 3. Willow, alder, poplar, and spruce seedling densities from seeds sown on treated and untreated seedbeds in three successional stages, mean  $\pm$  SE. Treated seedbeds had mineral soil exposed by removal of the O1 and O2 soil horizons. Sample size is  $n = 16$  (treated),  $n = 12$  (untreated).

showed  $>0.2\%$  survivorship two full years after sowing (Walker 1985).

#### Transects

Colonization by all four study species began within 5 yr of silt bar formation (Fig. 4; see description of site dating below). Willow and poplar seedlings and saplings were most abundant until the transition to the alder stage, after which alder and spruce seedlings and saplings were more common. Willow and poplar stems  $< 50$  mm dbh were not present in stands older than 30 yr, indicating that establishment of these species is limited to early successional stages on this river sys-

tem. Small alder stems recorded in poplar and spruce stands were all stump sprouts derived from mature individuals. In contrast, spruce seedlings were found in all stages, although they were in low abundance during the first 10 yr of succession. Thus, with the exception of spruce, no colonization was observed after the initial stages of succession.

Spruce seedling age was more closely correlated with terrace height ( $r^2 = 0.84$ ) than with age of the site ( $r^2 = 0.25$ ), presumably because terrace height determines frequency and intensity of flood events. Spruce establishment appears to be episodic, as the variation in age of seedlings within each stage was small. Spruce estab-

TABLE 3. Maximum seedling densities (an index of germination) in first summer after sowing for seed sown at different planting dates on untreated and treated seedbeds. Means  $\pm$  SE are from arcsine transformed data,  $n = 16$  (treated),  $n = 12$  (untreated). Mean values within stages and treatments followed by the same letter are not significantly different ( $P > .05$ ).

Species	Treatment*	Planting date	Successional stage				
			Vegetated-silt	Willow	Alder	Poplar	Spruce
Maximum first summer seedling density (% of viable seed sown)							
Willow	Untreated	8-10 Jun 1982	35.5 $\pm$ 3.8 a	14.3 $\pm$ 4.3 a	0.0 $\pm$ 0.0 a	0.0 $\pm$ 0.0 a	0.2 $\pm$ 0.1 a
		17-18 Jun 1982	15.5 $\pm$ 3.0 b	0.7 $\pm$ 0.2 b	<0.1 a	<0.1 a	2.1 $\pm$ 0.8 b
		1-3 Jun 1983	4.7 $\pm$ 1.5 c	0.3 $\pm$ 0.2 b	0.0 $\pm$ 0.0 a	0.0 $\pm$ 0.0 a	0.0 $\pm$ 0.0 c
	Treated	8-10 Jun 1982	56.6 $\pm$ 4.4 a	17.0 $\pm$ 4.3 a	15.5 $\pm$ 2.8 a	18.4 $\pm$ 5.2 a	16.3 $\pm$ 2.1 a
		17-18 Jun 1982	13.3 $\pm$ 2.3 b	14.4 $\pm$ 5.4 a	3.3 $\pm$ 1.4 b	9.4 $\pm$ 3.2 a	15.6 $\pm$ 3.1 a
		1-3 Jun 1983	2.9 $\pm$ 0.7 c	0.6 $\pm$ 0.4 b	0.8 $\pm$ 0.3 b	0.6 $\pm$ 0.4 b	1.4 $\pm$ 0.6 b
Alder	Untreated	22-23 Sep 1982	14.9 $\pm$ 5.2	5.7 $\pm$ 2.2	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
	Treated	22-23 Sep 1982	9.7 $\pm$ 2.2	17.5 $\pm$ 7.2	12.5 $\pm$ 2.4	11.8 $\pm$ 3.7	8.1 $\pm$ 4.4
Poplar	Untreated	9-12 Jul 1982	3.1 $\pm$ 1.4 a	1.8 $\pm$ 1.0 a	0.1 $\pm$ 0.1 a	0.6 $\pm$ 0.2 a	0.7 $\pm$ 0.2 a
		17 Jul 1982	0.5 $\pm$ 0.3 a	0.4 $\pm$ 0.2 a	0.1 $\pm$ 0.1 a	0.1 $\pm$ 0.1 a	1.4 $\pm$ 1.0 a
		28 Jun 1983	23.8 $\pm$ 2.1 b	15.9 $\pm$ 3.7 b	0.2 $\pm$ 0.1 a	0.8 $\pm$ 0.2 a	2.3 $\pm$ 1.0 a
	Treated	9-12 Jul 1982	1.7 $\pm$ 0.8 a	2.8 $\pm$ 1.3 a	0.5 $\pm$ 0.2 a	4.8 $\pm$ 1.0 a	1.8 $\pm$ 0.6 a
		17 Jul 1982	0.1 $\pm$ 0.1 b	0.5 $\pm$ 0.5 b	12.5 $\pm$ 2.1 b	11.5 $\pm$ 2.8 b	16.9 $\pm$ 3.1 b
		28 Jun 1983	35.5 $\pm$ 3.4 c	23.2 $\pm$ 5.3 c	15.5 $\pm$ 2.9 b	9.9 $\pm$ 2.0 b	28.7 $\pm$ 5.4 b
Spruce	Untreated	24 May 1982	13.1 $\pm$ 3.2 a	12.1 $\pm$ 3.2 a	13.3 $\pm$ 3.3 a	1.1 $\pm$ 0.3 a	0.3 $\pm$ 0.2 a
		9-10 Sep 1982	6.7 $\pm$ 3.0 a	3.6 $\pm$ 1.3 b	0.0 $\pm$ 0.0 b	0.0 $\pm$ 0.0 b	0.0 $\pm$ 0.0 b
	Treated	24 May 1982	26.1 $\pm$ 2.8 a	11.8 $\pm$ 3.7 a	2.8 $\pm$ 0.9 a	8.8 $\pm$ 2.7 a	1.5 $\pm$ 0.3 a
		9-10 Sep 1982	1.4 $\pm$ 0.4 b	0.1 $\pm$ 0.1 b	0.4 $\pm$ 0.2 b	1.1 $\pm$ 0.4 b	0.3 $\pm$ 0.1 b

\* Treated seedbeds had mineral soil exposed by removing the forest floor (O1 and O2 layers). Untreated seedbeds were left intact.

lishment on early successional silt bars is not always successful because slow-growing spruce seedlings are unable to survive burial by silt during major floods.

#### Herbivory

All four species were browsed heavily by snowshoe hares (*Lepus americanus*). Browsing was predominantly in mature alder thickets, which provide cover for the hares. Highest densities of dead stems were also found in mature alder thickets (Walker 1985) and were associated consistently with evidence of past herbivory, suggesting that herbivory may contribute to the significant ( $P < .05$ ) decline in live willow and poplar stem densities in the alder stage (Fig. 4). Thus, hare damage may be important in preventing natural regeneration and limiting longevity of the four species.

#### Longevity

Ages of the largest mature individuals of each species in each successional stage indicate nearly simultaneous arrival of all species (Table 4). Willow was the first of the four species studied to establish on the silt bars. A few individuals persisted into the poplar stage and reached a maximum age of 48 yr. Alder and poplar established within 2 yr after willow. Individual alder stems lived for  $\approx 25$  yr, with a maximum age of 34 yr. Alder continued to regenerate by stump sprouting, so that individual genets may be older than the ages we determined. Aerial photographs showed that alder initially established as isolated individuals. These initial

colonizers apparently expanded to form a dense stand both by enlargement of individuals and by rapid establishment of seedlings derived from seed of initial colonizers. Individuals of poplar survived for  $\approx 100$  yr. The maximum age of poplar measured in this study was 116 yr. However, trunk rot made it difficult to age older poplar stems. Spruce colonization occurred either simultaneously or within 10 yr of alder and poplar colonization. Spruce was unique in that it continued to establish throughout succession and attained ages near 400 yr on these sites.

Alder and poplar stems sampled from the  $12 \times 12$  m clearcuts differed in age distribution, density of stems, and diameter growth. These differences indicate potentially distinct successional roles for each species. Diameter growth at both sites was significantly greater ( $P < .05$ ) in alder than in poplar (Table 5). However, density of alders decreased dramatically from the alder to the poplar site, indicating a drastic self-thinning. In contrast, densities of poplar stems did not change from the alder to the poplar site. Alder stems were considerably younger than the poplar in the poplar site. In the poplar site, alder exhibited a bimodal age distribution (Walker 1985). Field observations indicated no regeneration of alder seedlings in recent years, but vigorous stump sprouting helped maintain a wide age distribution of alder stems. In contrast, the poplar stems in the poplar site were primarily from the initial decade of colonization,  $\approx 50$  yr previously. The greater longevity of poplar helps explain its predominance in later successional stages.



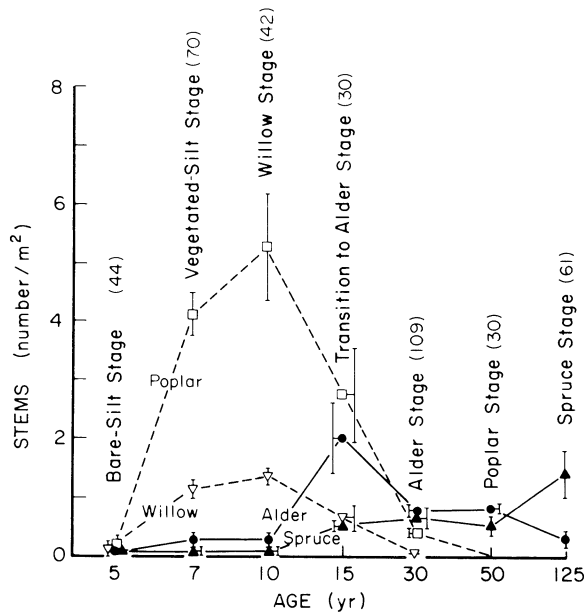


FIG. 4. Stem densities of  $\nabla$  willow,  $\bullet$  alder,  $\square$  poplar, and  $\blacktriangle$  spruce in seven successional stages, mean  $\pm$  SE. All stems  $< 2$  m tall and  $< 50$  mm dbh were recorded. Numbers of  $1 \times 5$  m quadrats sampled in each successional stage are in parentheses. Approximate age of each stage is shown across the bottom of the figure.

#### DISCUSSION

Fluvial processes are an essential stochastic component of successional change on the Tanana River floodplain. The river erodes forested banks and deposits silt bars available for plant colonization. Seasonal changes in water level control soil moisture, silt deposition, and seedling inundation and burial. Typically, flooding occurs twice yearly, during spring runoff and during midsummer when warm days melt glaciers at the river's headwaters, but flood heights are highly variable. The timing, intensity, and scale of this riverine disturbance determine the overall pattern of floodplain colonization. Life history traits of the four major species are then sufficient to explain observed patterns of successional replacement on the silt bars.

The quantity of seed available for colonization of floodplain sites by these species is primarily the result of the annual seed rain. We found no evidence of a seed bank containing these species in floodplain soils. Seeds of willow and poplar do not become incorporated into a seed bank, because they germinate within a few days after dispersal or die (Densmore and Zasada 1983). Although seeds of spruce, alder, and similar species (e.g., black spruce, paper birch) can survive for 1–2 yr (Fraser 1976, Zasada et al. 1983), the majority of these seeds germinate during the first growing season after dispersal.

Seed rain, both in terms of seed quantity and quality, varies annually and provides an additional stochastic element to controls over seedling establishment. Dur-

ing a 13-yr observation period on a site near those used in this study, four crops of white spruce seeds were greater than those reported here (41–178 viable seeds/m<sup>2</sup>). Maximum seed rain was 1480 seeds/m<sup>2</sup> (total seed rain) and 950 seeds/m<sup>2</sup> (viable seeds). For the remaining 9 yr, seed crops were equal to or less than those reported here (Zasada et al. 1978, J. C. Zasada, *personal observation*). The maximum seed rain reported for white spruce in Alaska is 4000 seeds/m<sup>2</sup> (total seed fall) and 2600 seeds/m<sup>2</sup> (viable seeds) (Zasada and Viereck 1970).

Seed production in two *Alnus tenuifolia* stands in Finland (14-yr study period) exceeded the estimates for this study in 85 and 65% of the years studied. Maximum seed production was 14 100 seeds/m<sup>2</sup> in one stand and 8600 seeds/m<sup>2</sup> in the other (Koski and Tallquist 1978).

Seed rain and periodicity of production of willow and poplar seeds have received less attention. Moore (1983) reported maximum seed rain of feltleaf willow on the Sagavanirktok River of 380 seeds/m<sup>2</sup>. J. C. Zasada (*personal observation*) estimated seed rain in *Salix repens* clones at between 8500 and 20 000 seeds/m<sup>2</sup>. Schopmeyer (1974) reported that seed production by individual *Populus* trees could be as high as 30–50  $\times 10^6$  seeds per tree. In general, very large willow and poplar seed crops occur more frequently than in spruce and at about the same frequency as alder (Schopmeyer 1974). Thus, the seed rain of our four study species is highly variable, particularly for white spruce, but the values we observed appear representative for the species.

All four species in this study were present within 5 yr of silt bar formation, although the light-seeded willow and poplar arrived at newly formed silt bars in greater numbers and established in greatest abundance. Only spruce continued to establish in later successional stages. The abundant early establishment of willow and poplar was due primarily to their high seed rain; their survivorship on untreated early successional silt sites was less than spruce and similar to alder. Due to the extremely short period of viability of willow and poplar seeds, successful establishment depends on dispersal coinciding with high but receding water levels of spring floods. This condition provides newly exposed mineral soil seed beds and the moist surface optimal for germination of poplar (Wilson 1970) and willow (Sigafos 1964, Nechaev 1967, Densmore and Zasada 1983, Moore 1983). Once established, rapid root growth anchors seedlings and reduces desiccation (Nechaev 1967) so that, following initial establishment, moisture may not strongly limit the growth and distribution of willows (Wilson 1970, McLeod and McPherson 1973). A period of several years without extreme flooding allows seedlings to become established. However, in the limited course of this study, silt deposition by floods severely restricted 1st- and 2nd-yr survivorship of willow and poplar seedlings on silt bars. Estimates of seedling establishment rates from our measurements of seed

TABLE 4. Ages of largest mature individuals of willow, alder, poplar, and spruce, obtained from growth ring counts, mean  $\pm$  SE. n.d. indicates no data available. Sample sizes are in parentheses.

Species	Successional stage				
	Vegetated-silt	Willow	Alder	Poplar	Spruce
Willow	6.7 $\pm$ 0.3 (15)	9.2 $\pm$ 1.0 (17)	Age (yr) 26.0 $\pm$ 1.8 (6)	47.0 $\pm$ 0.5 (2)	n.d.
Alder	5.0 $\pm$ 0.2 (15)	6.5 $\pm$ 0.8 (15)	20.0 $\pm$ 0.4 (9)	34.0 $\pm$ 0.0 (1)	n.d.
Poplar	5.3 $\pm$ 0.3 (17)	7.2 $\pm$ 0.2 (17)	21.4 $\pm$ 1.0 (7)	42.6 $\pm$ 2.0 (12)	101.7 $\pm$ 4.3 (8)
Spruce	5.0 $\pm$ 0.0 (6)	4.0 $\pm$ 0.0 (3)	12.9 $\pm$ 0.8 (26)	15.1 $\pm$ 1.2 (29)	128.5 $\pm$ 7.1 (22)

rain and survivorship yielded values roughly similar to observed seedling densities.

In our study and in a northern Alaskan floodplain (Moore 1983), colonization of silt bars was almost entirely by seed. However, vegetative reproduction is sometimes also important in the colonization of willow and poplar. Both species regenerate from river-borne stems that have pre-formed root primordia (Carlson 1950, Wilson 1970, Schier and Campbell 1976). These initial stands (poplar only) may then spread by root suckers (M. E. Krasny, *personal communication*). Similarly, river bars may be colonized by vegetative propagation from nearby forest stands (Dahlskog 1966).

Establishment of alder and spruce seedlings may be episodic due to variable seed production and dispersal. Alder seedlings were not common during the present study, but Van Cleve et al. (1971) found numerous alder seedlings on the Tanana River floodplain in 1968 and 1969. Alder seed dispersal is by both wind and water. Successful colonization may depend on flood waters depositing the corky seeds above frequently flooded levels. The establishment of alder-dominated stands on the silt bars may be a two-step process whereby a few initial colonizers act as seed sources for a second, denser stand. This nucleation process has been observed in postglacial (Cooper 1931) and sand dune succession (Yarranton and Morrison 1974). Sequential aerial photographs (1948–1978) suggest that alder thickets establish by nucleation on Tanana River silt bars as well.

Forest litterfall can inhibit seedling establishment (Gregory 1966). We found that removal of the forest

floor in the alder, poplar, and spruce stages improved seedling establishment. Only spruce seedlings colonized these successional stages naturally. This occurred when a year of high seed production (e.g., 1970) followed a high flood (e.g., in 1967). Under such conditions, spruce seedlings established naturally on the silt that had been deposited over the forest floor. All species were capable of germination on artificially created mineral soil seed beds in the alder, poplar, and spruce stages. However, only spruce seedlings survived, suggesting that spruce is more tolerant of reduced light, reduced soil temperatures, and increased competition (Walker and Chapin 1986).

Herbivory can strongly affect the structure of successional plant communities (Cates and Orians 1975, Snyder and Janke 1976, Whitney 1984). Moose (*Alces alces*) alter the relative abundance of willow and alder on the Tanana River floodplain by preferential browsing of willow (Wolff and Zasada 1979). In our study, which was conducted during a period of high local hare populations (J. Bryant, *personal communication*), alder thickets provided cover for snowshoe hares, which accounted for the high proportion of browsed individuals (>90% for willow) in alder thickets. The combination of low shade tolerance (Walker and Chapin 1986) and intense browsing may explain the dramatic decline in abundance of willow and poplar in the alder community. Only those poplar individuals that grew rapidly enough to remain within or above the alder canopy survived. Although spruce were also browsed by hares, they are not a preferred food item (Bryant and Kuropat 1980), and their ability to withstand limited browsing

TABLE 5. Growth parameters of alder and poplar trees in 12  $\times$  12 m clearcuts in one alder and one poplar site, mean  $\pm$  SE.

Site	Species	No. stems	Growth parameters			
			Age (yr)	Diameter (mm)	Diameter growth (mm/yr)	Stem density (no./m <sup>2</sup> )
Alder	Alder	153	13.7 $\pm$ 0.4	37.3 $\pm$ 1.5	2.7 $\pm$ 0.1	1.09
	Poplar	44	16.2 $\pm$ 0.5	35.3 $\pm$ 2.3	2.2 $\pm$ 0.1	0.31
Poplar	Alder	30	16.7 $\pm$ 1.8	44.1 $\pm$ 6.0	2.6 $\pm$ 0.2	0.21
	Poplar	49	47.4 $\pm$ 1.0	87.0 $\pm$ 5.3	1.8 $\pm$ 0.2	0.35

in alder thickets may contribute to their dominance in later successional stages.

Growth rates may also be important in explaining patterns of successional dominance (van Andel and Dueck 1982, Hibbs 1983). Among our study species, seedlings of willow and poplar had a higher potential growth rate than alder, which grew much more rapidly than spruce (Chapin et al. 1983, Walker and Chapin 1986). Despite some tolerance of flooding (Ahlgren and Hansen 1957, Lees 1964) the slow-growing spruce are often buried by flood-deposited silt on low-lying silt bars. The faster growing willow, alder, and poplar were more successful in establishing under these conditions. Adventitious roots can be produced from buried stems of willow (Densmore and Zasada 1978, Jensen 1979), alder (M. Krasny, *personal communication*), poplar (Zasada et al. 1981), and spruce (Jeffrey 1959). However, willow and poplar resprout most rapidly after flooding, because they have pre-formed root primordia in their stems to exploit the new silt layers rapidly. Although spruce seedlings grew slowly when artificially sown or planted on the silt bars, they had the highest survivorship of all species. This applied as well to the other stages where spruce seedlings were least affected by forest litter. High survivorship may be the result of a slow-growing yet stress-tolerant growth pattern (Grime 1979, Chapin 1980). These different growth patterns led to the immediate establishment of the deciduous trees but the continual establishment of spruce.

Once colonization has occurred, a combination of growth rates and longevity may explain subsequent successional changes (Fagerstrom and Ågren 1979, Hibbs 1983). In our study there was nearly simultaneous colonization by willow, alder, poplar, and spruce, with successive dominance and death, first, of the short-lived, rapid-growing willow and alder, followed by poplar, and finally the long-lived, more slowly growing spruce. We conclude that the pattern of tree and tall shrub species replacement in this primary successional sequence is adequately explained by (1) stochastic events related to flooding and seed dispersal, and (2) the life history traits of the dominant species. The extent to which this basic pattern is modified by facilitative or competitive interactions among species is examined in a companion study (Walker and Chapin 1986).

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