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THE PROCESSES CONTROLLING PRIMARY SUCCESSION ON AN ALASKAN FLOOD PLAIN

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THE PROCESSES CONTROLLING
PRIMARY SUCCESSION
ON AN ALASKAN FLOOD PLAIN

A THESIS

Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
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Fairbanks, Alaska
May 1985

THE PROCESSES CONTROLLING
PRIMARY SUCCESSION
ON AN ALASKAN FLOOD PLAIN

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ABSTRACT

Life history and competitive processes were more important than facilitative processes in controlling seedling establishment during primary succession on an Alaskan river flood plain. These experimental results contrast with the widely held assumption that facilitation is essential to primary succession.

Low soil and plant nitrogen levels in early succession are ameliorated by stands of alder associated with nitrogen-fixing bacteria. Yet seedlings transplanted into each successional stage grew least in alder stands where available nitrogen was highest. Increases in litter depth, root competition, and shade from alder limit most natural seedling establishment to river banks where alder stands have not yet formed but where mineral soil seed beds are available for germination. Colonization of the river banks is also influenced by stochastic factors such as seed production, seed dispersal, and fluctuating river levels.

Distinct growth responses of seedlings to successional changes in light, water, and nutrient regimes alter the relative dominance of species in each successional stage. Rapidly growing willow, alder, and poplar seedlings were more tolerant of flooding and silt deposition but less shade-tolerant than the slowly growing spruce. Consequently, only spruce seedlings continued to establish in later stages. Relative longevities are therefore important in explaining the succession: the short-lived willow and alder die first, followed by poplar, and finally the long-lived spruce.

Life history (regeneration, growth rate, and longevity), competitive, stochastic, and perhaps facilitative processes were important in the flood plain succession. Understanding plant succession requires examination of the role of each of these processes during establishment, maturation, and senescence phases of the life cycle of each species, rather than differentiation among complex but mutually exclusive successional models.

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INTRODUCTION

Many theories have been developed which advance different mechanisms or models of succession. Each model emphasizes certain kinds of species interactions and life history or ecosystem processes. Yet none of these models appears adequate to explain the majority of successional systems studied. In particular, there is a lack of evidence from terrestrial primary succession, and few experimental studies have been done in successional systems. This dissertation examines the successional processes that are important in determining species changes on a primary flood plain succession in interior Alaska.

Clements (1916, 1928, 1936) developed a theory that succession is a predictable series of species invasions on a site where early colonizers change the environment so that it is less favorable for themselves but more favorable for those species that follow. Clements further suggested that successional development of an ecosystem is analogous to the ontogeny of an individual organism. The end point is convergence to a predictable (monoclimax) formation (Clements 1936) within a given climatic zone, regardless of the starting point. The climax concept became a central theme in successional literature (Tansley 1920, Whittaker 1953) and was modified extensively to recognize the importance of biotic (Shelford 1932), edaphic, and topographic (Nichols 1923, Tansley 1929) influences in addition to climate. Modern proponents of this view (Margalef 1963, Odum 1969) are termed holists by Finegan (1984). They generally disregard the organismal analogy but emphasize the development of ecosystem-level properties. Terrestrial primary succession is often used as an example of this type of succession.

An alternative view of succession de-emphasizes the role of ecosystem development, focusing instead on attributes of individual species. Gleason (1926) proposed that plant associations resulted from a coincidence of migration and natural selection over a given area and time. This individualistic concept was later incorporated into Egler's suggestion (1954) that successional plant communities are determined by the initial floristic composition of the pioneer stage. Successive dominance of later species is explained by the relative longevity of each species.

Modern explanations of this reductionistic approach (Finegan 1984) have focused on a variety of life history parameters. Grubb (1977) noted the importance of the regeneration niche in determining successional patterns. White (1979) and Noble (1981) addressed the role of disturbance, while Harper and White (1974) stressed the importance of microhabitat and intraspecific variation. Others (Horn 1976, Pickett 1976) have emphasized competition as a force in structuring successional communities. Physiological traits (Bazzaz 1979, Lugo and McCormick 1981, chapter 3) may also be important in determining species replacements.

Connell and Slatyer (1977) incorporated many of these approaches into three successional models that examine the mechanisms of species interactions. Their facilitation model includes the classical Clementsian view that early colonizers improve the environment for later arrivals. Their inhibition model suggests that early colonizers dominate the resources, inhibiting later colonization. In their tolerance model neither facilitative nor inhibitory interactions are assumed for species colonization. After colonization, different processes may explain species interactions. For example, their tolerance and facilitation models suggest that competitive interactions determine the next series of species replacements whereas with their competitive inhibition model, the relative longevities of the original colonizers determines when they are replaced. Thus, these three models recognize that several types of species interactions occur at each developmental phase of a successional sequence. Despite their utility in focusing discussion, these models have led to confusion about successional mechanisms (McIntosh 1980). Terms such as facilitation, inhibition, tolerance, and initial floristic composition acquire multiple connotations when used both as names of successional processes and as names of models implying several types of species interactions.

One predictive framework for terrestrial succession that is more process-centered than previous models has been described by Noble and Slayter (1980) and Noble (1981). They group species attributes into those concerning the method of arrival or persistence of a species after a disturbance, those concerning the ability to establish and grow to maturity, and those influencing the time taken for a species to reach critical stages in its life. This last point emphasizes developmental phases, permitting identification of different successional mechanisms that occur during the life-time of a species. For example, their tolerant species can establish both immediately after a disturbance and indefinitely thereafter, intolerant species can establish only after a disturbance, and a third group of species needs some form of site enhancement before establishment is possible.

The present study addresses some of the unresolved issues in succession described above. It takes the view that succession is fundamentally a combination of several basic processes. The relevance of each process to an Alaskan flood plain succession is discussed.

The flood plain of the Tanana River was chosen because earlier studies have established the vegetation chronosequence (Viereck 1970, Van Cleve et al. 1980, Viereck et al. 1983), and the distribution of soil nutrients (Van Cleve et al. 1971, Van Cleve and Viereck 1972). Demographic aspects of dominant species (Zasada et al. 1978, Zasada and Densmore 1983) and the role of herbivory (Wolff and Zasada 1979, Bryant and Kuropat 1980) have also been examined. With this background information, the Tanana River flood plain is an ideal location to study primary succession. Only four major woody species dominate the sequence for the first 200 years. The successional communities often have only one or two dominant species and the life histories of these species are distinct.

The first chapter examines how the physical and chemical properties of the soil (particularly various nitrogen fractions) change through succession, how these changes modify plant establishment and growth, and how these changes are modified by the plants themselves. Chapter two examines the effect of seed rain, germination requirements, seedling survival, and species longevities on the successional pattern. Chapter three reports seedling responses to experimental manipulations of light and nutrient levels and discusses to what degree these responses determine the course of successional replacements. Competitive and facilitative interactions between species are also discussed. Special emphasis is placed on the role of the N-fixing alder. The first three chapters follow an experimental approach with replicate study sites within each successional stage of a chronosequence. This approach allowed analysis of variation both between and within stages, and included soil analyses, seed rain measurements, sowing experiments, transplanting of seedlings, and physiological measurements of seedling responses to shading and fertilizer. Chapter four defines and examines evidence for four kinds of processes that may be important in determining species changes in succession. Initial steps toward an examination of the relative importance of each process are suggested in light of the evidence presented in the first three chapters.

CHAPTER ONE: Soil Development

INTRODUCTION

An understanding of the process of soil development is essential to interpreting vegetation changes in terrestrial primary succession. Primary succession may be defined as ecosystem development that begins on raw parent material with no soil profile and no vegetation. One view of plant succession (Clements 1936, Odum 1969) states that vegetation development on primary substrates is an orderly progression of species whose abilities to colonize differ. According to this view, early colonizers improve the soil conditions, thereby facilitating the establishment of later colonizers. Nitrogen addition by fixation is considered critical to this process of soil development. The validity of this "facilitation" model of succession (Connell and Slatyer 1977) can be tested by documenting successional changes in soil nitrogen (N) levels and determining to what degree these soil parameters direct species replacements.

Soil development in primary succession has been described for glacial moraines (Crocker and Major 1956, Viereck 1966), lava flows (Vitousek et al. 1983), sand dunes (Olson 1958, Walker and Syers 1976, Robertson and Vitousek 1981) and flood plains (Van Cleve et al. 1971). Soil N levels are typically low in early primary successional stages (Walker and Syers 1976), presumably favoring vascular plants with symbiotic N-fixers (Stevens and Walker 1970, Walker and Syers 1976, Gorham et al. 1979) and limiting the growth of plants that lack the ability to fix nitrogen. Yet changes in levels of N that are in forms available for plant uptake have rarely been measured in primary succession (Robertson and Vitousek 1981, Vitousek et al. 1984).

This study documents changes in N levels on a primary flood plain succession on the Tanana River, near Fairbanks, Alaska. The relationship between these N levels and physical soil parameters (pH, moisture retention, particle size, and bulk density) is examined. In addition, this paper examines the influence of all these soil parameters, including N levels, on vegetation change. Trenching experiments examine the effect of eliminating plant uptake on nitrogen mineralization and nitrification.

METHODS

Study area

The study was conducted along a 10 km length of the glacially-fed Tanana River, adjacent to Bonanza Creek Experimental Forest (64° 40' N, 148° 15' W), approximately 32 km SW from Fairbanks, Alaska (Fig. 1-1). The climate of the area is strongly continental, with large annual temperature variation (- 50 to + 35 degrees C., mean - 3.5 degrees C.). The average annual precipitation is 286 mm, 30% of which falls as snow. The taiga vegetation is dominated by birch, spruce, aspen, and poplar forests and is typically underlain by permafrost except on south-facing slopes and flood plains (Viereck et al. 1983).

The successional sequence on the Tanana River flood plain (Fig. 1-2) begins with silt deposition on the inside of river meanders. Gradual aggradation of these bars due to additional silt deposits 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 within one year of silt bar formation. However, frequent flooding of the lowest silt bars often delays successful establishment. Within five years, seedlings of _Salix interior_ Rowlee, _S. alaxensis_ (Anderss.) Cov., and _Populus balsamifera_ L. are abundant. _Alnus tenuifolia_ Nutt. and _Picea glauca_ (Moench) Voss seedlings are often present but less abundant. Dense feltleaf willow (_Salix alaxensis_) stands may form on wetter soils.

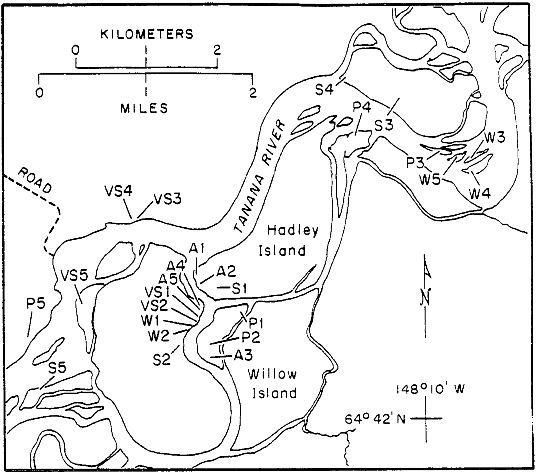
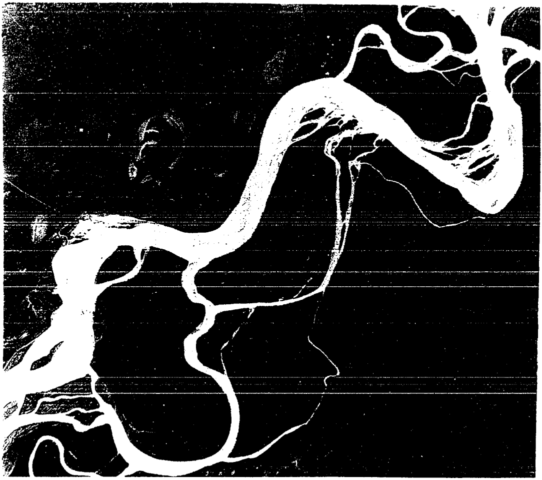


Fig. 1-1. Aerial photograph of the study area (NASA-JSC386, Roll 23 Frame 117). Five replicate study sites are located in each of five successional stages: vegetated-silt (VS1-5), willow (W1-5), alder (A1-5), poplar (P1-5), and spruce (S1-5).



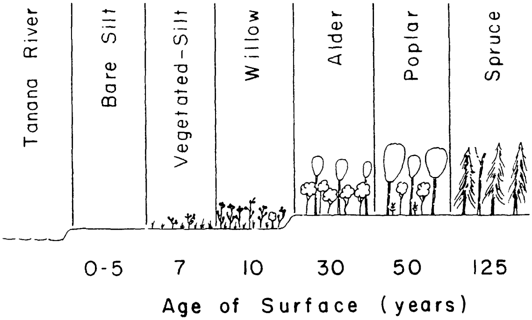


Fig. 1-2. Primary successional stages on the Tanana River flood plain in interior Alaska (modified from Viereck 1970).

Thinleaf alder (Alnus tenuifolia) thickets predominate from about 20-50 years, with balsam poplar (Populus balsamifera) as a significant component of the canopy. White spruce (Picea glauca) seedlings are sometimes common in alder thickets. Pure stands of poplar commonly predominate from about 50-100 years after initial colonization, and these stands are gradually replaced by spruce stands, which usually predominate more than 100 years after colonization (Viereck 1970, Van Cleve et al. 1980). Measurements of stand ages are discussed in chapter two.

Five replicate study sites (Fig. 1-1) were chosen in each of five successional stages. These stages were named for the dominant species and were chosen to include, where possible, seedlings of each species studied (willow: Salix alaxensis; alder: Alnus tenuifolia; poplar: Populus balsamifera; spruce: Picea glauca). The vegetation characteristics used in selecting these stages were: (1) vegetated-silt stage - plants 0.3-0.6 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^2; (4) poplar stage - a poplar canopy, more poplar than alder stems, > 1 spruce seedling/m^2 and spruce seedlings < 1 m tall; (5) spruce stage - a spruce canopy. Additional criteria emphasizing links between successional stages were used: spruce stands were required to have standing dead poplar and poplar stands were required to have dead alder stems to ensure that a true chronosequence was being studied. Vegetation types not included in this study were dry silt bars where

Salix interior was dominant and older spruce stands with no evidence of a previous poplar stage remaining. An outline of experiments for the entire study, including those reported on in later chapters, is shown in Table 1-1.

Field methods

The flood plain soils examined in this study are Typic Cryofluvents (Soil Conservation Service 1979) that are well-drained and lack permafrost. Height of the river terrace was measured at each study site on 18 September 1983, when the river gauge heights at Fairbanks and Nenana were, respectively, 130 m and 104 m above mean sea level (R. L. Burrows, United States Geological Survey, personal communication). Five replicate samples of both the forest floor and mineral soils were randomly collected from each of the 25 sites. Also sampled were five sites in the bare silt stage (mineral soil only) at the edge of the river ("time zero"). All collections were made in September 1982, and the samples were frozen at -20 degrees C. until analyzed in January 1983. Forest floor samples were obtained by pooling the O1 and O2 horizons. Mineral soils were sampled from the A1 horizon. Forest floor and mineral soil horizons were collected (excluding large roots), to a depth of 250 mm using a 64 mm diameter soil corer. The depth of each layer was measured in adjacent areas not compacted by the soil corer. Bulk densities of each horizon were obtained by dividing soil dry mass by volume. Depth, bulk densities, and N concentrations of each respective horizon were used to estimate

Table 1-1. Experiments on four flood plain species discussed in chapters one, two and three. Analyses performed and replicate stages, sites within a stage, and individuals within a site are listed.

Experiment	Stages 1)	Replicate sites per stage	Replicate individuals per site	Analyses
Soil experiments				
Forest floor	5	5	5	pH, particle size, H_2O retention, bulk density, KCl extractable NH_4 and NO_3, Kjeldahl N, soluble organic N (3 stages), N pool sizes
Mineral soil	6	5	5	same as above
Trench	2	5	3	KCl extractable NH_4 and NO_3, Kjeldahl N, N pool sizes; only in alder and poplar stages
Clearcut	2	1	5	same as above
Life history experiments				
Seed traps	5	3	4-5	water traps (willow, poplar, 5/site), screen traps (alder, spruce, 4/site)
Sowing	5	4	3-4	weekly seedling counts, survivorship, height, 1-3 sowings/species
Transects	-	-	14	stem density, height, age, herbivory, independent of study sites
Longevity	5	5	3-10	age by ring counts
Clearcut	2	1	31-79	stem counts (alder, poplar) in 12 X 12 m experimental clearings in alder and poplar stages
Physiology experiments				
Transplants 2)				
Control	5	5	4	dry mass, total N and P concentrations
Fertilizer	5	5	4	dry mass, total N and P, fertilizer applied May 1982, May 1983
Shade	3	5	4	dry mass, total N and P, only in vegetated-silt, willow and poplar stages
Clearcuts	2	1	4	dry mass, total N and P, only in alder and poplar stages
Photosynthesis	2	4	0-4	on control transplants only, vegetated-silt and alder stages

Table 1-1. (continued)

Experiment	Stages	Replicate sites per stage	Replicate individuals per site	Analyses
Physiology experiments (continued)				
Natural seedlings 3)				
Control	0-4	0-5	6-15	dry mass, total N and P, relative growth rate
Fertilizer	0-4	0-5	5-15	dry mass, fertilizer applied July 1981, May 1982, May 1983
Shade	0-2	0-5	5-15	dry mass, vegetated-silt and willow stages
Trench	2	5	4-25	dry mass, total N and P (spruce only), alder and poplar stages
Water relations	1-2	1	10	on shaded seedlings (willow, poplar), control and fertilizer (willow, poplar, spruce)
Photosynthesis	1-2	1	4-15	on control, fertilizer, and shade (willow, poplar)
Vegetation	5	5	1 plot	cover, dry mass (all vascular species) before (July 1981) and after (July 1983) fertilization and shade
Greenhouse experiments				
Fertilization and shade	-	-	2-36	5 treatments: vegetated-silt stage soil (control, fertilizer, shade), alder soil (control, fertilizer), dry mass, total N and P, P uptake
Nitrogen	-	-	8-15	3 treatments: 0, 50, 500 mg/L N on vegetated-silt stage soil

1) stages: bare silt (chapter one), vegetated-silt, willow, alder, poplar, spruce

2) willow, alder, and poplar transplants age 3 mo when planted (17 mo at harvest), spruce: 23 and 40 mo respectively

3) natural seedlings of willow and poplar (vegetated-silt and willow stages) and spruce (all stages - see Fig. 2-7), no physiological measurements done on willow stage spruce seedlings

N pool size for each of five replicate cores per site. Buried organic horizons (see Viereck et al. 1983) contributed < 2% to extractable and Kjeldahl N pools (see below) and were not included in pool size calculations because of the variability among sites in depth and number of buried horizons. Instead, it was assumed that mineral soil extended continuously from the base of the forest floor to the bottom of the 250 mm core.

To determine whether N uptake by tree roots depleted soil N pools, mineral soil samples were taken from two experimental treatments in the alder and poplar stages: trenched plots and small experimental clearcuts. Trenches were dug 0.6 m deep around ten 2 X 2 m plots, one in each of the five alder and five poplar sites. The trenches were initially dug in August 1981, lined with tar paper, and refilled. All trees and saplings were cut and removed from these plots and stump sprouts were kept pruned. In May 1983, the deteriorating tar paper was removed and replaced with two layers of 0.15 mm (6 mil) plastic. Three replicate mineral soil samples from the top 200 mm of the A1 horizon were randomly collected from each of the ten trenched plots and from adjacent, untreated controls one year after the treatment began.

One 2 X 2 m plot was located in the center of each of two 12 X 12 m experimental clearings. All trees were removed at ground level in July 1981 and subsequent stump sprouts were kept pruned. Five replicate mineral soil samples were collected from each of these two plots and from adjacent, uncleared control plots in August 1982.

Laboratory methods

Soil pH was determined on a saturation paste using a PHM64 Research pH meter. Soil particle size (% sand, silt, and clay) was determined by the hydrometer method (Day 1965). Moisture retention of saturated A1 horizon mineral soils was measured at 0.03 and 1.5 MPa tension using a ceramic pressure plate extractor (Soil Moisture Equipment Company Model #1500 and methods of Richards 1965). Instantaneous pool sizes of nitrate and ammonium in forest floor and mineral soils were determined by extraction with 2N KCl using methods outlined by Bremner and Mulvaney (1982). Extracts were done on 20 mg of freshly thawed soils but expressed on a dry mass basis. Kjeldahl nitrogen content of 20 mg air-dried soil was established by a macroKjeldahl method (Bremner and Mulvaney 1982). Soluble organic nitrogen was estimated by acid digestion (modified microKjeldahl, Bremner and Mulvaney 1982) of the KCl extracts after subtraction of extractable ammonium. Ammonium and nitrate values were estimated after extraction with an autoanalyzer using methods outlined by Technicon (Whitledge et al. 1981).

Statistical analysis

Means were compared with two-sample t-tests (Zar 1974). Nested analysis of variance (BMDP 3V, Dixon 1981) was used to compare differences among sites within a stage and differences among stages. Simple linear correlations (Zar 1974) were performed on moisture retention, nitrogen concentrations, and soil particle size. Significance was determined at the 5% level.

RESULTS

Terrace heights (Table 1-2) increased significantly ($P < 0.05$) due to silt accumulation between the vegetated silt and willow stages and between the willow stage and all later successional stages. Forest floor depths (Table 1-2) increased from the bare silt stage which had no forest floor, to the vegetated-silt and willow stages (< 10 mm), the alder and poplar stages (30-60 mm), and finally the spruce stage (10-180 mm). The forest floor depth was more variable among the five spruce sites than in earlier stages and depended upon their respective flooding histories: frequently flooded sites (flooded in the last 15 years) had a thin forest floor but several (up to five) buried organic horizons from previous forest floors. Spruce sites not flooded in the last 50 years had deeper forest floors on the surface and fewer buried organic horizons. Buried organic horizons were also present in the poplar stage. Flooding history was estimated from known rates of litterfall (Viereck et al. 1983) and dates of severe floods (L. A. Viereck, United States Forest Service, personal communication). Bulk densities (Table 1-2) of mineral soils were relatively constant among stages, while forest floor bulk densities decreased as forest litter accumulated.

The clay fraction of A1 horizon mineral soils (Fig. 1-3) was consistently < 6%. Mineral soils of the willow stage had the highest clay percentage. The sand and silt fractions varied inversely, and willow stage soils had the highest percentages of silt and lowest

Table 1-2. Terrace heights, thickness of forest floor and buried organic horizon, and bulk densities in soil profiles from six successional stages, mean ± SE. Terrace heights are heights above mean river level on 18 September 1983, n = 5. See text for terrace reference levels. Depths at which buried organic horizons occur are in parentheses. Spruce stages were categorized either as "often flooded" or "not often flooded." See text for details. Sample sizes are n = 15 for bare silt and spruce, n = 25 for all other stages. " - " indicates absence of forest floor or buried organic horizon.

						Spruce stage	
	Bare silt stage	Vegetated-silt stage	Willow stage	Alder stage	Poplar stage	Often flooded	Not often flooded
Terrace height (m)	1.11 ± 0.05	1.11 ± 0.05	1.33 ± 0.06	2.45 ± 0.19	2.70 ± 0.22	2.65 ± 0.11	2.59 ± 0.17
Forest floor thickness (mm)	-	9 ± 1	9 ± 1	50 ± 8	36 ± 2	13 ± 3	125 ± 13
Buried organic horizon thickness (mm)	-	-	-	-	20 ± 2 (78 ± 5)	46 ± 8 (113 ± 7) 35 ± 7 (269 ± 15)	-
Bulk density (g/cm^3)							
Surface forest floor	-	1.24 ± 0.10	0.86 ± 0.08	0.14 ± 0.01	0.10 ± 0.01	0.42 ± 0.07	0.17 ± 0.01
Buried forest floor	-	-	-	-	0.61 ± 0.04	0.41 ± 0.04	-
Mineral soil	1.26 ± 0.02	1.21 ± 0.03	1.14 ± 0.01	1.12 ± 0.02	1.00 ± 0.05	1.15 ± 0.04	1.04 ± 0.06

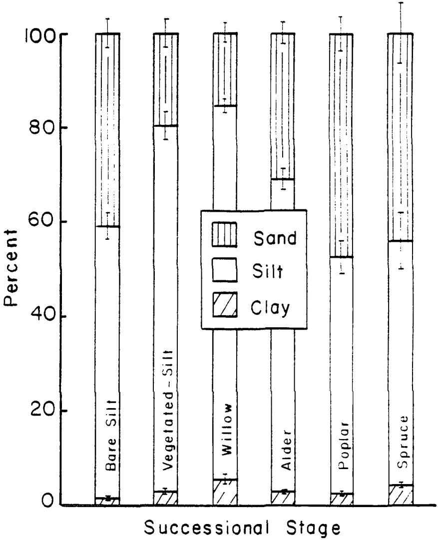


Fig. 1-3. Percentages of sand, silt, and clay in six successional stages, mean ± SE, n = 15 (bare silt), n = 25 (all other stages).

percentages of sand. Soils in the bare silt, poplar, and spruce stages were more sandy ($P < 0.05$) than mid-successional soils. Moisture retention at 0.03 MPa (Fig. 1-4) tended to be higher in the vegetated-silt and willow stages than in the bare silt and later successional stages, but this difference was not significant ($P > 0.25$) because 90% of the total variance was explained by variance among sites within stages. Only 6% of the variance was explained by differences among stages. Moisture retention at 1.5 MPa followed a similar pattern but varied less among stages. Moisture retention at 0.03 MPa was strongly correlated ($P < 0.001$) with percent silt (Table 1-3) both within and among stages. Moisture retention at 0.03 MPa was also strongly correlated within and among stages (Table 1-3) with extractable ammonium and total N concentrations (Table 1-4).

Soil pH was higher (pH 7.7-7.8) in early than in late successional stages (pH 6.6-7.4) for both mineral soils and the forest floor (Fig. 1-5). This successional decrease ($P < 0.05$) was most abrupt from willow to alder in the forest floor and from poplar to spruce in the mineral soil.

Kjeldahl N pools for forest floor and mineral soils combined (Fig. 1-6), were higher ($P < 0.05$) in alder and poplar stages than in early successional stages (vegetated-silt and willow stages). This difference, which was significant only when the highly variable N pools in the spruce stage were omitted from the nested ANOVA, resulted mostly from increased N pool sizes in the forest floors of alder and

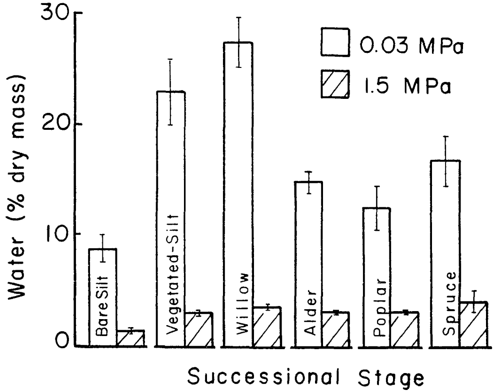


Fig. 1-4. Moisture retention of mineral soils at 0.03 and 1.5 MPa in six successional stages, mean ± SE, n = 15 (bare silt), n = 25 (all other stages).

Table 1-3. Correlation coefficients (r values) for moisture retention versus percent silt, for extractable NH_4 concentration (mg/kg) versus moisture retention, and for total N concentration (mg/kg) versus moisture retention. Correlations comparing variables with all stages treated as sone population are in the last column. Moisture retention was measured at 0.03 MPa tension. Sample sizes are in parentheses. Site means of five samples were used as individual data points in the correlation analysis. Significance levels for r are shown by symbols: NS, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

	Bare silt stage (n = 15)	Vegetated-silt stage (n = 25)	Willow stage (n = 25)	Alder stage (n = 25)	Poplar stage (n = 25)	Spruce stage (n = 25)	Among stages (n = 140)
Moisture retention versus: % silt	.77**	.79***	.77***	.91***	.88***	.82***	.76***
Extractable NH_4 versus: moisture retention	.59*	.51**	.68***	.65***	.78***	.86***	.26**
Kjeldahl N versus: moisture retention	.84***	.90***	$.32^{NS}$	.84***	.98***	.98***	.51***

Table 1-4. Extractable NH_4, extractable NO_3, soluble organic nitrogen (SON), and Kjeldahl N concentrations in forest floors and mineral soils from six successional stages, mean ± SE. Forest floors are from pooled O1 and O2 horizons. Mineral soils are from the top 200 mm of the A1 horizon. Sample sizes for extractable and Kjeldahl N are n = 15 (bare silt), n = 22 (poplar), and n = 25 for all other stages. SON sample sizes are n = 6 (willow), n = 15 (alder and spruce). n.d. = no data available. " - " indicates forest floor absent.

Soil type	N fraction (mg/kg)	Bare silt stage	Vegetated-silt stage	Willow stage	Alder stage	Poplar stage	Spruce stage
Forest floor	NH_4	-	4.3 ± 0.5	8.0 ± 1.7	64.6 ± 13.9	24.0 ± 1.3	11.5 ± 1.0
	NO_3	-	0.0 ± 0.0	0.8 ± 0.4	64.8 ± 8.6	0.07 ± 0.03	0.02 ± 0.01
	Kjeldahl N	-	1515.7 ± 146.2	2106.5 ± 321.0	9765.1 ± 1489.1	27545.3 ± 4094.3	6094.3 ± 450.4
Mineral soil	NH_4	0.7 ± 0.1	0.9 ± 0.1	0.8 ± 0.2	1.5 ± 0.1	1.6 ± 0.4	1.0 ± 0.3
	NO_3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.4	0.0 ± 0.0	0.3 ± 0.2
	SON	n.d.	n.d.	1.8 ± 0.4	4.7 ± 0.6	n.d.	4.1 ± 0.6
	Kjeldahl N	161.3 ± 25.3	27820 ± 2.0	344.4 ± 15.1	491.6 ± 27.2	425.4 ± 62.9	606.0 ± 104.9

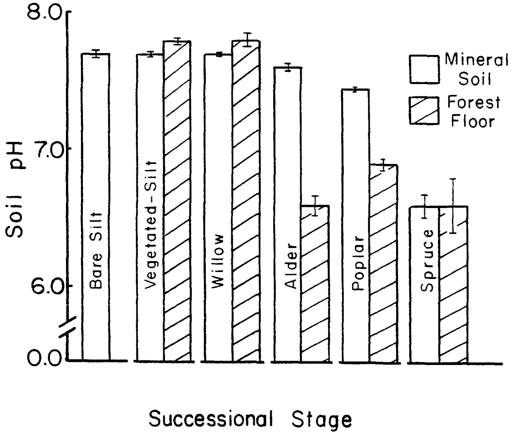


Fig. 1-5. Soil pH for mineral soil and forest floors in six successional stages, mean ± SE, n = 15 (bare silt), n = 25 (all other stages).

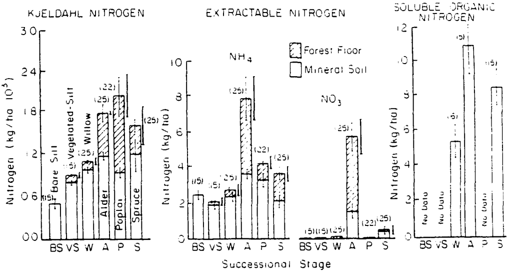


Fig. 1-6. Soil N pools in forest floor and mineral soils of six successional stages to a depth of 250 mm, mean ± SE. Nitrogen fractions include Kjeldahl N, KCl extractable NH_4 and NO_3, and soluble organic N. Successional stages are bare silt (BS), vegetated-silt (VS), willow (W), alder (A), poplar (P), and spruce (S). Note differences in scale between Kjeldahl N and the other N fractions. Forest profile depths are listed in Table 1-1. Mineral soil depths are the difference between 250 mm and forest floor depths. Buried organic horizons were not included in N pool calculations. Heavy bars are standard errors for total pool values (forest floor and mineral soil combined). Sample sizes are in parentheses.

poplar stage soils. The percentage of total variance explained by differences among sites within each stage was 63% with the spruce stage included but only 24% without the spruce stage. Stage differences accounted for 9% of the total variance with the spruce stage and 63% without the spruce stage included. Thus, most of the variance was found among sites within the spruce stage.

Pool sizes of extractable ammonium (Fig. 1-6) were higher ($P < 0.05$) in the alder stage than in early and late successional stages, again due primarily to increased N pool sizes in forest floors. Differences among sites within stages accounted for 23% of the total variance for extractable ammonium, whereas differences among stages acccounted for 20%. Extractable nitrate from the forest floor was mostly limited to the alder and spruce stages, with very low values (< 0.02 kg/ha) in the vegetated-silt, willow, and poplar stages. In mineral soils, extractable nitrate was found only in the alder and spruce stages. Soluble organic N pool sizes in mineral soils (Fig. 1-6) were often higher in alder than in willow stages, although the differences were not significant ($P > 0.05$) due to large variability within stages. More than 90% of the total variance for soluble organic N pools was explained by differences among sites within each stage. Despite high within-stage variability, these results suggest that the immediate influence of alder upon soil is to increase extractable forms of N. Extractable N thereafter declines, but total N pools remain high as N is increasingly bound in organic residues in the forest floors of the poplar and spruce stages.

Mineral soils from trenched and clearcut plots (Fig. 1-7) in the alder and poplar stages had higher ($P < 0.05$) extractable ammonium and nitrate pool sizes one year after initiation of treatment than did adjacent untreated control plots. These differences do not appear to be a result of spatial variation within each site, because within-site variation was small. Kjeldahl N tended to increase in mineral soil of trenched ($0.05 < P < 0.10$) and clearcut ($P < 0.05$) alder plots, decreased ($P < 0.05$) in clearcut poplar plots, and did not change in trenched poplar plots.

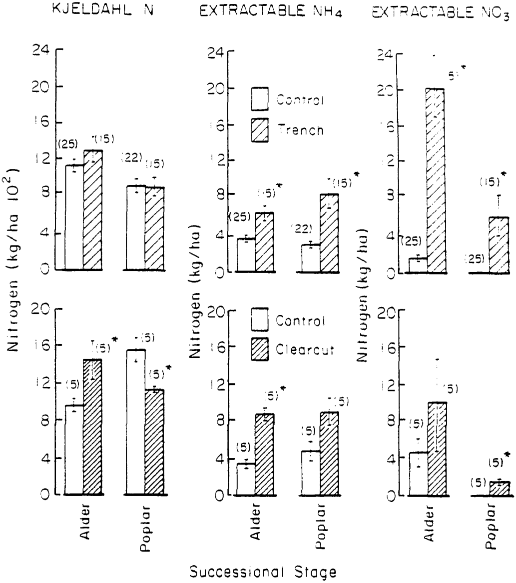


Fig. 1-7. Nitrogen pool sizes in mineral soils from alder and poplar stages as affected by trenching (top row) and clearcutting (bottom row), mean ± SE. Note difference in scales between Kjeldahl N and the extractable N fractions.

DISCUSSION

Soil development during the primary successional sequence on the Tanana River is initially controlled by physical factors (Van Cleve et al. 1980). Soil particle size is determined by the sediment load and flow rate of the river at the deposition site (Lindsey et al. 1961) and is often highly variable among successional stages. Soil moisture is affected by particle size, organic matter content, height of the terrace above water table, and seasonal changes in river levels. These factors in turn affect riparian vegetation (Viereck 1970, Johnson et al. 1976). For example, Gill (1972) found that coarse-textured point bar environments favored colonization by deep-rooted Populus balsamifera. Terrace levels on the Missouri River coincided with successive bands of even-aged Populus sargentii (Everitt 1968), while elevational gradients determine flood plain herb distributions in Wisconsin (Menges and Waller 1983). Nechaev (1971) found that intra- and inter-seasonal moisture levels (determined by terrace height above water table) controlled Salix spp. and Populus suaveolens regeneration on the Bureya River in the Priamur region of the Soviet Union.

On the Tanana River, early successional mineral soils (excluding "time-zero" soils) are characterized by small particle size and high moisture retention. These conditions should favor seed germination, provided that short periods of seed viability (Salicaceae) coincide with high water levels. Nevertheless, drought stress can occur even in these wetter stages as shown by low transpiration rates and high stomatal resistance of willow and poplar seedlings (chapter three). Distribution of seedlings did not appear to be strongly related to soil particle size on the Tanana River (M. E. Krasny, University of Washington, personal communication). As terrace levels increase from silt deposition on river flood plains, coarser sediments are often deposited (Nechaev 1971). However, soils on the Tanana River show highest sand content on unvegetated silt bars as well as on the higher terraces (i.e., the alder, poplar, and spruce stages). The combination of sandy soils and elevated terraces results in reduced moisture retention in these latter stages.

The frequency and rate of sedimentation affect riparian vegetation (Dahlskog 1966), because plant colonization is dependent on substrate stability as well as on flooding frequency and moisture availability. Rapid growth rates of roots and shoots (Nanson and Beach 1977), adventitious rooting of buried stems (Gill 1973), and dormancy during spring floods (Lindsey et al. 1961) are some of the adaptations to flood plain environments. Depth and particle size of flood sediments influence the degree of root anaerobiosis (Gill 1970), and flood plain colonizers often show high tolerance to anoxic conditions (Gill 1970, Hook and Brown 1973). Yet on the Tanana River flood plain, annual depositions of silt frequently buried seedlings in early successional stages (chapter two), indicating the importance of sedimentation in controlling plant colonization.

Nutrient availability is also initially controlled by physical factors. Van Cleve et al. (1971) reported total N pool sizes of 112 kg/ha to a depth of 150 mm depth of soil in time-zero soils. Values in the present study were 2.7 times higher (500 ± 74 kg/ha per 250 mm depth), after differences in sampling depths were accounted for. The river alluvium therefore contains substantial N when it is deposited. N fixation by blue green algae (Lawrence 1979, Buresh et al. 1980) and Hedysarum alpinum (Gill 1972) may also contribute to the N supply and may explain the increase in total N from the bare silt to the vegetated-silt stage. Ammonium was the predominant form of extractable N on the time-zero soils along the Tanana River. Rapid recycling may have made nitrate difficult to detect.

Following plant colonization, biotic influences on soil development become important (Lindsey et al. 1961, Gill 1973, Nanson and Beach 1977). Initial colonizers provide substrate stability (Wilson 1970), thereby reducing erosion. Subsequent forest floor accumulation is associated with increasing moisture retention capacity in surface layers, lower pH, and generally higher nutrient availability. Crocker and Major (1955) noted that alder litter accumulation coincided with a lowering of soil pH from pH 8.0 to pH 4.0. Soil pH also declined in the present study (pH 7.7 to pH 6.6). Extractable and Kjeldahl N pools on the Tanana River flood plain increase dramatically when N-fixing alder (Alnus tenuifolia) thickets form, approximately 15-20 yr after silt bar formation (chapter two). Van Cleve et al. (1971) reported Kjeldahl N values of 937 kg/ha per

250 mm depth of soil from a 20-year-old alder stand on the Tanana River, about a five-fold increase over time-zero soils. Krasny et al. (1984) reported 1117 kg/ha per 100 mm soil in a 15-year-old alder stand on the Tanana River, a three-fold increase from their four-year-old pre-alder stands. My study (Fig. 1-6) found similar results (1754 ± 14 kg/ha per 250 mm) in 20-year-old alder stands, a 3.5-fold increase from time zero. Extractable N pool sizes (ammonium and nitrate) also increased significantly in the alder-dominated stage. Extractable ammonium levels were 2.3 ± 0.2 kg/ha per 250 mm depths in time-zero soils as compared to 7.9 ± 1.2 kg/ha per 250 mm in alder soils. These results are again comparable to results from Krasny et al. (1984) who measured 1.3 kg/ha extractable N in a four-year-old stand and 4.9 kg/ha in a 15-year-old alder stand. This increase was mostly encountered in the developing forest floor. Organic matter is generally considered the principle source of available N (Rosswall 1976), but was not measured in this study.

Instantaneous pool sizes of nitrate were negligible except in the alder stage. Low nitrate values in early succession may be due to low substrate availability for nitrifiers, low initial populations of viable nitrifiers (Sabey et al. 1959), high pH (Alexander 1976), or leaching conditions. Alternatively, rapid recycling may result in low instantaneous pool size measurements. Low nitrate levels in later successional stages may be a result of late successional inhibition of nitrification (Rice and Pancholy 1972, Rice 1984), low substrate availability, low pH (Weber and Gainey 1962), or rapid recycling (see below). The similarity between extractable ammonium and nitrate patterns among successional stages on the Tanana River supports the idea that ammonium availability limits nitrification in all but the alder stage. Adequate moisture may limit both mineralization and nitrification, as suggested by the significant correlations between moisture retention and concentrations of both extractable ammonium and Kjeldahl N. These correlations may also reflect organic matter content of the soil which increases with successional development on the flood plain (Van Cleve et al. 1971). Increased levels of organic matter are often associated with increased moisture retention and N availability (Van Cleve et al. 1980). Moisture retention is in turn correlated with soil particle size. These data support the suggestion (Robertson and Vitousek 1981) that soil texture not only directly affects vegetation and rates of succession (Coile 1940, Odum 1960), but also influences nutrient availability.

Trenching (the prevention of nutrient and water uptake by tree roots) and clearcutting increased extractable forms of N in alder- and poplar-dominated stages. These increases suggest that prior to disturbance there is substantial uptake and recycling of N (see Vitousek et al. 1982) by alder and poplar roots. Alternatively, increased N mineralization and nitrification after disturbance could be due to increased soil moisture and temperature (Marks and Bormann 1972, Harcombe 1977), increased substrate for mineralization from root decay (Johnson and Edward 1979, Rice 1979), or reduced production of nitrification inhibitors (Rice 1984, but see Robertson and Vitousek 1981). An extensive analysis of the effects of trenching on soil nitrogen levels (Vitousek et al. 1982) concluded that the degree of nitrate loss was related to the initial N availability in the system. Low nitrate losses were associated with infertile systems. In my study, levels of extractable nitrate in the five trenched plots in the alder stage increased in proportion to extractable nitrate levels in adjacent, untrenched control plots ($r = 0.95$, $P < 0.05$). This supports the idea that sites with high nitrification rates are more susceptible to nitrate loss when disturbed. Extractable ammonium in trenched plots did not vary as closely with control levels in the alder ($r = 0.73$, $0.10 < P < 0.20$) and the poplar ($r = 0.64$, $0.20 P < 0.50$) stages. Thus, these results indicate that despite relatively high levels of ammonium, nitrate, and Kjeldahl N in the alder and poplar stages, root competition and recycling or inhibition may limit availability of N for plant use.

Phosphorus (P) may also be important in limiting growth in primary succession (Walker et al. 1981). On the Tanana River flood plain P may be limited by alkaline conditions in early succession (Van Cleve et al. 1980), by rapid recycling in the alder stands, or by acidic conditions in late successional spruce stands. The importance of P availability to species replacements in this flood plain succession remains to be studied.

Physical factors initially control both soil development and vegetation change on the Tanana River flood plain. Increases in terrace levels reduce moisture availability but also result in reduced seedling mortality from burial by flood-deposited silt. Although time-zero river alluvium contains substantial N when it is deposited, alder colonization leads to dramatic increases in N levels. Biotic influences also increase moisture retention in surface layers and lower soil pH. Root uptake and rapid recycling of large N pools in alder- and poplar-dominated soils may limit availability of N for seedling growth. Thus, physical factors affecting both soil development and plant colonization in the early stages of succession become less important as biotic influences increase with time.

CHAPTER TWO: Life History Traits

INTRODUCTION

Recent studies (Drury and Nisbet 1973, Horn 1974, Pickett 1976, Connell and Slatyer 1977, Dean and Hurd 1980) have questioned the classical explanation of succession (Clements 1916, 1928, 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, Sousa 1979, van Hulst 1979) or on life history traits such as arrival time, growth rates and longevity patterns (Glenn-Lewin 1980, Noble and Slatyer 1980, van der Valk 1981, Hils and Vankat 1982, Hibbs 1983) to explain successional change. However, critical tests of these various successional models are few. This is due in part to semantic problems in interpreting and evaluating the models and in part to the complexity of species interactions. It seems probable that there is no one model or interaction type directing any given successional pattern but rather a combination of interaction types, each one important (Collins and Quinn 1982, Turner 1983).

Current research on succession is primarily in terrestrial secondary successional systems (cf. Austin and Belbin 1981, Collins and Quinn 1982, Parrish and Bazzaz 1982a, Runkle 1982) or marine systems (Sutherland 1974, Sousa 1979) where life history traits and competition are often considered important in directing succession. Others consider facilitative interactions important in decomposer (Richardson 1980) or marine communities (Dean and Hurd 1980, Gallagher et al. 1983, Turner 1983). Studies of terrestrial primary succession are few (cf. Crocker and Major 1955, Olson 1958, Viereck 1966, 1970, Reiners et al. 1971, Smathers and Gardner 1979, 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 flood plains may be influenced by such life history traits as the reproductive habits of potential colonizers. For example, the timing of seed dispersal (Sigafoos 1964, Nechaev 1967) must coincide with receding water levels (to provide moist banks but no immediate flooding) for some species to germinate. 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 flood plain 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 flood plains.

The present study examines the degree to which life history characteristics direct a primary successional sequence on an Alaskan flood plain. The establishment patterns of four dominant woody species were examined by measuring seed rain and responses of sown seed to different surface treatments in each successional stage. These measurements show that colonization by all species occurred early in the successional sequence where the process of flooding and silt deposition strongly influenced establishment. Some seedling establishment continued throughout the sequence when flood deposition of silt provided a mineral soil surface. The relative age and longevity of each species in each successional stage support the explanation that successional replacement occurs by long-lived species remaining on a site after shorter-lived species die.

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), approximately 32 km SW from Fairbanks, in interior Alaska (see chapter one and Table 1-1 for more details).

Five replicate study sites were chosen in each of five successional stages. Four of these stages were named for the dominant species (willow: Salix alaxensis; alder: Alnus tenuifolia; poplar: Populus balsamifera; spruce: Picea glauca). The fifth stage, the "vegetated-silt" stage, was characterized by willow and poplar plants < 0.6 m tall. A "bare silt" stage (referring to the river edge or "time-zero") and a "transition" stage between willow and alder were less intensively studied. All stages included, where possible, natural seedlings of each of the four study species. Additional criteria for site selection are discussed in chapter one. At each site a 2 m high, 25 mm mesh wire fence was erected to keep snowshoe hares (Lepus americanus) from browsing seedlings. Unfenced control plots were established outside each exclosure and vegetation cover values within and outside each exclosure were compared. Table 1-1 provides an outline for all the experiments in the entire study.

Seed rain

Seed rain was measured for willow, alder, poplar, and spruce to determine the potential seed pools of each species in each successional stage. Rectangular plastic trays (0.35 m X 0.26 m X 0.08 m; Growers Supply Company, Ann Arbor, Michigan) with a surface area of 0.09 m^2 were kept filled with water to trap willow and poplar seeds. Four or five of these trays were placed on the ground in each of 15 sites (three of the five replicate sites in each successional stage 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 felt-leaf willow (Salix alaxensis) and balsam poplar (Populus balsamifera) were removed and counted every two to four days. Most willow and poplar seeds germinated in the traps, but viability tests were not done. It is reasonable to assume nearly 100% germination for Salix alaxensis under such moist conditions (Densmore and Zasada 1983).

Four square traps (0.50 m X 0.50 m; 0.25 m^2) with a screen bottom and muslin covering were located on the ground in each of the same 15 sites to trap 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 degrees C. and under continuous light. Germination was defined as 1 mm hypocotyl extension from the seed. Distance to seed source was measured at each study site as the distance to the nearest reproductive individual of each species, so that dispersal distances could be qualitatively discussed. Irregular spacing of traps from seed sources did not allow numerical analysis of dispersal distances. Seed rain was calculated for each study species from the sum of seed collected in each tray over the course of each year.

Sowing experiment

Seeds of willow, alder, poplar, and spruce were sown on natural substrates in each successional stage to measure the effect of stage on germination and seedling survival. Seeds were also sown on an artificially treated surface to measure the effects of forest floor removal on germination in each stage. Within a 25 m^2 area at each of 20 sites (four of the five described above in each successional stage), four 1 m^2 quadrats were randomly chosen and cleared of leaf litter and organic soil to provide a mineral soil ("treated") seed bed. Three 1 m^2 quadrats were chosen at each of the 20 sites 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 formed by the capillary rise of soil solution from a shallow ground water table and surface evaporation with formation of calcium sulfate and calcium carbonate salts (Van Cleve et al. 1980).

Seeds of each species were collected, cleaned, and sown as indicated in Table 2-1. Balsam poplar and willow seeds were collected at the time seed dispersal began and just prior to the first and third sowing. Seeds were stored at -10 degrees C. between the first and second sowings. White spruce and alder seeds were collected in early September. With the exception of the first sowing of white spruce, seeds of all four species were sown during the period of maximum seed dispersal for each species. Seeds for the first sowing of white spruce were stratified to simulate overwintering.

Sowing rates were based on estimates of field germination (willow 1%, poplar 5%, alder and spruce 10%) and survivorship (50%) obtained from previous studies (Ganns 1977, Densmore 1979, Zasada et al. 1983) and experience from unpublished experiments. Sowing density of willow was reduced by 50% after the first sowing due to higher than expected germination. Prior to each sowing, laboratory germination tests were conducted to obtain an estimate of viable seeds that could be used in determining the amount of seed needed for sowing. The quantity of seed for each species was determined by weighing seeds and not by counts of individual seeds.

Seedlings of all species were counted weekly, and treated seed beds were kept litter free. Seedlings from adjacent unseeded plots were subtracted from the counts to allow for seedlings from natural seed rain. When the density of seedlings was > 300 per 0.2 X 0.3 m rectangle, seedlings in three randomly selected subsamples of 0.06 m^2 each were counted and the average multiplied by 24 to estimate density

Table 2-1. Sowing date and seed densities at which seeds of each study species were sown in experimental plots.

Species	Sowing date	Seed density (viable seed/m^2)
Willow		
First sowing	6/8-10/82	48,000
Second sowing	6/17-18/82	24,000
Third sowing	6/1-8/83	24,000
Alder		
First sowing	9/22/82	3,500
Poplar		
First sowing	7/9-12/82	13,800
Second sowing	7/17/82	13,800
Third sowing	6/28/83	13,800
Spruce		
First sowing	5/24-27/82	10,100
Second sowing	9/9-10/82	10,100

in the 0.2 X 0.3 m rectangle. High seedling densities made following individuals difficult, so seasonal patterns of seedling densities were recorded. The maximum number of seedlings during the first summer after sowing was used as a measure of the ability of the site to support germination. Maximum seedling density was determined from the date during the first summer with the highest mean seedling density. Maximum seedling densities, first, and second year survivors were counted for each species/stage/treatment combination and were expressed as the percentage of viable seed sown. Seed beds with no survivors were included in the calculations. In August 1983, heights of all surviving seedlings were measured in 10 mm height classes.

Transects

Densities of natural seedlings and saplings were measured along fourteen 2 m-wide transects chosen at regular (0.8 km) intervals along the main river channel to provide seedling density estimates independent of density measurements at the primary study sites. These transects extended at least 50 m inland, perpendicular to the river course, and ended either in a mature spruce community or at a maximum distance of 300 m. Eight, 1 X 5 m quadrats were sampled along each of the 14 transects at randomly chosen intervals in each of the five successional stages (vegetated-silt, willow, alder, poplar, and spruce) that the transects encountered. 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. Seedling and sapling ages were determined by ring counts. Larger individuals were less intensively sampled (see below). The density of standing dead stems was also recorded.

Longevity

The maximum age of each species was estimated in each successional stage to test the idea that successional replacements may be primarily due to long-lived species remaining on a site when short-lived plants die. Growth rings were counted on three to ten of the largest individuals at each of the five primary study sites in each successional stage. Ages of stems > 100 mm dbh were determined with an increment borer used at stump height. Site ages were estimated from ring counts of stems, and these ages were confirmed by examination of aerial photographs of the study area taken in 1948, 1958, 1962, 1968, 1971, and 1978. Alder cover was estimated from the photographs in four cover classes (1-25%, 26-50%, 51-75%, 76-100%) at each of 10 locations near the study sites where silt bars had formed around 1940. In one alder site and one poplar site all alder and poplar stems in a 12 X 12 m area were sampled to determine the ages and densities of all individuals present.

Statistical analysis

Statistical analyses included t-tests for comparisons of means (Zar 1974) and one-way analysis of variance (BMDP 7D, Dixon 1981), which provided pairwise t-tests with Bonferroni probabilities for multiple comparisons. This method is conservative, tending to reject differences. All percentages were treated with arc-sin transformation (Zar 1974). Significance was determined at the 5% level.

RESULTS

Seed rain

The availability of alder, poplar, and spruce seeds was highest ($P < 0.05$) in the successional stage dominated by that species (Table 2-2). The availability of willow seeds was highest in the willow and alder stages in 1982 and highest in the vegetated-silt and willow stages in 1983. Most seeds of the four study species fell within 50 m of the nearest sexually mature individual of that species. Wind-dispersed willow and poplar seeds were found at greater distances from seed sources than the heavier alder and spruce seeds. However, winged spruce seeds were capable of dispersal to distances over 250 m (some spruce seeds were found 460 m from the nearest possible source) and were also found in early successional sites. Similarly, early successional willow seeds were found in late successional spruce forests. Seed dispersal of willow and poplar (Fig. 2-1) was limited to several weeks in June (willow) or July (poplar). Alder and spruce seeds (Fig. 2-1) dispersed primarily in late fall.

Water provided an alternative mode of dispersal for all four study species. Flood waters may be particularly important for dispersal of the corky alder seeds, which were observed germinating on riverbanks at the high water mark. High alder seedling mortality resulted from silt deposition by subsequent flooding, suggesting that alder establishment on early successional silt bars may be dependent

Table 2-2. Total seed rain in five successional stages in 1982 and 1983, mean ± SE, n = 12. Number of viable seeds/m^2 are shown 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 (see text). Mean values of number of seeds in each row followed by the same letter are not significantly different ($P > 0.05$).

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

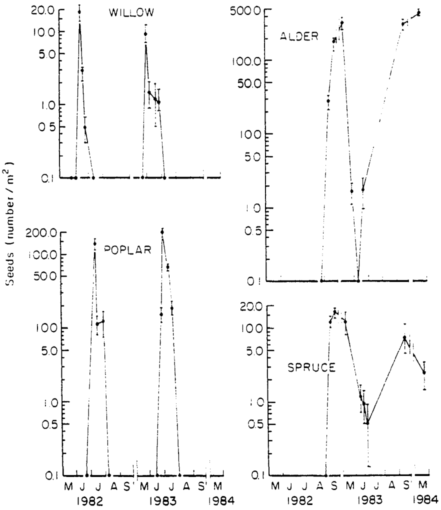


Fig. 2-1. Seasonal pattern of seed rain of willow, alder, poplar, and spruce from successional stages dominated by these species, in 1982, 1983, and 1984, mean ± SE, n = 12 seed traps. Note log scale.

on flooding followed by several years without flooding.

Sowing experiment

Seedling survivorship

Survivorship of all species sown on untreated seed beds was higher ($P < 0.05$) in early than in late successional stages. This is shown for sowing dates with the highest germination (the first sowing of willow, alder, and spruce, and the third sowing of poplar; Table 2-3), but other sowings showed the same pattern (Table 2-4). In fact, willow, alder, and poplar showed negligible establishment on untreated seed beds except in the vegetated-silt and willow stages. This pattern was true for maximum seedling densities during the first summer, for first year, and for second year survivorship. Less than 5% of the viable spruce seeds sown and < 1% of the willow, alder, and poplar seeds sown on untreated seed beds survived for two years.

On treated (mineral soil) seed beds, maximum seedling densities, first year, and second year survivorship were also generally greater in early than in late successional stages for the high germination plots (Table 2-3). However, this difference between early and late successional stages was less pronounced than on untreated seed beds. Removal of the forest floor had a dramatic effect in later stages where maximum seedling densities were usually more than ten times higher on treated seed beds than on untreated seed beds. This suggests that the forest floor inhibits germination and seedling survival in the alder, poplar, and spruce stages. This inhibition may

Table 2-3. Maximum first summer seedling densities, first, and second year survivorship for seedlings from sown seed of willow, alder, poplar, and spruce in seed beds in five successional stages. Means ± SE are from arc sin transformed data, n = 16 (untreated), n = 12 (treated). Treated seed beds had mineral soil exposed by removing the forest floor (01 and 02 layers). Untreated seed beds were left intact. Percentages of plots with survivors are shown in parentheses. Mean values in each row followed by the same letter are not significantly different ($P > 0.05$). Data are from the sowing date with the highest seedling density for each species (Table 2-4).

		Maximum first summer seedling density (% of viable seed sown)				
Species	Treatment	Vegetated-silt stage	Willow stage	Alder stage	Poplar stage	Spruce stage
Willow	Untreated	35.5 ± 3.8 a (100)	14.3 ± 4.3 b (100)	0 ± 0 c	0 ± 0 c	0.2 ± 0.1 d (58.3)
	Treated	56.6 ± 4.4 a (100)	17.0 ± 4.3 b (100)	15.5 ± 2.8 b (100)	18.4 ± 5.2 b (93.7)	16.3 ± 2.1 b (100)
Alder	Untreated	14.9 ± 5.2 a (100)	5.7 ± 2.2 a (91.7)	0 ± 0 b	0 ± 0 b	0 ± 0 b
	Treated	9.7 ± 2.2 a (87.5)	17.5 ± 7.2 a (100)	12.5 ± 2.4 a (93.7)	11.8 ± 3.7 a (87.5)	8.1 ± 4.4 a (75.0)
Poplar	Untreated	23.8 ± 2.2 a (100)	15.9 ± 3.7 a (100)	0.2 ± 0.1 b (50.0)	0.8 ± 0.2 b (100)	2.3 ± 1.0 b (75.0)
	Treated	35.5 ± 3.4 a (100)	23.2 ± 5.3 a (100)	15.5 ± 2.9 ab (100)	9.9 ± 2.0 b (100)	28.7 ± 5.4 a (93.7)
Spruce	Untreated	13.1 ± 3.2 a (100)	12.1 ± 3.3 a (100)	13.3 ± 3.4 a (75.0)	1.1 ± 0.2 b (100)	0.3 ± 0.2 b (66.7)
	Treated	26.1 ± 2.8 a (100)	11.8 ± 3.7 b (100)	2.8 ± 0.9 c (100)	8.8 ± 2.7 b (100)	1.5 ± 0.3 c (87.5)

Table 2-3. (continued)

		First year survivorship (% of viable seed sown)				
Species	Treatment	Vegetated silt stage	Willow stage	Alder stage	Poplar stage	Spruce stage
Willow	Untreated	7.2 ± 1.2 a (100)	0.4 ± 0.2 b (66.7)	0 ± 0 c	0 ± 0 c	< 0.1 c (37.5)
	Treated	5.4 ± 2.1 a (100)	0.5 ± 0.2 b (81.2)	0.6 ± 0.1 b (43.7)	1.2 ± 0.6 b (56.2)	4.2 ± 2.2 a (75.0)
Alder	Untreated	2.4 ± 2.0 a (42.0)	0.1 ± 0.1 a (25.0)	0 ± 0 b	0 ± 0 b	0 ± 0 b
	Treated	0.1 ± 0.1 a (19.0)	0.8 ± 0.6 a (44.0)	< 0.1 b (6.0)	0 ± 0 b	1.6 ± 1.2 a (50.0)
Poplar	Untreated	1.4 ± 1.0 a (25.0)	0.8 ± 0.5 a (17.0)	0 ± 0 b	0 ± 0 b	0 ± 0 b
	Treated	0.1 ± 0.1 a (25.0)	< 0.1 ab (12.5)	< 0.1 ab (25.0)	0 ± 0 b	1.9 ± 1.0 a (75.0)
Spruce	Untreated	15.2 ± 3.3 a (100)	11.1 ± 3.7 a (83.3)	0.5 ± 0.3 b (8.0)	0.5 ± 0.3 b (42.0)	0.5 ± 0.3 b (17.0)
	Treated	25.8 ± 2.1 a (100)	6.8 ± 2.7 b (87.5)	1.9 ± 0.5 c (100)	7.7 ± 2.5 b (100)	1.4 ± 0.3 c (81.0)

Table 2-3. (continued)

		Second year survivorship (% of viable seed sown)				
Species	Treatment	Vegetated silt stage	Willow stage	Alder stage	Poplar stage	Spruce stage
Willow	Untreated	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a
	Treated	< 0.1 a (6.0)	0 ± 0 a	0 ± 0 a	0 ± 0 a	0.2 ± 0.1 b (50.0)
Alder	Untreated	< 0.1 a (17.0)	< 0.1 a (8.0)	0 ± 0 a	0 ± 0 a	0 ± 0 a
	Treated	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	< 0.1 a (25.0)
Poplar	Untreated	< 0.1 a (25.0)	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a
	Treated	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	< 0.1 a (25.0)
Spruce	Untreated	4.8 ± 1.5 a (75.0)	3.2 ± 1.6 a (25.0)	0 ± 0 b	< 0.1 b (17.0)	< 0.1 b (50.0)
	Treated	4.2 ± 1.6 a (69.0)	2.3 ± 1.7 ab (44.0)	0.7 ± 0.3 b (81.0)	4.9 ± 2.0 a (100)	0.8 ± 0.3 b (67.0)

Table 2-4. Maximum seedling densities in first summer after sowing for seed sown at different planting dates on untreated and treated seed beds. Means ± SE are from arc sin transformed data, n = 16 (treated), n = 12 (untreated). See Table 2-3 for treatment explanation. Mean values within stages and treatments followed by the same letter are not significantly different ($P > 0.05$).

			Maximum first summer seedling density (% of viable seed sown)				
Species	Treatment	Planting date	Vegetated silt stage	Willow stage	Alder stage	Poplar stage	Spruce stage
Willow	Untreated	6/8-10/82	35.5 ± 3.8 a	14.3 ± 4.3 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.2 ± 0.1 a
		6/17-18/82	15.5 ± 3.0 b	0.7 ± 0.2 b	< 0.1 a	< 0.1 a	2.1 ± 0.8 b
		6/1-3/83	4.7 ± 1.5 c	0.3 ± 0.2 b	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 c
	Treated	6/8-10/82	56.6 ± 4.4 a	17.0 ± 4.3 a	15.5 ± 2.8 a	18.4 ± 5.2 a	16.3 ± 2.1 a
		6/17-18/82	13.3 ± 2.3 b	14.4 ± 5.4 a	3.3 ± 1.4 b	9.4 ± 3.2 a	15.6 ± 3.1 a
		6/1-3/82	2.9 ± 0.7 c	0.6 ± 0.4 b	0.8 ± 0.3 b	0.6 ± 0.4 b	1.4 ± 0.6 b
Alder	Untreated	9/22-23/82	14.9 ± 5.2	5.7 ± 2.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Treated	9/22-23/82	9.7 ± 2.2	17.5 ± 7.2	12.5 ± 2.4	11.8 ± 3.7	8.1 ± 4.4
Poplar	Untreated	7/9-12/82	3.1 ± 1.4 a	1.8 ± 1.0 a	0.1 ± 0.1 a	0.6 ± 0.2 a	0.7 ± 0.2 a
		7/17/82	0.5 ± 0.3 a	0.4 ± 0.2 a	0.1 ± 0.1 a	0.1 ± 0.1 a	1.4 ± 1.0 a
		6/28/83	23.8 ± 2.1 b	15.9 ± 3.7 b	0.2 ± 0.1 a	0.8 ± 0.2 a	2.3 ± 1.0 a
	Treated	7/9-12/82	1.7 ± 0.8 a	2.8 ± 1.3 a	0.5 ± 0.2 a	4.8 ± 1.0 a	1.8 ± 0.6 a
		7/17/82	0.1 ± 0.1 b	0.5 ± 0.5 b	12.5 ± 2.1 b	11.5 ± 2.8 b	16.9 ± 3.1 b
		6/28/83	35.5 ± 3.4 c	23.2 ± 5.3 c	15.5 ± 2.9 b	9.9 ± 2.0 b	28.7 ± 5.4 b
Spruce	Untreated	5/24/82	13.1 ± 3.2 a	12.1 ± 3.2 a	13.3 ± 3.3 a	1.1 ± 0.3 a	0.3 ± 0.2 a
		9/9-10/82	6.7 ± 3.0 a	3.6 ± 1.3 b	0.0 ± 0.0 b	0.0 ± 0.0 b	0.0 ± 0.0 b
	Treated	5/24/82	26.1 ± 2.8 a	11.8 ± 3.7 a	2.8 ± 0.9 a	8.8 ± 2.7 a	1.5 ± 0.3 a
		9/9-10/82	1.4 ± 0.4 b	0.1 ± 0.1 b	0.4 ± 0.2 b	1.1 ± 0.4 b	0.3 ± 0.1 b

be through allelopathic chemicals, lack of a mineral soil seed bed, or limitation of water or light. However, removal of litter and salt crust also improved seedling survival of willow, poplar, and spruce seedlings in early succession where less litter accumulated. This indicates that other factors like surface crusts or surface hydrology may affect germination and seedlng survival in early succession.

Density of willow seedlings from the first sowing date (Fig. 2-2) declined significantly ($P < 0.05$) during the first summer on both treated and untreated seed beds in the vegetated-silt and willow stages, but slight declines in the spruce stages were not significant. Significant treatment effects on willow seedling densities were only found in the spruce stage (Fig. 2-2) where density of seedlings was consistently higher ($P < 0.05$) on treated than on untreated seed beds. Density of willow seedlings in the alder and poplar stages also declined significantly ($P < 0.05$) on treated seed beds during the first summer (Table 2-5). No willow seedlings were observed on untreated seed beds in the alder and poplar stages. Inundation and silt deposition from summer floods were in part responsible for high willow seedling mortality during the summer. So, despite higher germination on early (than on late) successional seed beds, densities of willow seedlings were similar among all stages by the end of the summer.

Alder seedlings only survived on untreated seed beds in the vegetated-silt and willow stages (Fig. 2-3). They showed a more gradual increase in density than willow seedlings during the first

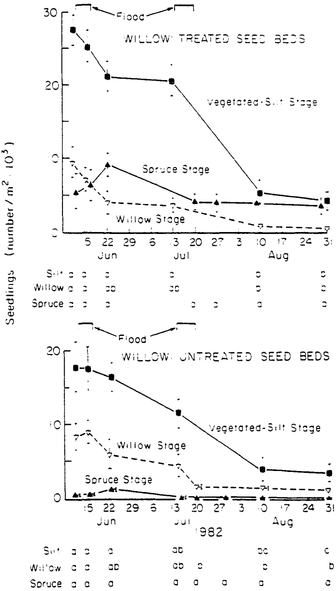


Fig. 2-2. Willow seedling densities from seed sown on treated and untreated seed beds in three successional stages, mean ± SE. Seeds were sown 8 - 10 June 1982. Sample size is n = 16 (treated), n = 12 (untreated). See Table 2-3 for treatment explanation and Table 2-5 for the alder and poplar stages. Mean values in each row followed by the same letter are not significantly different (P > 0.05).

Table 2-6. Seedling densities of the four study species in the alder and poplar stages of succession on treated and untreated seed beds, mean ± SE, n = 16 (treated), n = 12 (untreated). See Table 2-3 for treatment and letter explanations. See Fig. 2-2, 2-3, 2-4, 2-5 for the vegetated-silt, willow, and spruce stages. " - " indicates seed not sown.

			Date (1982)								
Species	Stage	Treatment	6/1	6/8	6/15	6/22	7/13	7/20	7/27	8/10	8/31
Willow	Alder	Untreated	-	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a
		Treated	-	2789 ± 451 a	8166 ± 1452 b	5761 ± 801 ab	551 ± 334 c	317 ± 184 c	150 ± 83 c	134 ± 67 c	118 ± 65 c
	Poplar	Untreated	-	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a
		Treated	-	9251 ± 1987 ab	10120 ± 1970 a	9686 ± 1937 a	2154 ± 802 bc	1737 ± 618 bc	1520 ± 518 c	1169 ± 501 bc	1319 ± 451 c
Poplar	Alder	Untreated	-	-	-	-	25 ± 17 a	25 ± 17 a	33 ± 17 a	2 ± 0.2 a	0 ± 0 b
		Treated	-	-	-	-	90 ± 33 a	319 ± 75 a	252 ± 73 a	102 ± 32 a	75 ± 27 a
	Poplar	Untreated	-	-	-	-	123 ± 33 a	40 ± 18 a	15 ± 8 a	4 ± 3 a	3 ± 3 a
		Treated	-	-	-	-	1516 ± 249 a	1157 ± 200 a	1052 ± 204 a	651 ± 154 a	716 ± 142 a
Spruce	Alder	Untreated	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	12 ± 7 b	112 ± 57 b	237 ± 130 b	247 ± 103 b	108 ± 38 b
		Treated	0 ± 0 a	0 ± 0 a	15 ± 5 b	252 ± 90 b	431 ± 134 b	437 ± 132 b	384 ± 113 b	306 ± 83 b	257 ± 72 b
	Poplar	Untreated	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	3 ± 2 b	28 ± 10 b	108 ± 23 c	72 ± 23 bc	92 ± 35 bc
		Treated	0 ± 0 a	4 ± 3 b	810 ± 250 bc	1114 ± 314 bc	1391 ± 317 bc	1359 ± 329 bc	1257 ± 334 c	1257 ± 334 bc	1097 ± 272 bc

Table 2-5. (continued)

Species	Stage	Treatment	5/24	5/31	6/7	6/14	6/21	7/5	7/19	8/16	9/7
Alder	Alder	Untreated	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a
		Treated	7 ± 5 a	137 ± 48 a	479 ± 68 b	447 ± 68 b	446 ± 63 b	105 ± 55 a	103 ± 58 a	45 ± 28 a	3 ± 3 a
	Poplar	Untreated	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a
		Treated	48 ± 20 ac	337 ± 144 abc	533 ±157 ab	445 ± 102 b	154 ± 45 abc	5 ± 3 c	20 ± 20 ac	5 ± 5 c	0 ± 0 d

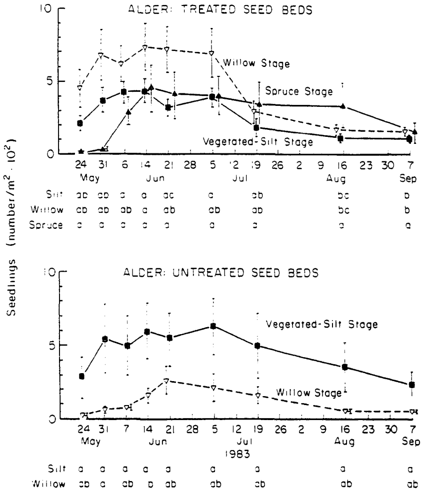


Fig. 2-3. Alder seedling densities from seed sown on treated and untreated seed beds in three successional stages, mean ± SE. Seeds were sown 22 September 1982. Sample size is n = 16 (treated), n = 12 (untreated). See Table 2-3 for treatment explanation and Table 2-5 for the alder and poplar stages. Mean values in each row followed by the same letter are not significantly different (P > 0.05).

summer after the September sowing. Although seedling densities then declined, this trend was not significant ($P > 0.05$). Alder seedlings on treated seed beds did not show significant seasonal trends in density in the vegetated-silt, willow, or spruce stages (Fig. 2-3) while seasonal trends in density were slightly more pronounced in the alder and poplar stages (Table 2-5). Densities of first summer alder seedlings were similar among stages. There was a small positive treatment effect on alder seedling densities in the willow stage.

Poplar seedlings survived in all stages on untreated seed beds but densities tended to be higher (nonsignificant) in the vegetated-silt, willow, and spruce stages (Fig. 2-4) and lowest in the alder and poplar stages (Table 2-5). Densities tended to be higher in the poplar and spruce stages on treated beds, suggesting that removal of the forest floor improves poplar seedling establishment.

The density of spruce seedlings (Fig. 2-5) did not decline significantly ($P > 0.05$) during the season as did the densities of willow. There was more variation among sites at a given date than between dates. However, a significant positive treatment effect was obtained by removal of the forest floor in the alder and poplar stages (Table 2-5). Germination occurred earlier in the summer on treated than on untreated seed beds in the alder, poplar, and spruce stages.

Within and between season differences ($P < 0.05$) in maximum seedling densities of willow, poplar, and spruce were found in the first summer following different sowing dates (Table 2-4). Survival

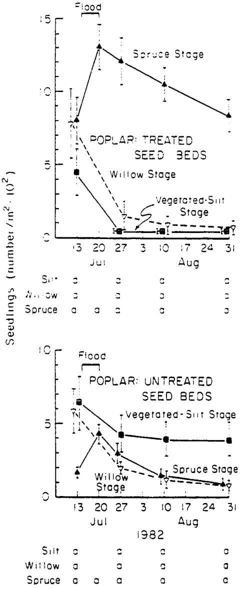


Fig. 2-4. Poplar seedling densities from seed sown on treated and untreated seed beds in three successional stages, mean ± SE. Seeds were sown 9 - 12 June 1982. Sample size is n = 16 (treated), n = 12 (untreated). See Table 2-3 for treatment explanation and Table 2-5 for the alder and poplar stages. Mean values in each row followed by the same letter are not significantly different (P > 0.05).

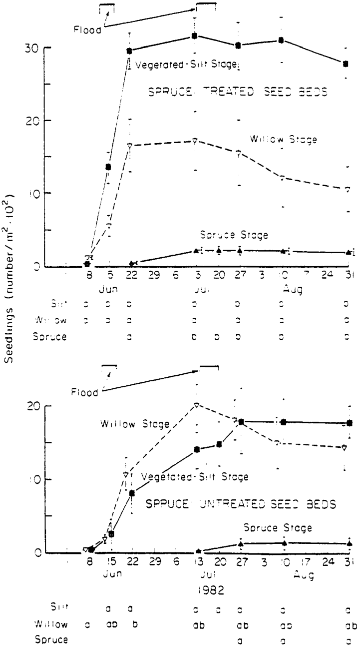


Fig. 2-5. Spruce seedling densities from seed sown on treated and untreated seed beds in three successional stages, mean ± SE. Seeds were sown 24 - 27 May 1982. Sample size is n = 16 (treated), n = 12 (untreated). See Table 2-3 for treatment explanation and Table 2-5 for the alder and poplar stages. Mean values in each row followed by the same letter are not significantly different (P > 0.05).

in the vegetated-silt and willow stages was most variable due to changes in surface moisture and silt deposition resulting from fluctuating river levels.

Seedling height

All seedlings from spring 1982 sowings that survived one year on treated seed beds grew taller in spruce sites than in vegetated-silt sites (Fig. 2-6). (First year survivorship on untreated seed beds was too low to compare.) The tall seedlings appeared healthy, and they were not etiolated. This difference in height was particularly pronounced for willow seedlings (spruce sites>>poplar sites>vegetated-silt sites). Spruce seedlings grew tallest in alder sites (alder sites>poplar and spruce sites>willow sites>vegetated-silt sites). The year or season of planting did not affect this basic pattern. The improved seedling growth may accrue from the removal of an inhibiting forest floor or may reflect the influence the forest floor had on the nutrient status of the mineral soil beneath it.

Transects

Ages of the successional stages were approximated by determining the age of largest individuals of each species at each site (see longevity). Colonization by all four study species began within five years of silt bar formation (Fig. 2-7). Willow and poplar seedlings and saplings were predominant until the transition to the alder stage, after which alder and spruce seedlings and saplings were more common. Willow stems < 50 mm dbh were not present in stands older than 30

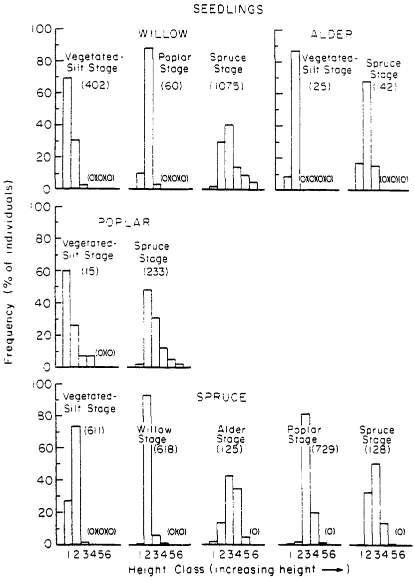


Fig. 2-6. Frequency of first year surviving seedlings of willow, alder, poplar, and spruce in six height classes in two - five successional stages. Seedlings were from seed sown on treated seed beds in 1982. Only successional stages with surviving seedlings are included. Samples sizes are in parentheses. Height classes are 1: 0-10 mm, 2: 11-20 mm, 3: 21-30 mm, 4: 31-40 mm, 5: 41-50 mm, 6: > 51 mm.

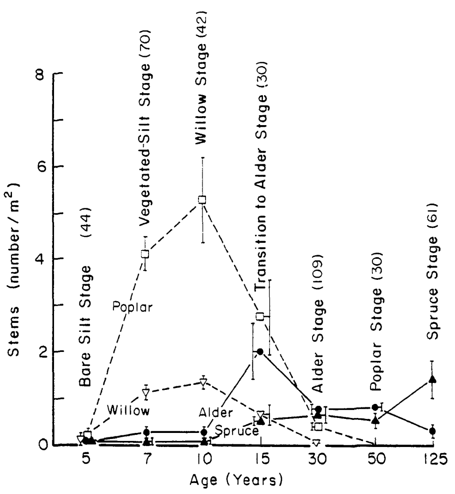


Fig. 2-7. Stem densities of willow, alder, poplar, and spruce in seven successional stages, mean ± SE. All stems < 2 m tall and < 50 mm dbh were recorded. Numbers of 1 X 5 quadrats sampled in each successional stage are in parentheses. Approximate age of each stage is shown across the bottom of the figure.

years, suggesting that the presence of willow is limited to early successional stages on this river system. Small alder stems recorded in poplar and spruce stands were all stump sprouts derived from mature individuals. No establishment of poplar seedlings was observed within mature poplar forests. This was despite successful germination of poplar on artificially exposed mineral soils (Fig. 2-4). Herbivory (see below) on young poplar seedlings or physiological factors (chapter three) may limit growth of young poplar seedlings when they do establish on exposed soils in poplar forests. Spruce seedlings were found in all stages (below). Thus, with the exception of spruce, no colonization was observed after the initial stages of succession. Initial floristic composition of the stand is therefore important in determining the successional pattern (Egler 1954).

There was little variation in age of spruce seedlings sampled from a given successional site (Fig 2-8). Seedling age was more closely correlated with terrace height ($r = 0.96$) than with age of the site ($r = 0.50$). Terraces are the result of silt deposition by floods, and flooding provides a litter-free, mineral soil surface for seedling establishment. Spruce establishment on early successional silt bars is not always successful, however, because slow-growing spruce seedlings are unable to survive burial by silt during major floods. Spruce establishment in later successional stages is dependent on silt deposits providing a mineral soil surface. For example, a 1967 flood followed by a large spruce seed crop in 1970 (Zasada et al. 1978)

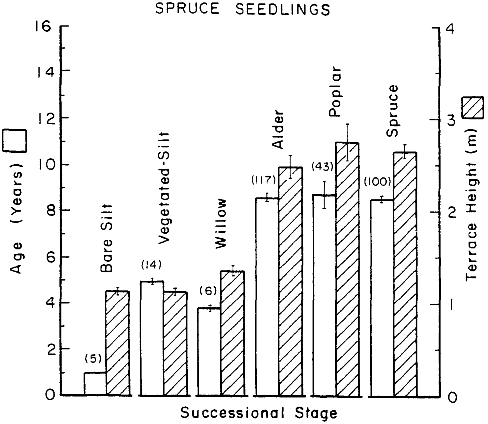


Fig. 2-8. Spruce seedling ages and terrace heights in six successional stages, mean ± SE. Samples sizes of ages are in parentheses. Samples sizes of terrace heights is n = 5. See text for terrace reference level. Terrace height data are also reported in Table 1-2.

resulted in numerous spruce seedlings establishing in later successional stages. The periodicity of white spruce seed production further limits natural spruce regeneration.

Herbivory

All four study species were browsed heavily by snowshoe hares (Fig. 2-9). Browsing was predominantly in mature alder thickets which provide cover for the hares. Willow, poplar, and spruce stems all received a higher percentage of browsing than alder in these heavily browsed alder stands. Further, willow was more heavily browsed in alder than in willow stands and spruce was more heavily browsed in alder than in spruce stands. This selection for less abundant plant species may accelerate successional transitions. Highest densities of dead stems (Fig. 2-10) were also found in mature alder thickets, suggesting that herbivory may contribute to the significant ($P < 0.05$) decline in live willow and poplar stem densities in the alder stage (Fig. 2-7). Thus, hare damage may be important in preventing natural regeneration and limiting longevity of the four study species.

Longevity

Ages of the largest mature individuals of each species in each successional stage indicate nearly simultaneous arrival of all species except spruce (Table 2-6). 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 very soon after the willow. Individual alder stems

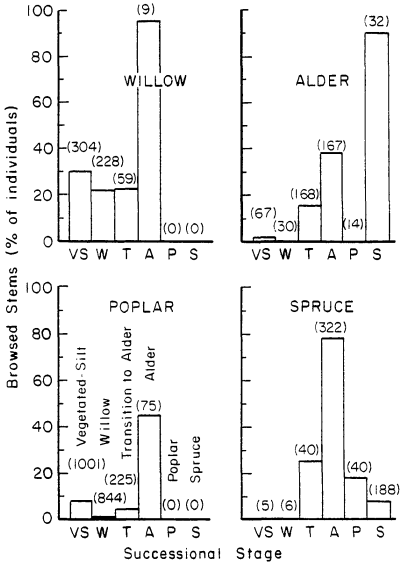


Fig. 2-9. Browsed stems of willow, alder, poplar, and spruce in six successional stages. Browse from hare (Lepus americanus) and moose (Alces alces) was combined. All stems < 2 m tall and < 50 mm dbh were combined. Total numbers of stems (browsed and unbrowsed) are in parentheses. Successional stages are vegetated-silt (VS), willow (W), transition to alder (T), alder (A), poplar (P), and spruce (S).

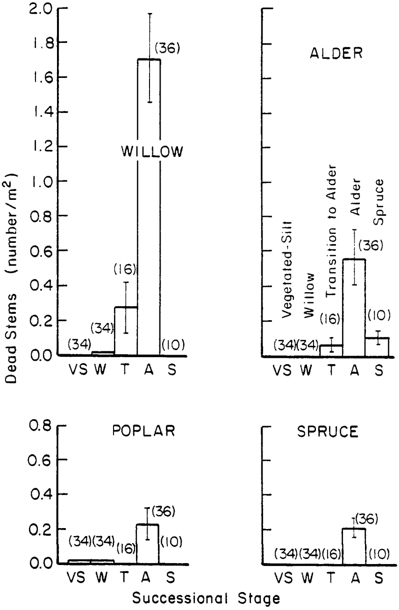


Fig. 2-10. Standing dead stems of willow, alder, poplar, and spruce in five successional stages, mean ± SE. Numbers of 1 X 1 m quadrats sampled in each successional stage are in parentheses. See Fig. 2-9 for successional stage abbreviations. No dead stems were found in the poplar stage.

Table 2-6. Ages of largest mature individuals of willow, alder, poplar, and spruce, obtained from growth ring counts, mean ± SE. n.d. indicates no data available. Sample sizes are in parentheses.

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

lived for about 25 yr, with a maximum age of 34 yr (see below). Alder continued to regenerate by stump sprouting, so that individual genets may be older than the ages I determined. Examination of aerial photographs indicated gradual increases in alder cover (Fig. 2-11). This may be both from stump sprouting and from establishment of seedlings derived from seed of initial colonizers. Individuals of poplar survived for about 100 yr. The maximum age of poplar measured in this study was 116 yr; however, trunk rot (Viereck et al. 1983) 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.

Alder and poplar stems sampled from the 12 X 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 was significantly greater ($P < 0.05$) in alder than in poplar (Table 2-7). However, density of alders decreased dramatically from the alder to the poplar stage, indicating a drastic self-thinning. In contrast, densities of poplar stems did not change from the alder to the poplar stage. Alder stems were considerably younger than the poplar in the poplar site. In the poplar site, alder exhibited a bimodal age distribution (Fig. 2-12). Field observations indicated no sexual regeneration of alder seedlings in recent years. Instead, vigorous stump sprouting occurred,

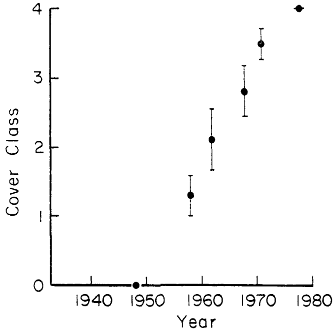


Fig. 2-11. Estimates from aerial photographs of percent alder cover on silt bars formed around 1940, mean ± SE, n = 10. Cover classes are 1: 1-25%, 2: 26-50%, 3: 51-75%, 4: 76-100%.

Table 2-7. Growth parameters of alder and poplar trees in clearcuts in one alder and one poplar site, mean ± SE. Sample sizes are in parentheses.

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

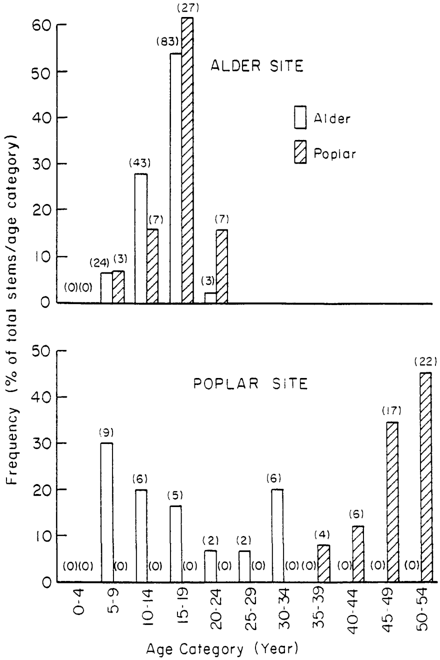


Fig. 2-12. Age distribution of alder and poplar trees in one alder and in one poplar site as determined by sampling of all stems in a 12 X 12 m area. Sample sizes are in parentheses.

maintaining a wide age distribution of alder stems. The oldest stems probably represent a generation of stump sprouts from the original colonizing stems which have since decayed. In contrast, the poplar stems in the poplar site were primarily from the initial decade of colonization, about 50 years ago. Thus, the greater longevity of poplar helps explain its predominance in later successional stages.

DISCUSSION

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

All four species in this study arrived within five years of silt bar formation. Only spruce continued to establish in later successional stages. Seed production, seed dispersal, seed longevity, and seedling mortality distinguished their respective colonization patterns. Wind-dispersed willow and poplar seeds often arrived at newly-formed silt bars in greater numbers than the heavier alder and spruce seeds. Despite a shorter dispersal time, short (7-14 d) seed viability (Densmore and Zasada 1983), small seed reserves, and high seedling mortality, germination and initial seedling growth of willow and poplar were frequent on the silt bars. This is in part due to the almost immediate germination of these two species, along with rapid root growth, which anchors the seedlings and reduces desiccation (Nechaev 1967). Due to the extremely short period of viability of willow and poplar seeds, successful establishment is dependent on the coincidence of dispersal times with high but receding water levels. This condition provides newly exposed mineral soil seed beds and the moist or temporarily flooded surfaces optimal for germination of poplar (Wilson 1970) and willow (Sigafoos 1964, Nechaev 1967, Moore 1983, Densmore and Zasada 1983). McLeod and McPherson (1973) found that once established, willows did not have a high moisture requirement, but that willow distribution in Oklahoma was limited by adequate moisture for seed germination. A period of several years without flooding allows seedlings to establish. However, in the limited course of this study, silt deposition by floods severely restricted first and second year survivorship of willow and poplar seedlings on silt bars.

Vegetative reproduction may sometimes be a more successful method of colonization for willow and poplar. Both species may regenerate from river-borne stems that have pre-formed root primordia (Carlson 1950, Schier and Campbell 1976). Bliss and Cantlon (1957) noted few seedlings of Salix alaxensis on the gravel bars of the Colville River in arctic Alaska, but numerous examples of vegetative propagation of willow from river-borne soil clumps. In contrast, Moore (1983) found S. alaxensis establishment along the Sagavanirktok River, also in arctic Alaska, was primarily from seed. Wilson (1970) found sand bar colonization by *Populus deltoides* in South Dakota was primarily from root suckers. Water tables at 100-200 mm depths were not adequate for seeds that needed constant moisture for 14 days after dispersal. Vegetative propagation may also be important in the colonization of narrow bars from nearby forest stands (Dahlskog 1966). M. E. Krasny (University of Washington, *personal communication*) found that *Populus balsamifera* produced numerous root suckers on some sites along the Tanana River. However, nearly 100% of the plants sampled in this study originated from seed.

Both alder and spruce are normally dispersed in the fall and germinate in the spring. Their seeds were less numerous than willow and poplar seeds during this study, but are larger and viable for longer periods (about 12 months; J. C. Zasada, United States Forest Service, *personal communication*) allowing germination and seedling growth to occur when microsite conditions (particularly water levels) are favorable. Yet establishment of alder and spruce seedlings may be more episodic due to more variable seed production and dispersal. Alder seedlings were not common in the present study, but Van Cleve et al. (1971) found numerous alder seedlings on the Tanana River flood plain 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. Cooper (1931) has suggested this process of nucleation may be important in post-glacial succession. Yarronton and Morrison (1974) observed it on sand dune succession. Evidence from aerial photographs of the gradual increase in density of alder on the Tanana River silt bars suggests that nucleation occurs in this system as well.

Spruce seed production has large annual variation (Zasada et al. 1978, Zasada 1980). Germination of spruce was comparable to germination of other species in this study but seed rain was lower. Establishment may be significant only in mast years. Vegetative reproduction is not important for spruce or alder colonization, but stump sprouting may extend the life of alder stands (L. Huenneke, Stanford University, personal communication).

In addition to the temporal changes in availability of water and seeds, spatial heterogeneity of seed beds may affect colonization patterns. A surface crust of calcium salts was found on early successional silt bars. Its distribution was not uniform, and its thickness depended on time elapsed since flooding. Artificial removal of the crust resulted in greater germination of willow, poplar, and spruce seeds. The surface crust may inhibit germination mechanically by keeping seeds from ground water or by osmotic or chemical inhibition (Van Cleve et al. 1980).

Forest litterfall has been found to inhibit seedling establishment (Gregory 1966). I found that artificial 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 spruce are the most tolerant of reduced light, reduced soil temperatures, and increased competition (chapter three). Yet spruce seedlings may be sensitive to soil drought and overheating on mineral soil beds (Ganns 1977). Studies in upland sites in interior Alaska have also shown that mineral soil seed beds have more favorable soil temperature and soil moisture conditions than organic horizons for germination of _Salix_ _alaxensis_ and _Populus_ _balsamifera_ (Zasada et al. 1983), and _Picea_ _glauca_ (Zasada and Gregory 1969). Litter in the vegetated-silt and willow stages on the Tanana River was not thick enough to impede seedling establishment.

Herbivory is a factor affecting the structure of successional plant communities (Cates and Orians 1975, Snyder and Janke 1976, Whitney 1984). Moose (_Alces_ _alces_) may alter the relative abundance of willow and alder on the Tanana River flood plain by preferential browsing of willow (Wolff and Zasada 1979). In my study, which was conducted during a period of high local hare populations (J. Bryant, University of Alaska, _personal_ _communication_), alder thickets provided cover for hares (_Lepus_ _americanus_). Preferential browsing of the early successional willow stems (Bryant and Kuropat 1980) hastened their decline. Larger and older willow stands have been observed on the Kobuk River in Alaska (J. C. Zasada, United States Forest Service, personal communication), perhaps indicating less severe browsing or less competition from other species. Hares also graze young seedlings of willow and poplar in the alder, poplar, and spruce dominated stages. Thus, in combination with litter, hares effectively prevent stand regeneration. However, willow and poplar are sometimes able to establish in spite of heavy browsing (L. A. Viereck, United States Forest Service, personal communication). Further, in the absence of browsing, establishment of willow, alder, or poplar in the alder, poplar, and spruce stages, is unlikely, even if mineral soils are available, due to physiological restraints (chapter three). Although spruce are also browsed by hares, they are not a preferred food item and their ability to withstand some browsing in alder thickets may contribute to their dominance in later successional stages.

Growth rates may be important in explaining density patterns of successional species (Andel and Dueck 1982, Hibbs 1983). Because of the early arrival of all major species in my study, differences in growth rates influenced the pattern of successional change. For example, growth rates (chapter three) were important on the Tanana River flood plain in determining seedling survival on the frequently flooded silt bars. Despite some tolerance of flooding (Ahlgren and Hansen 1957, Lees 1964) the slow-growing spruce were 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 (J. C. Zasada, United States Forest Service, personal communication), poplar (Schier and Campbell 1976, Zasada et al. 1981), and spruce (Jeffrey 1959). However, willow and poplar appear to be better adapted than alder and spruce to the early flood plain environment because they have pre-formed root primordia in their stems to rapidly exploit the new silt layers (see above). Yet, when artificially sown or planted on the silt bars, spruce seedlings had the highest survivorship of all species. This applied as well to the other stages where spruce seedlings were least affected by forest litter. This high survivorship may be the result of a slow-growing yet stress-tolerant growth pattern (Grime 1979, Chapin 1980). These 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 the pattern of successional changes observed (Fagerstrom and Ågren 1979, Hibbs 1983). In this study there was nearly simultaneous colonization by willow, alder, poplar, and spruce, with successive dominance and death of, first the short-lived, rapid-growing willow and alder, followed by poplar, and finally the long-lived spruce. This sequence is adequately explained by differences in growth rates and longevity.

Facilitation of the establishment and growth of late successional species by early colonizers is a commonly held tenet for primary successional systems (Connell and Slatyer 1977). If any facilitative interactions occurred in this study they did not fit the classical description of facilitation, in which the presence of a colonizing species is required to make the environment favorable for species that follow. Instead, in this study all species established only on early successional mineral surfaces or flooded later successional forest floors. More important to understanding the sequence are the "accidents of dispersal" emphasized by Crocker and Major (1955) for post-glacial succession. Plant establishment is influenced by the interaction of abiotic factors such as sedimentation, flooding, and erosion (Bliss and Cantlon 1957) with biotic factors such as seed production, seed arrival times and germination requirements.

Once plants are established, the successional sequence is adequately explained by plant growth rates, herbivory, and longevity. To the extent that early successional species affect the establishment of later successional species, they appear to inhibit rather than facilitate their establishment. For example, alder thickets provide cover for herbivores and produce litter that inhibits germination. However, it is possible that species interactions occur that do facilitate seedling establishment. For example, the early colonizers willow and poplar are often deep-rooted. They may stabilize the silt bars (Jensen 1979), reducing erosion and facilitating colonization by spruce and alder. Further studies (chapter three) evaluate the degree to which facilitation of plant growth and competition modify species interactions subsequent to the establishment phase. Annual variability is high in seed production, seed dispersal, seed germination, river levels, and terrace formation. Therefore, studies of greater duration will be needed to verify the basic pattern that has been described here.

CHAPTER THREE: Seedling Physiology

INTRODUCTION

The mechanisms by which successional communities replace each other in time are not well understood (McIntosh 1981, Finegan 1984). Some authors (Margalef 1968, Odum 1969, 1971, 1981) support the classical view (Clements 1928, 1936) that early successional species "improve" the environment, thereby facilitating the establishment and growth of later arrivals but simultaneously making conditions more difficult for their own regeneration. Alternatively, colonizers may inhibit subsequent colonization by other species by pre-empting the resources of a particular site (Niering and Goodwin 1974, Harcombe 1977, van Hulst 1979). In this scenario, succession is delayed until the colonizers die. A third alternative is the absence of facilitative or inhibitory interactions between successional species. Evidence for this view (Noble 1981, Hils and Vankat 1982, Hibbs 1983, Uhl and Jordan 1984) suggests that successional replacement occurs primarily from the different arrival times, growth rates, and longevities of the species involved.

Studies supporting the view that early colonizers competitively inhibit later arrivals have found annuals inhibiting perennials (Keever 1950, Brown and Roti 1963, McCormick 1968, Parenti and Rice 1969, Abul-Fatih and Bazzaz 1979, Hils and Vankat 1982), shrubs resisting invasion by trees (Niering and Egler 1955, McCormick 1968, Webb et al. 1972, Niering and Goodwin 1974), and early successional marine colonizers resisting invasion by later colonizers (Sutherland 1974, Sousa 1979). The mechanisms by which successional replacement is resisted may be through root competition (Korstian and Coile 1938, Lutz 1945, Shirley 1945), shading (Bray 1956, Westman 1968, Oliver and Stephens 1977, Hibbs 1982), allelopathy (Whittaker 1970, Rice 1974, 1984), or pre-emption of colonizable surfaces such as intertidal rocks (Sousa 1979) or mineral soils in forests (Gregory 1966, chapter two) or abandoned fields (Keever 1950, Parenti and Rice 1969, Connell and Slatyer 1977).

Studies of terrestrial primary succession (Crocker and Major 1955, Olson 1958, Lawrence 1979, Van Cleve et al. 1980, Van Cleve and Viereck 1981) have suggested that soil improvement by colonizing nitrogen fixers facilitates the establishment and growth of later species. On the Tanana River flood plain in central Alaska, Van Cleve et al. (1971) documented the role of nitrogen-fixing alder (Alnus tenuifolia) in increasing soil nitrogen. The specific interactions of nitrogen fixers and neighboring species, however, have not been closely examined (but see Taylor 1932, 1935, Schoenike 1958, Lawrence et al. 1967, Bradshaw 1983).

Biotic interactions in primary flood plain successions are complicated by the dominant influence of such abiotic events as rapidly changing water levels, silt deposition and erosion in early succession (Viereck 1970, Nechaev 1971, Gill 1972, Johnson et al. 1976). However, successional development on flood plains proceeds more rapidly than on volcanic ash (Griggs 1933, Vitousek et al. 1983), or glacial moraine (Lawrence 1979), making it more amenable to experimental investigation.

The present study examines the interactions of alder with three other woody colonizing species (*Salix alaxensis*, *Populus balsamifera*, and *Picea glauca*) on the Tanana River flood plain to determine to what extent facilitation and competitive inhibition influence the establishment of these species. Seedlings of the four species were transplanted into each successional stage and their growth responses were compared in pre-alder, alder, and post-alder stages to test the hypothesis that alder facilitates seedling establishment. Increased growth in alder stands would suggest facilitation whereas decreased growth would suggest inhibition. Responses of naturally occurring seedlings to alder were also measured, and greenhouse experiments were performed with the same species on pre-alder and alder soils. Despite their role in increasing nitrogen availability, alder thickets inhibited establishment and growth of understory seedlings by root competition and shading. In addition, development of a thick forest floor eliminated "safe sites" for germination. Seedlings of all species were found in pre-alder sites, which contrasts with the widely held view that nitrogen fixers are necessary precursors to successional development in primary succession.

METHODS

Five replicate study sites were chosen in each of five successional stages along a 10 km length of the Tanana River in interior Alaska (64° 40' N, 148° 15' W; see chapter one and Table 1-1 for more details). The five stages and their approximate ages from the time of silt bar formation or "time-zero" (see chapter two) were: "vegetated-silt" stage (7 yr), willow stage (10 yr), alder stage (30 yr), poplar stage (50 yr), and spruce stage (125 yr). These stages were named for the dominant species and were chosen to include, where possible, naturally occurring seedlings of each species studied (willow: *Salix alaxensis*; alder: *Alnus tenuifolia*; poplar: *Populus balsamifera*; spruce: *Picea glauca*). Not all sites contained seedlings of all four study species. Spruce stands with standing dead poplar and poplar stands with old alder stems were chosen to ensure that a true chronosequence was being studied. At each site a 2 m high, 25 mm mesh wire fence was erected to keep snowshoe hares (*Lepus americanus*) from browsing on natural and transplanted seedlings.

Physiological responses of transplanted and naturally occurring seedlings to pre-alder, alder, and post-alder stages were used to asses the influence of alder. Response of seedlings to fertilization, shading, and trenching (to remove root competition) were experimentally demonstrated in field experiments and complemented by similar experiments in a greenhouse. Seedling concentrations of nitrogen and phosphorus, photosynthetic rates, water potential, and transpiration were also measured. An outline of experiments is shown in Table 1-1.

Transplants

Seedlings from locally collected flood plain seed were grown in a greenhouse at the Alaska State Forest Nursery in Palmer, Alaska. The willow, poplar, and alder seeds were collected in May, June, and September 1981, respectively. The spruce seeds were collected in September 1977. Willow, alder, and poplar seedlings were grown for three months (April to June 1982) and spruce seedlings for 23 months (July 1980 to June 1982) in a 1:1 soilless medium of sphagnum peatmoss and coarse vermiculite at pH 5.5 for spruce and pH 6.5 for the other species. Seedlings were grown in 3 in^3 Ray Leach "Fir Cells" (willow, alder, and poplar) or 4 in^3 Ray Leach "Pine Cells" (spruce). Soluble NPK fertilizer was applied in the irrigation water (whenever watering was necessary) to willow, alder, and poplar seedlings at the rate of 100 ppm nitrogen (or 100 parts N per million parts water), 47 ppm phosphorus (P), and 83 ppm potassium (K) (NPK 20:20:20). Spruce seedlings were initially fertilized as above, but for the second year they were fertilized with 100 ppm N, 235 ppm P, and 138 ppm K (NPK 9:45:15). Natural light was supplemented (430 lux, 16 h photoperiod) until the natural photoperiod exceeded 16 h. Greenhouse temperatures were kept at 20 $\pm$ 2 degrees C.

In June 1982, 268 seedlings of each species were hardened for 10 d by placing them outside, and then transplanted (18 - 21 June) into the hare exclosures. At each study site, the seedlings were planted into mineral soil, and litter was removed weekly throughout the growing season. Within each of the fenced sites, four seedlings of each species were randomly located in a rectangular grid in each of two or three, 2 X 2 m plots, each seedling separated from its nearest neighbors by 0.5 m. Plots were then randomly assigned to the following treatments: control (5 sites X 5 stages), fertilizer (5 sites X 5 stages), shade (5 sites X 3 stages: vegetated-silt, willow and poplar stages). Eight seedlings of each species were transplanted into clearcut sites (see below).

Fertilizer plots received 50 g/m^2 (500 kg/ha) commercial fertilizer (NPK 20:10:10) containing 10.0 g N/m^2 (as ammonium nitrate), 2.4 g P/m^2 (as P_2O_5), and 4.0 g K/m^2 (as K_2O). Shaded plots had all wavelengths of light reduced by 40% with commercial shade cloth from June to September 1982 and May to September 1983. Shade cloths were not used in the alder stage because of the dense alder stems. One small, experimental clearcut was made at one alder site and at one poplar site in July 1981 by removing all trees and saplings at ground level in a 12 X 12 m area; stump sprouts appearing later were also removed. The two clearings were made in the alder and poplar stages because that is where root or light competition was expected to be most limiting. A single fenced 2 X 2 m plot was located in the center of each of the two clearings into which four seedlings of each species were transplanted. Licor-190S quantum sensors and Licor-500 integrators were used to measure incoming photosynthetically active radiation (PAR) for the vegetated-silt, alder, poplar, and spruce stages and for the clearcut plots. All measurements were taken at ground level, and PAR values were integrated over two week periods (336 h) in July and August 1981.

In August 1983, after two growing seasons in the field, surviving transplants from all treatments were harvested at ground level. Willow, alder, and poplar were separated into 1983 leaves plus stems and 1982 stems. Spruce was separated into 1983 needles plus stems and pre-1983 needles plus stems. All parts were oven-dried at 70 degrees C. for 72 h, weighed and analyzed for total N and P (Kedrowski 1983).

Dry mass of current (1983) leaves and stems was combined and analyzed for differences among sites and among stages. Nutrients were compared among stages with analyses done on two to five replicates of tissue pooled from sites within a stage. Treatment effects were expressed as ratios of dry mass of treated plants divided by dry mass of controls.

Natural seedlings

Spruce seedlings occurred naturally in all successional stages except the willow stage, but varied in age (Fig. 2-8) and size. Willow and poplar seedlings occurred naturally in the vegetated-silt and willow stages, and their ages in each stage were similar (Table 2-6). Natural seedlings occurring within the same exclosures as the transplanted seedlings (but in a different group of randomized plots) received the same fertilizer and shade treatments as the transplanted seedlings, except that both treatments began in July 1981 rather than June 1982. Relative growth rates (the natural logarithm of total dry mass minus the natural logarithm of pre-1983 dry mass divided by one year) of natural seedling controls were compared among successional stages.

To examine the effect of the proximity of alder shrubs on spruce, current-year growth of 20 naturally occurring four-year-old spruce seedlings growing within a 1 m radius of each of 10 large (> 2 m tall) isolated alder stems was compared with that of spruce seedlings growing > 2 m away from the same alder stems.

Trench experiment

An additional treatment examined the effect of root competition from overstory trees on growth of understory seedlings. To do this, one 0.6 m deep trench was dug around a 2 X 2 m plot containing natural spruce seedlings in each of the five alder and five poplar sites. The trenches were initially dug in August 1981, lined with tar paper and refilled. All trees and saplings were removed from these plots and stump sprouts were kept pruned. Due to the small area and low angle of the sun, changes in the light regime of these trenched plots were probably not affected. In May 1983, the deteriorating tar paper was removed and replaced with two layers of 0.15 mm (6 mil) plastic. Natural seedlings from all treatments were harvested in August 1983 at ground level and separated into 1983 leaves and stems and 1982 stems.

In spruce, 1982 leaves and stems were also weighed and analyzed separately. All seedlings were oven-dried and analyzed for total N and P.

Water relations

To compare fertilizer and shade treatments with controls, water relations of natural willow, poplar, and spruce seedlings at one vegetated-silt site and one alder site were measured in the early afternoon on 25 June 1983. Shade cloths were removed 0.5 h before measurements were taken. Diffusive resistance (a measure of stomatal closure) and transpiration were measured on intact leaves with a Licor steady state porometer. Xylem water potential was measured with a Scholander pressure bomb. Measurements were taken in full sunlight, and quantum readings did not vary significantly within the time of measurement for each species.

Photosynthesis

Maximum potential photosynthesis was measured between 25 June and 1 July 1983, using a 6 cm^3 cuvette for ^{14}C exposure modified from Bigger and Oechel (1982) to control temperature with a Peltier control unit. Measurements on transplants from control plots were done at 25 degrees C. in full sunlight (vegetated-silt stage) and in ambient shade (alder stage). Natural seedlings were measured in fertilized, shaded, and control plots from one vegetated-silt site. Measurements were taken on the uppermost fully expanded healthy leaf. Shade cloths were removed for at least 0.5 h before measurements began. Leaf discs from labeled leaves were placed in dimethylsulfyloxide (DMSO) and counted by liquid scintillation (P. M. Miller and W. C. Oechel, San Diego State University, unpublished manuscript).

Vegetation

In July 1981, before treatments began, and again in July 1983, prior to seedling harvests, vegetation cover values (Braun-Blanquet 1965) were estimated for each vascular species in the 2 X 2 m fertilized and shaded plots without transplants. Cover values at each site were compared between dates to detect fertilization or shade effects. Fertilization effects on dry matter production were examined in August 1983 by harvesting all living herbaceous and woody (< 2 m tall and < 50 mm dbh) plant material from control and fertilizer plots in vegetated-silt, alder, and spruce stages. All harvested material was then separated by species (combining all herbaceous species) and oven-dried at 70 degrees C. for 72 h. Fertilization effects on dry matter production were expressed as the ratio of the dry mass of fertilized plots divided by the dry mass of controls. At each study site, cover values in one 2 X 2 m unfenced control plot (located outside each exclosure) were compared to cover values in a fenced control plot.

Greenhouse experiments

Seedlings of willow, alder, poplar, and spruce were grown from local flood plain seeds in two greenhouse experiments to investigate the physiological responses of flood plain species to shade, fertilization, and different mineral soil types (alder and pre-alder) under controlled conditions. All plants were grown in flood plain soils under VHO cool bulb fluorescent lights at a 20 h photoperiod supplemented by natural light. Pot locations were randomized, and all pots were moved once every two weeks. Air temperatures were held at 20 ± 5 degrees C. Plants were watered as needed with tap water. Nutrient solutions were adjusted to pH 6.0 and were added at the rate of 50 ml per pot per week.

Fertilization and shade experiment

Seeds of flood plain willow, alder, poplar, and spruce were germinated on washed sand and watered weekly with a complete nutrient solution (Ingestad 1971) modified to contain 14 mg N/L (in an ammonium-N to nitrate-N ratio of 40 to 60). Spruce seeds were planted to germinate around 13 February 1981, alder around 14 May 1981, and poplar and willow around 20 June 1981. Seedlings were transplanted on 3 August 1981 to 1 L pots containing mineral soil from either the vegetated-silt stage or the alder stage. Seedlings were thinned to one per pot by 16 September 1981, at which point nutrient solution addition stopped and five treatments were begun: control, fertilizer, and shade on mineral soil from the vegetated-silt stage, and control and fertilizer on mineral soil from the alder stage. Fertilization was with NPK 20:20:20, diluted 1:256 (on a volume to volume basis) and was applied weekly at 50 ml per pot. The shade treatment duplicated the field experiments with a 40% light reduction. All seedlings were harvested 1-8 February 1982 and analyzed for survivorship, P absorption, dry mass of shoots and roots, and total N and P. The rate of P absorption was measured on the fine roots of each species from a solution of 0.5 mM calcium chloride and NaH_2PO_4 labeled with ^{32}P and maintained at 25 degrees C. (Chapin and Bloom 1976). The radioactivity of the roots was determined by liquid scintillation using Cerenkov radiation (Chapin and Holleman 1974). Measurements were made at two P concentrations (1 and 10 µM) to cover the probable range of P concentrations in the flood plain soil solution.

Nitrogen Experiment

In order to measure the response to different levels of N, flood plain seeds of willow, alder, poplar, and spruce were planted directly into 1 L pots containing flood plain soil from the vegetated-silt stage. Spruce seeds were planted to germinate around 18 December 1982, alder around 4 February 1983, and willow and poplar around 20 February 1983. Seedlings were thinned to one plant per pot and were watered with full strength Hoagland's minus N until treatments began on 24 March 1983. Treatments consisted of complete Hoagland's solutions and modified to have 0, 50, or 500 mg N/L, applied weekly. Seedlings were harvested 20-24 June 1983, and analyzed for dry mass of roots and shoots.

Statistical analysis

Nested analysis of variance (BMDP 3V, Dixon et al. 1981) was used to detect differences among sites and differences among stages. Student Neuman Keuls multiple range tests (Zar 1974) were then used to compare individual stages when differences were found among all stages. Covariate analysis (BMDP 1V, Dixon et al. 1981) was used to compare relative growth rates of natural seedlings, with age as the covariate. Two-way analysis of variance (BMDP 2V, Dixon et al. 1981) was used on measurements of spruce seedlings growing adjacent to alder shrubs. Paired t-tests (Zar 1974) were used to compare vegetation cover on different dates. Kruskall Wallis multiple comparisons (Conover 1980) were used to compare plant nutrient concentrations and Mann Whitney tests (Zar 1974) were used on treatment/control ratios, measurements of photosynthesis and water relations, and on the greenhouse experiments where assumptions of normality were violated. Significance was determined at the 5% level.

RESULTS

Transplants

Current-year aboveground growth of two-year-old transplanted alder seedling controls (Fig. 3-1) was significantly higher ($P < 0.05$) in the willow stage where available soil N pools were low (8.9×10^3 kg/ha; chapter one) than in the high-N alder stage (25.7×10^3 kg/ha). Twenty-seven percent of the total variance in current year alder seedling dry mass was explained by the variance among stages. Total dry mass of two-year-old alder and poplar control seedlings (Table 3-1) was significantly higher ($P < 0.05$) in early and late successional stages than in alder stages, with 28% of the total variance explained by variance among stages for both species. Alder transplants in the alder stage showed a decline in total shoot dry mass between the time of transplanting and harvest (Table 3-1). Current (Fig. 3-1) and total (Table 3-1) aboveground dry mass of willow and spruce transplant controls did not differ significantly among stages, although current-year growth of spruce tended (nonsignificantly) to be greater in the alder and poplar stages. Patterns of 1982 dry mass were similar to patterns of 1983 dry mass for all four species. Dry mass did not vary significantly ($P > 0.05$) among sites within each stage for any species. Spruce sites were most variable with 15% of the total variance explained by variance among sites. These results show that transplanted willow, alder, and poplar seedlings either had no

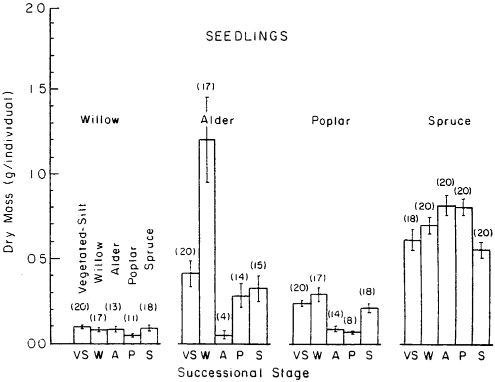


Fig. 3-1. Dry mass of current year aboveground growth of control seedlings of major flood plain species transplanted into five successional stages, mean ± SE. Samples sizes are in parentheses. Willow, poplar, and alder seedlings were 17 months old at harvest, spruce seedlings were 37 months old. Successional stages are vegetated-silt (VS), willow (W), alder (A), poplar (P), and spruce (S).

Table 3-1. Total shoot dry mass of seedlings before transplanting ("initial dry mass"), and when harvested, after two growing seasons ("final dry mass"), mean ± SE. Sample sizes (number of seedlings) are in parentheses.

		Final dry mass (g)				
Species	Initial dry mass (g)	Vegetated silt stage	Willow stage	Alder stage	Poplar stage	Spruce stage
Willow	0.19 ± 0.02 (10)	0.40 ± 0.03 (20)	0.30 ± 0.03 (17)	0.24 ± 0.03 (13)	0.24 ± 0.03 (11)	0.30 ± 0.03 (18)
Alder	0.21 ± 0.02 (10)	0.72 ± 0.12 (20)	1.77 ± 0.36 (17)	0.13 ± 0.03 (4)	0.55 ± 0.12 (14)	0.56 ± 0.11 (15)
Poplar	0.18 ± 0.02 (10)	0.43 ± 0.03 (20)	0.51 ± 0.07 (17)	0.21 ± 0.03 (14)	0.22 ± 0.03 (8)	0.37 ± 0.04 (18)
Spruce	1.53 ± 0.13 (10)	2.84 ± 0.23 (18)	2.91 ± 0.23 (20)	2.86 ± 0.14 (20)	3.09 ± 0.18 (20)	2.74 ± 0.17 (20)

differences in aboveground dry matter production across stages or less dry matter production in the high-N alder stage than in other stages. This suggests an inhibitory rather than facilitative effect of alder on these understory seedlings. Aboveground dry matter production of transplanted spruce seedlings was not significantly affected by alder during the course of this study. However, relative growth rates of natural seedlings (see below) suggest that spruce growth may be inhibited by alder.

Fertilization

The aboveground response of transplanted seedlings to fertilization indicated nutrient limitations were most pronounced in early and late succession (Fig. 3-2). Willow dry mass was significantly higher ($P < 0.05$) in fertilized than in control plots in all successional stages. Willow seedlings were most responsive to fertilization in the vegetated-silt and spruce stages. Poplar seedlings responded to fertilization most strongly in the vegetated-silt stage but also showed significant differences between the dry mass of fertilized and control transplants in the poplar and spruce stages. Alder transplants were only nutrient-limited in the vegetated-silt stage, and spruce transplants were nutrient-limited in all stages except the alder stage. Willow was most responsive to fertilization whereas spruce was least responsive.

Leaf and stem concentrations of N (Fig. 3-3) and P (Fig. 3-4) in 1983 growth of transplanted seedlings were higher ($P < 0.05$) in all

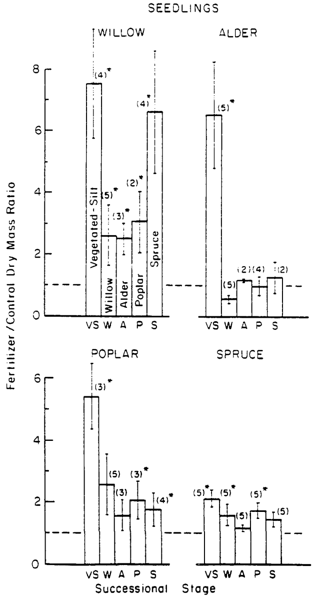


Fig. 3-2. Ratio of dry mass of fertilized to unfertilized control seedlings transplanted into five successional stagess, mean ± SE. Dry mass is from current-year tissue. Sample sizes are in parentheses and represent site ratios, obtained from four seedlings per treatment per site. * indicates a significant fertilization effect. See Fig. 3-1 for stage abbreviations.

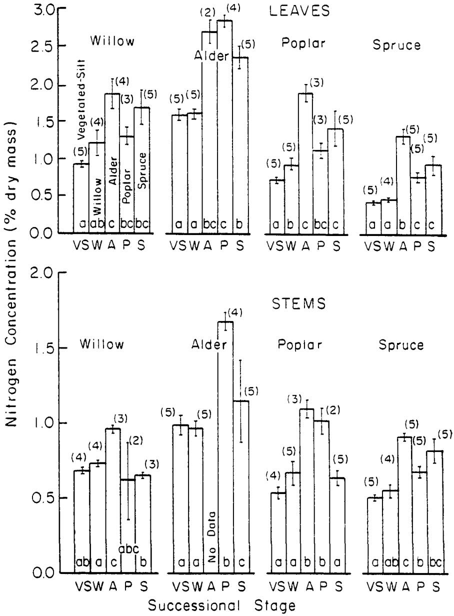


Fig. 3-3. Nitrogen concentration of current year leaves and stems of control seedlings transplanted into five successional stages (% dry mass), mean ± SE. Note difference in scale between leaves and stems. Concentrations followed by the same lower case letter within a species are not significantly different ($P > 0.05$). Sample sizes are in parentheses. See Fig. 3-1 for stage abbreviations. Leaf N concentrations before transplanting ($n = 4$) were: willow (1.73 ± 0.08%), alder (2.19 ± 0.13%), poplar (1.94 ± 0.06%), and spruce (1.32 ± 0.07%).

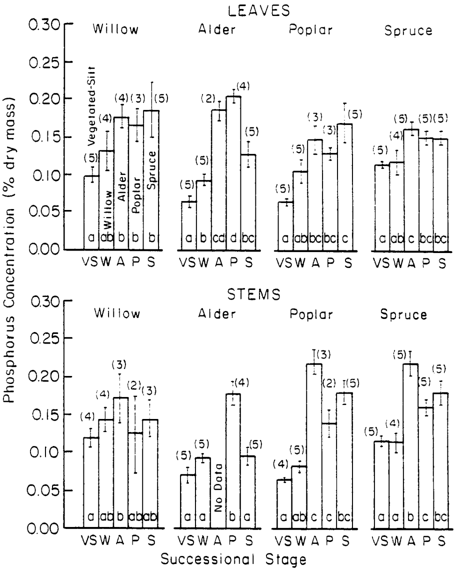


Fig. 3-4. Phosphorus concentrations of current year leaves and stems of control seedlings transplanted into five successional stages (% dry mass), mean ± SE. Concentrations followed by the same lower case letter within a species are not significantly different ($P > 0.05$). Sample sizes are in parentheses. See Fig. 3-1 for stage abbreviations. Leaf P concentrations before transplanting ($n = 4$) were: willow (0.21 ± 0.01%), alder (0.34 ± 0.02%), poplar (0.26 ± 0.01%), and spruce (0.22 ± 0.01%).

species in the alder stage than in early successional vegetated-silt and willow stages. These results suggest the transplants were responding to natural fertilization from alder by concentrating N and P (Figs. 3-3, 3-4) rather than by increased aboveground growth (Fig. 3-1). Concentrations of N and P in fertilized transplants generally did not differ from controls, suggesting growth dilution of N and P in response to fertilization in early and late succession. Willow, alder, and poplar seedlings had fertilizer-to-control ratios of N concentrations of < 1 in the vegetated-silt and willow stages. Fertilized seedlings of willow and alder had significantly lower N concentrations than controls in the vegetated-silt stage, again suggesting dilution of N by growth. Spruce transplants were the exception, with consistently higher N concentrations in fertilized 1983 leaves and stems than in control tissue (Table 3-2). This indicates a more nutrient-conserving strategy for spruce than for the three deciduous species and less mobilization of nutrients to support growth. Fertilizer-to-control ratios of N and P concentrations in spruce transplants showed a tendency to increase with successional time. In alder sites, fertilized transplants may be nutrient-saturated or have competitors for N and P that maintain transplant nutrient concentrations of fertilized individuals similar to controls.

Shade

There was a 70% attenuation of integrated PAR values from the vegetated-silt stage (average 1,420 $\mu E \cdot m^{-2} \cdot s^{-1}$) to the alder and

Table 3-2. Ratio of nitrogen and phosphorus concentrations of seedlings transplanted into fertilized plots to seedlings in unfertilized plots. Concentrations are from current year growth. Sample sizes are n = 3 to 5 sites. * indicates a significant fertilizer effect ($P < 0.05$). n.d. indicates insufficient plant tissue for analysis.

		Fertilizer/control nitrogen concentration ratio				
Species	Plant part	Vegetated-silt stage	Willow stage	Alder stage	Poplar stage	Spruce stage
Willow	leaves	0.94	1.04	1.14	1.27	1.50
	stems	0.66*	0.91	1.10	1.25	2.10*
Alder	leaves	0.82	1.04	1.03	0.92	1.10
	stems	0.71*	0.96	n.d.	0.95	1.31
Poplar	leaves	1.26	1.00	1.24	1.34	1.69
	stems	0.91	0.80	1.90*	1.06	1.78*
Spruce	leaves	1.25*	1.46*	1.55*	1.77*	2.08*
	stems	1.25	1.13	1.90*	1.68*	2.27*
		Fertilizer/control phosphorus concentration ratio				
Willow	leaves	0.83	1.10	0.80	0.96	1.49
	stems	0.60	0.75	0.75	1.22	1.35
Alder	leaves	1.51	1.38	1.11	1.18	1.34
	stems	1.24	1.19	n.d.	1.50	1.04
Poplar	leaves	1.40	1.16	1.00	1.16	1.25
	stems	1.00	1.24	1.30	1.01	1.13
Spruce	leaves	0.68	0.69	0.99	0.92	1.03
	stems	0.96	1.05	1.03	1.17	1.24

poplar stages and a 50% reduction from the vegetated-silt to the spruce stage. A 40% reduction in light from the shade cloths did not result in significantly decreased growth of transplanted seedlings when compared to unshaded controls (Table 3-3) in the vegetated-silt, willow, and poplar stages. Only N concentrations of alder seedlings in the poplar stage were significantly lower ($P < 0.05$) in shaded plants. Phosphorus concentrations of shaded willow transplants in the poplar stage and shaded alder stems in the willow stage were significantly higher than for unshaded seedlings. This suggests that these seedlings are not strongly light-limited in these stages.

Clearcuts

Clearcuts had between a 50% and 100% increase in integrated PAR values over adjacent uncut control plots. Willow, alder, and poplar (but not spruce) transplants in clearcut areas grew significantly more than controls ($P < 0.05$; Table 3-4). The lack of a response to shade and a generally strong response to fertilization suggest that increased growth in clearcut plots is more likely the result of increased soil nutrients than increased light. However, some seedlings (e.g. alder in the poplar stage) showed no response to either fertilization or shade yet did show increased growth in cleared plots. Either the response was due to a factor other than light or nutrients or to a synergism between light, nutrients, and perhaps water or soil temperature. Nitrogen concentrations of willow, alder, and poplar transplants in clearcuts did not increase significantly over controls

Table 3-3. Ratio of dry mass, and N and P concentrations of seedlings (% dry mass) transplanted into shaded plots to seedlings in unshaded plots. Data are from current year tissue. Sample sizes are n = 3 to 5 sites. * indicates a significant treatment effect. n.d. indicates insufficient plant tissue for analysis.

		Shade/control ratio		
Species	Analysis	Vegetated-silt stage	Willow stage	Poplar stage
Willow	Dry mass	0.92	1.19	0.71
	N leaves	1.12	1.20	1.31
	stems	0.91	1.12	1.16
	P leaves	1.09	1.03	1.57*
	stems	0.83	1.01	1.55*
Alder	Dry mass	1.20	0.84	0.53
	N leaves	n.d.	0.98	0.84*
	stems	n.d.	1.08	0.95
	P leaves	n.d.	1.20	0.76
	stems	n.d.	1.32*	0.83
Poplar	Dry mass	1.06	1.12	0.74
	N leaves	1.03	1.08	1.14
	stems	1.02	1.05	0.85
	P leaves	1.08	1.15	1.04
	stems	0.93	1.00	0.98
Spruce	Dry mass	1.12	1.06	0.91
	N leaves	1.03	1.26	1.22
	stems	1.05	1.10	0.99
	P leaves	0.96	1.04	1.03
	stems	1.04	1.20	1.18

Table 3-4. Ratio of dry mass of seedlings transplanted into clearcut plots to control seedlings in two successional stages. * indicates a significant clearcut effect. n.d. indicates insufficient plant tissue for analysis.

	Clearcut/control seedling dry mass ratio	
Species	Alder stage	Poplar stage
Willow	n.d.	4.8*
Alder	6.8*	2.7*
Poplar	8.3*	14.4*
Spruce	1.5	1.9

despite increases in soil N in clearcuts (chapter one). This may reflect a dilution of N and P from increased growth. Spruce transplant N and P concentrations in clearcuts tended to be higher than in controls, though this difference was not significant. Again, this suggests that spruce seedlings responded differently to changes in the environment than did the other three species.

Photosynthesis

In situ photosynthetic rates of willow, alder, poplar, and spruce transplants were all significantly lower ($P < 0.05$) in the alder stage than in the vegetated-silt stage (Fig. 3-5) due to the decreased light intensity in the alder stage. Photosynthetic rates of spruce were five to seven times less than those of willow, alder, or poplar regardless of stage.

Natural Seedlings

Spruce seedlings were found in each of the five successional stages and in most of the 25 sites. Spruce seedlings in the willow stage were found in transects (chapter two) and some of the study sites, but their densities were too low to harvest for growth measurements. Natural spruce seedling ages (Fig. 2-8) and sizes differed. Therefore, comparisons were made using relative growth rates, which account for size differences, and covariate analysis which accounts for age differences. The relative growth rate of naturally occurring spruce seedlings (Fig. 3-6) was significantly greater in the vegetated-silt stage than in the alder stage. This

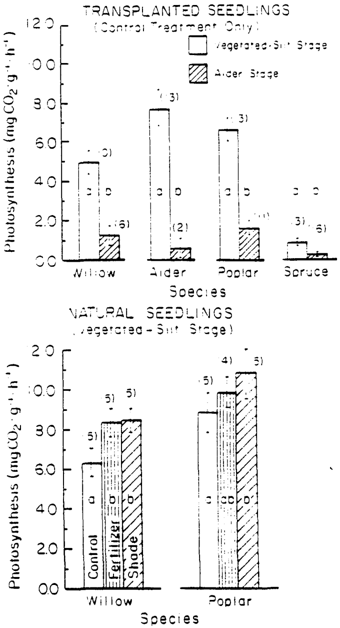


Fig. 3-5. Photosynthetic rates of control seedlings transplanted into vegetated-silt and alder stages and naturally occurring seedlings in control, shade, and fertilized plots at one vegetated-silt site, mean ± SE. Measurements were taken between 25 June and 1 July, 1983, in full sunlight (vegetated silt stage) and ambient shade (alder stage) at 25 degrees C. Measurements followed by the same letter within a species are not significantly different ($P > 0.05$).

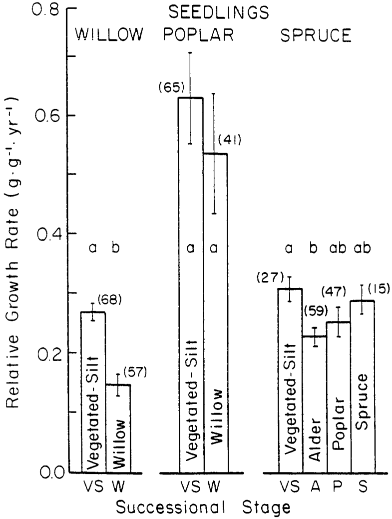


Fig. 3-6. Relative growth rate for current year growth (leaves and stems combined) of naturally occurring willow, poplar, and spruce control seedlings in the successional stages in which they occur, mean ± SE. Analysis of covariance permitted comparison of seedlings of different ages (see text). Relative growth rate = ln (total dry mass) - ln (total - current growth). Growth rates followed by the same lower case letter within a species are not significantly different ($P > 0.05$). See Fig. 3-1 for stage abbreviations. Sample sizes are in parentheses.

resembles the growth response of alder and poplar seedlings transplanted into alder sites (Figure 3-1) and suggests inhibition of seedling growth in alder stands despite high N availability in the soils (chapter one) and high concentrations of N and P in spruce seedlings in the alder stage (Fig. 3-7).

Willow and poplar seedlings were only found in the vegetated-silt and willow stages of succession where they differed only slightly in age (Table 2-5). The relative growth rate (Fig. 3-6) of naturally occurring willow seedlings (*Salix alaxensis*) decreased significantly ($P < 0.05$) from the vegetated-silt to the willow stage, suggesting intraspecific competition among willow seedlings. Poplar seedlings had higher relative growth rates than willow but no significant difference between stages.

Current-year growth of natural spruce seedlings within a 1 m radius of alder stems were not significantly different ($P > 0.05$) from growth of spruce seedlings > 2 m from the same alder stems. These results indicate the absence of inhibition or facilitation of spruce by isolated stems of alder in early succession.

Fertilization and shade

Natural spruce seedlings showed no increase in aboveground dry mass to shade or fertilizer ($P > 0.05$, Table 3-5) except in the vegetated-silt stage, where both shade and fertilizer had a positive effect on growth (the sample size was too small for statistical tests). Willow and poplar stem growth increased significantly ($P <$

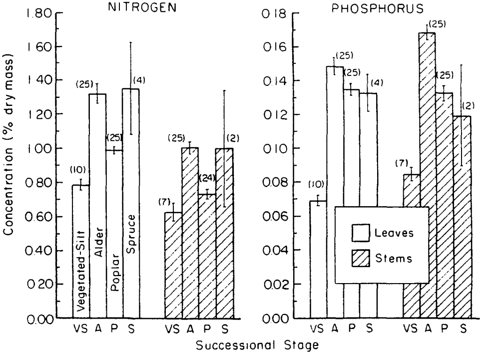


Fig. 3-7. Nitrogen and phosphorus concentrations in current year tissue of naturally occurring spruce control seedlings in four successional stages, mean ± SE. See Fig. 3-1 for stage abbreviations. Sample sizes are in parentheses. Note the difference in scale between nitrogen and phosphorus.

Table 3-5. Ratio of dry mass of fertilizer to control and shade to control seedlings of naturally occurring willow, poplar, and spruce seedlings in five successional stages, mean ± SE, n = 5 sites unless indicated otherwise by numbers in parentheses. Ratios are means of site ratios, obtained from at least five seedlings per treatment per site. Spruce dry mass is from current year leaves and stems. Willow and poplar dry mass is from current year stems only. n.d. indicates no data available.

		Treatment/control dry mass ratio				
Species	Treatment	Vegetated-silt stage	Willow stage	Alder stage	Poplar stage	Spruce stage
Willow	Fertlizer	16.0 ± 3.3*	3.8 ± 1.1*	n.d.	n.d.	n.d.
	Shade	2.4 ± 0.5*	1.0 ± 0.1	n.d.	n.d.	n.d.
Poplar	Fertilizer	14.7 ± 3.4*	27.8 ± 17.5*	n.d.	n.d.	n.d.
	Shade	1.5 ± 0.5	1.8 ± 0.5	n.d.	n.d.	n.d.
Spruce	Fertilizer	3.2 ± 0.2 (2)	n.d.	1.3 ± 0.2	1.2 ± 0.1	1.0 ± 0.0 (2)
	Shade	3.1 ± 0.0 (1)	n.d.	n.d.	0.6 ± 0.2	n.d.

0.05) when fertilized (Table 3-5). Leaf growth was not reported due to considerable leaf senescence prior to harvest. Willow growth in the vegetated-silt stage showed a significant positive response ($P < 0.05$) to shade (Table 3-5), perhaps reflecting an improved moisture regime (see below), but no other significant responses to shade were observed.

Trench experiment

Spruce seedlings in poplar sites (Table 3-6) did not grow significantly better in trenched than in control plots, suggesting that root competition between poplar trees and spruce seedlings was insufficient to affect spruce seedling growth. However, at three alder sites, dry mass of trenched spruce seedlings (Table 3-6) was significantly greater than untrenched control seedlings. Note that the age of spruce seedlings in alder and poplar sites is similar (Fig. 2-8). This again suggests an inhibitory effect of alder upon growth of understory seedlings. Spruce seedlings at one alder site showed a nonsignificant increase in dry mass whereas at another alder site a (nonsignificant) decrease in trenched seedling dry mass was measured. Concentrations of N and P in trenched spruce seedlings were greater than in untrenched seedlings (Table 3-6) in all poplar sites and in four of the five alder sites. The variable response of natural spruce seedlings to trenching and fertilization despite increases in nutrient concentration may reflect a lack of responsiveness to variation in the environment or the inhibition of growth by other (unmeasured) factors

Table 3-6. Ratio of dry mass, nitrogen, and phosphorus concentrations of naturally occurring spruce seedlings in trenched plots to untrenched controls in alder and poplar sites. Dry mass is from current year tissue. Extractable soil NH_4 and NO_3 ratios are included for comparison (see chapter one for details). * indicates a significant treatment effect ($P < 0.05$). - indicates no ratio was calculated because no NO_3 was found in poplar control plots.

	Trench/control ratios						
Alder site number	Dry mass	Extractable NH_4	Extractable NO_3	Nitrogen concentration leaves	Nitrogen concentration stems	Phosphorus concentration leaves	Phosphorus concentration stems
1	2.0	1.4	8.7*	1.4*	1.3*	1.0	1.3*
2	2.4*	1.3	7.5*	1.1*	1.0	1.3*	1.1*
3	0.5	2.3	> 10.0*	1.3*	1.4*	1.3*	1.1
4	2.8*	1.3	9.7*	0.9	0.9	0.8	0.8
5	6.8*	3.7	> 10.0*	2.0*	1.5*	1.2*	1.2*
Poplar site number							
1	0.5	0.9	-	1.5*	1.6*	1.2*	1.4*
2	1.5	3.8	-	2.1*	1.6*	1.4*	1.4*
3	1.2	2.6	-	1.7*	1.6*	1.3*	1.5*
4	2.2	2.9	-	2.4*	2.0*	1.5*	0.9*
5	0.7	2.0	-	2.0*	1.7	1.3	1.2

such as low water levels.

Water relations

Drought stress can be a factor for naturally occurring willow and poplar seedlings in the vegetated-silt stage. These seedlings were less water stressed when grown under shade cloth than were unshaded control seedlings on a vegetated-silt site (Fig. 3-8). Stomatal resistance was significantly lower ($P < 0.05$) in shaded willow and poplar, and transpiration was significantly higher in shaded willow than in unshaded controls. Stomatal resistance and transpiration of fertilized seedlings did not differ from controls. Water potential of fertilized and shaded seedlings did not differ from controls with the exception of fertilized poplar seedlings, which had a lower (more negative) water potential than control seedlings. No significant difference was found in water potentials of natural spruce seedlings between vegetated-silt site controls (-0.55 ± 0.08 MPa) and either fertilized seedlings in vegetated-silt sites (-0.59 ± 0.09 MPa) or alder site seedlings (-0.68 ± 0.08 MPa).

Photosynthesis

Fertilization of natural seedlings at one vegetated-silt site (Fig. 3-5) increased photosynthetic rates of willow but not poplar. However, photosynthetic rates of seedlings of both species from shade plots (shade cloth removed) were higher than unshaded controls. This may reflect the reduced water stress of the shaded seedlings.

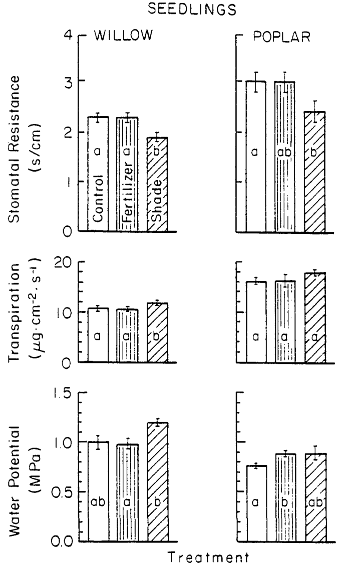


Fig. 3-8. Stomatal resistance (n = 10), transpiration (n = 10), and water potential (n = 5) for naturally occurring willow and poplar seedlings, mean ± SE. All measurements were taken 25 June 1983 at vegetated-silt sites. Measurements followed by the same letter are not significantly different ($P > 0.05$).

Vegetation

Vegetation Cover

Estimates of the total cover of all vegetation < 2 m tall and < 50 mm dbh before and after fertilization (Table 3-7) were significantly different ($P < .05$) at only three vegetated-silt sites and one spruce site. The cover of Populus balsamifera, five willow species, Equisetum spp., Epilobium angustifolium, and either Calamagrostis canadensis or bryophytes increased in fertilized vegetated-silt sites, whereas Rosa acicularis, Epilobium angustifolium, and bryophyte cover increased in the fertilized spruce site. Cover values for unvegetated ("bare") soil dropped significantly in all vegetated-silt and spruce sites when they were fertilized. This was due both to colonization by bryophytes and the increased cover values of the species mentioned above.

Total vegetation cover estimates in shaded plots before and after shading were different at only three willow sites. These differences were due to a decrease in the cover of three willow species, Populus balsamifera, and Equisetum spp. There was no detectable difference ($P > 0.05$) between vegetation cover values in unfenced control plots and fenced control plots before or after the study period, despite considerable browse by hares. Long-term maintenance of the exclosures may show measurable differences.

Biomass

Total sampled biomass was significantly greater ($P < 0.05$) in

Table 3-7. Vegetation cover of woody and herbaceous species in five sites in each of five successional stages in July 1981. Values are cover classes (" + " = < 1%, 1 = 1 - 5%, 2 = 6 - 25%, 3 = 26 - 50%, 4 = 51 - 75%, 5 = 76 - 100%. Species with < 1% cover at all sites combined were not included. Cover values in parentheses are from the same sites in August 1983 after 3 yr of fertilization with NPK 20:20:20 applied at 50 g/m^2 in July 1981, May 1982, and May 1983. Cover at the starred sites was significantly different after fertilization. Plant nomenclature follows Viereck and Little (1972) for woody plants and Hultén (1968) for herbaceous plants.

Species	Vegetated-silt stage 1 2* 3* 4* 5	Willow stage 1 2 3 4 5	Alder stage 1 2 3 4 5	Poplar stage 1 2 3 4 5	Spruce stage 1 2 3 4* 5
Woody plants					
Salix alaxensis	1 2 1 1 1 (3)(2)(2)(2)(1)	4 3 2 5 3 (3)(2)(1)(4)(2)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
S. interior	2 1 + + 1 (2)(1)(1)(0)(0)	1 3 1 + 1 (0)(1)(+)(+)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
S. glauca	0 0 0 0 1 (0)(0)(0)(1)(2)	0 0 0 0 0 (1)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
S. lasiandra	0 0 0 0 + (0)(1)(0)(1)(1)	1 0 0 0 1 (1)(1)(0)(0)(1)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
S. novae-angliae	1 1 + 1 1 (2)(2)(1)(2)(2)	0 + 0 0 0 (2)(1)(0)(2)(1)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
Alnus tenuifolia	0 0 0 2 0 (0)(0)(0)(2)(0)	0 1 0 0 0 (0)(2)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
Populus balsamifera	1 1 1 1 + (1)(3)(2)(2)(2)	3 1 2 1 1 (3)(2)(3)(2)(+)	0 0 + 0 0 (0)(1)(0)(0)(0)	0 + 0 + 0 (0)(+)(0)(+)(0)	0 0 0 0 0 (0)(0)(0)(+)(0)
Picea glauca	0 0 0 + 0 (0)(0)(1)(+)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	2 1 2 2 1 (2)(1)(3)(1)(1)	3 1 3 + + (3)(+)(3)(1)(+)	0 1 + + 0 (0)(+)(+)(+)(0)
Rosa acicularis	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	+ 0 0 0 0 (1)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 1 2 0 0 (0)(1)(3)(+)(0)
Cornus canadensis	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 + 2 0 0 (0)(+)(2)(0)(0)

Table 3-7. (continued)

Species	Vegetated-silt stage	Willow stage	Alder stage	Poplar stage	Spruce stage
Herbaceous plants					
Equisetum spp.	1 1 1 1 2 (1)(1)(2)(1)(2)	3 5 1 2 5 (2)(4)(1)(0)(5)	1 + 1 3 1 (3)(1)(+)(3)(3)	+ + 1 + 2 (+)(+)(2)(+)(5)	0 2 + + 0 (0)(5)(+)(+)(0)
Juncus spp.	2 0 0 0 2 (0)(0)(2)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
Carex spp.	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (+)(0)(0)(2)(+)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
Calamagrostis canadensis	0 0 0 0 0 (3)(3)(0)(0)(4)	0 0 0 0 0 (1)(+)(4)(1)(1)	+ 1 + 1 0 (0)(4)(1)(+)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
Erigeron acris	0 + + + + (0)(0)(+)(+)(+)	1 0 0 0 0 (+)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
Epilobium angustifolium	0 0 0 0 0 (0)(+)(0)(+)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 1 0 0 (0)(0)(1)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 + 0 0 0 (0)(1)(0)(+)(0)
Achillea sibirica	0 0 0 0 0 (0)(0)(0)(0)(0)	0 1 0 0 0 (1)(+)(0)(1)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
Hordeum jubatum	0 0 0 0 0 (0)(0)(0)(0)(0)	0 + 0 0 0 (0)(0)(1)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
Solidago canadensis	0 0 0 0 0 (0)(0)(0)(1)(0)	0 1 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
Triglochin palustris	0 0 + 1 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)
Pyrola asarifolia	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(1)(+)(0)	0 0 + 0 0 (0)(0)(0)(0)(0)
Geocaulon lividum	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 + 0 (0)(0)(0)(0)(0)	0 0 0 2 0 (0)(0)(0)(2)(0)
Linnea borealis	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 + 0 0 (0)(0)(1)(0)(0)
Bryophytes and lichens	0 0 + + 0 (+)(0)(5)(4)(0)	2 2 0 0 + (1)(+)(+)(0)(2)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 + + 0 + (0)(+)(0)(0)(0)	0 2 0 1 0 (0)(2)(1)(2)(0)
Bare soil	3 4 5 2 3 (+)(1)(+)(0)(1)	0 0 4 0 2 (1)(0)(2)(2)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 0 0 0 0 (0)(0)(0)(0)(0)	0 2 3 5 0 (0)(0)(0)(0)(0)

fertilized than in control plots in the vegetated-silt stage (Table 3-8) where fertilized plots produced about eight fold more biomass than control plots. In the alder and spruce stages about one and one half times more biomass was produced in fertilized than in control plots. The fertilization response was strongest in the herbaceous plants and willows in the vegetated-silt stage. The overall pattern resembles the fertilization response of the transplanted seedlings where nutrients appear to be more limiting in the vegetated-silt stage than in the alder stage.

Greenhouse experiments

The fertilization and shade experiment with potted plants was designed to complement the field experiments with transplants and natural seedlings. Survival of potted willow, alder, poplar, and spruce seedlings (Table 3-9) was independent of soil type (chi square analysis, $P > 0.05$), but not of treatment. Shade did not affect survivorship, whereas fertilization significantly decreased survivorship ($P < 0.05$) on both soil types for all four study species except spruce seedlings on silt soils.

Dry mass (combined roots and shoots) of potted willow and poplar seedlings was greater ($P < 0.05$) when grown on mineral soil from the alder stage than when grown on mineral soil from the vegetated-silt stage (Fig. 3-9). This contrasts with field results that showed decreased growth of poplar (and no change of willow growth) in alder stages as compared to earlier and later successional stages. This

Table 3-8. Dry mass of seedlings, saplings and herbaceous vegetation in fertilized and unfertilized plots in vegetated silt, alder, and spruce stages, mean ± SE, n = 5, 2 X 2 m plots per stage. All vegetation < 2 m tall and < 50 mm dbh was harvested. Fertilizer rates are discussed in the text. * indicates a significant fertilizer effect.

	Dry mass (g/m^2)					
	Vegetated-silt stage		Alder stage		Spruce stage	
Species	Control	Fertilizer	Control	Fertilizer	Control	Fertilizer
Herbs	22.2 ± 6.5	150.9 ± 21.7*	12.3 ± 2.0	23.3 ± 4.9	6.5 ± 3.4	16.2 ± 11.0
Salix alaxensis	8.6 ± 1.9	91.7 ± 37.1*	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
S. interior	9.2 ± 2.2	48.5 ± 24.9*	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
S. spp.	25.2 ± 3.3	238.7 ± 52.3*	9.6 ± 0.7	31.6 ± 13.2	0.0 ± 0.0	0.0 ± 0.0
Populus balsamifera	10.9 ± 5.9	58.1 ± 23.9*	19.4 ± 0.0	3.2 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Picea glauca	0.9 ± 0.0	1.5 ± 0.0	43.0 ± 15.2	49.1 ± 16.7	1.5 ± 1.3	3.4 ± 3.0
Rosa acicularis	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	20.1 ± 14.8	19.9 ± 13.4
Total biomass	72.7 ± 6.8	569 ± 75.3*	63.1 ± 15.4	85.7 ± 21.0	20.8 ± 14.6	31.7 ± 12.1

Table 3-9. Survivorship of potted seedlings grown in mineral soil from either the vegetated silt stage or the alder stage. Shade, fertilization, and control treatments were superimposed on these soil types. Sample sizes are in parentheses.

	Survivorship (% of individuals)				
	Vegetated-silt stage soil			Alder stage soil	
Species	Control	Shade	Fertilizer	Control	Fertilizer
Willow	90 (29)	93 (14)	29 (17)	87 (15)	13 (15)
Alder	43 (30)	40 (15)	27 (15)	53 (15)	13 (15)
Poplar	97 (36)	93 (15)	53 (17)	88 (17)	41 (17)
Spruce	100 (36)	100 (15)	100 (15)	93 (15)	66 (15)

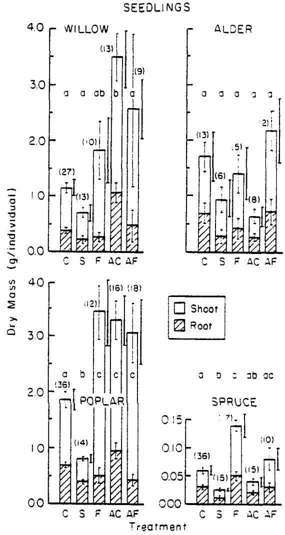


Fig. 3-9. Shoot and root dry mass of potted seedlings of four species grown on mineral soil from either the vegetated-silt stage or the alder stage, mean ± SE. Shade, fertilizer, and control treatments were superimposed on these soil types.
C = control on silt soil, S = shade on silt soil,
F = fertilizer on silt soil, AC = control on alder soil,
AF = fertilizer on alder soil. Sample sizes are in parentheses. Heavy bars are standard errors for total plant dry mass. Total plant dry mass values followed by the same letter are not significantly different (P > 0.05).

suggests that alder soils may be beneficial, but that the presence of alders may inhibit seedling growth. Dry mass of potted alder and spruce seedlings grown in alder soil did not differ significantly ($P > 0.05$) from seedlings grown in silt soil.

Poplar and spruce responded to NPK fertilization (Fig. 3-9) with significant ($P < 0.05$) growth increases over unfertilized controls on silt soils. Fertilized willows generally grew more than controls but the difference was not significant ($P > 0.05$). These fertilization responses resemble field results, where NPK fertilization also increased growth. However, fertilized alder seedlings on silt soils in pots did not grow more than unfertilized controls. On alder soils, which had higher KCl extractable N (chapter one), fertilization had no significant effect on total growth of any of the four study species, though spruce and alder shoots showed (nonsignificant) increases in dry mass in fertilized compared to unfertilized alder soils.

Growth of shaded seedlings (Fig. 3-9) was less than that of unshaded controls for all four study species, though the decrease was significant ($P <0.05$) for only poplar and spruce. This contrasts with field results where no significant shade response was found, perhaps because of higher light in the field. Shoot and root growth responses to the treatments were usually similar. However, fertilization raised the shoot to root ratios of willow (1.1 ± 0.1, $n=27$ to 7.6 ± 0.5, $n=10$) and poplar (1.9 ± 0.2, $n=36$ to 3.5 ± 0.6, $n=12$).

Phosphorus absorption was not significantly different ($P > 0.05$)

between control seedlings grown on silt versus alder soils (Table 3-10). However, P absorption of fertilized seedlings tended to be higher than unfertilized seedlings, though this difference was only significant for spruce seedlings.

Concentrations of N and P in potted seedling leaves, stems, and roots (Figs. 3-10, 3-11) were not higher in control seedlings in alder stage soils than bare silt soils, contrary to field grown seedling responses. For willow and poplar, this may have resulted from dilution by increased growth in the alder soils (Fig. 3-9). In addition, only mineral soils were used in pots, and most of the increase in soil N in the alder stage is in the organic horizon (chapter one). Willow and poplar N concentrations decreased in shade, and all species responded to fertilization with increases in both N and P concentrations on both vegetated-silt and alder stage soils.

When grown at different levels of N in silt soils, all four species grew significantly more ($P < 0.05$) with N fertilization than without (Fig. 3-12). All four species showed increases in dry matter accumulation from 0 to 50 mg N/L. Spruce and alder showed further increases in dry matter from 50 to 500 mg N/L, but willow and poplar did not. As with the previous experiment, shoot-to-root ratios increased with fertilization.

Table 3-10. Phosphorus absorption rate of excised roots of four species of potted seedlings in five treatments at either 1 μM or 10 μM, mean ± SE. Treatments are explained in Fig. 3-9. Sample sizes are in parentheses and values for each species that are followed by the same letter are not significantly different ($P > 0.05$). n.d. indicates no data available.

		Phosphate absorption rate (μ mol · g^{-1} · h^{-1})				
		Vegetated-silt stage soil			Alder stage soil	
Species	Phosphorus Concentration (μ mol/L)	Control	Shade	Fertilizer	Control	Fertilizer
Willow	1	0.43 ± 0.07 (6) a	0.25 ± 0.02 (5) a	n.d.	0.37 ± 0.04 (6) a	n.d.
	10	1.95 ± 0.16 (4) b	1.44 ± 0.11 (5) ab	4.15 ± 0.91 (5) b	1.85 ± 0.20 (6) b	n.d.
Alder	1	n.d.	0.31 ± 0.02 (4) a	n.d.	0.26 ± 0.07 (5) a	n.d.
	10	1.60 ± 0.27 (5) b	1.53 ± 0.11 (4) b	1.40 ± 0.04 (3) b	1.51 ± 0.31 (6) b	2.08 ± 0.16 (4) b
Poplar	1	0.37 ± 0.12 (6) a	0.32 ± 0.02 (6) b	0.66 ± 0.03 (5) a	0.36 ± 0.03 (6) a	0.29 ± 0.04 (5) a
	10	1.68 ± 0.10 (6) c	4.34 ± 0.20 (6) d	1.70 ± 0.12 (6) c	1.87 ± 0.15 (6) c	2.99 ± 0.0 (1) c
Spruce	1	0.13 ± 0.01 (6) a	n.d.	0.29 ± 0.02 (4) b	n.d.	n.d.
	10	0.79 ± 0.10 (4) abc	0.99 ± 0.09 (6) abc	1.43 ± 0.20 (5) c	0.80 ± 0.11 (5) abc	1.50 ± 0.21 (5) abc

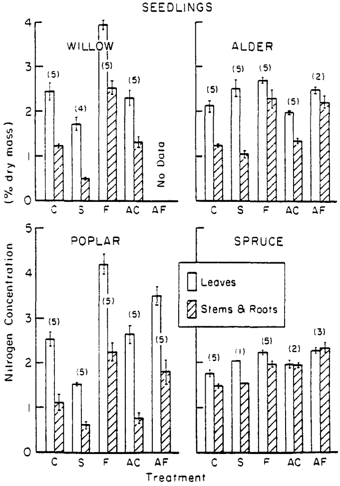


Fig. 3-10. Nitrogen concentrations of leaves and stems plus roots of seedlings grown in pots on mineral soil from either the vegetated-silt stage or the alder stage, mean ± SE. Shade, fertilizer, and control treatments were superimposed on these soil types. Treatment designations are defined in Fig. 3-9. Sample sizes for both bars are shown in parentheses over the first bar for each treatment.

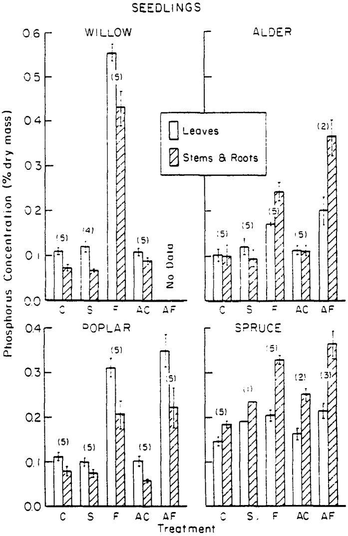


Fig. 3-11. Phosphorus concentrations of leaves, and stems plus roots of seedlings grown in pots on mineral soil from either the vegetated silt stage or the alder stage, mean ± SE. See Fig. 3-10 for further explanation.

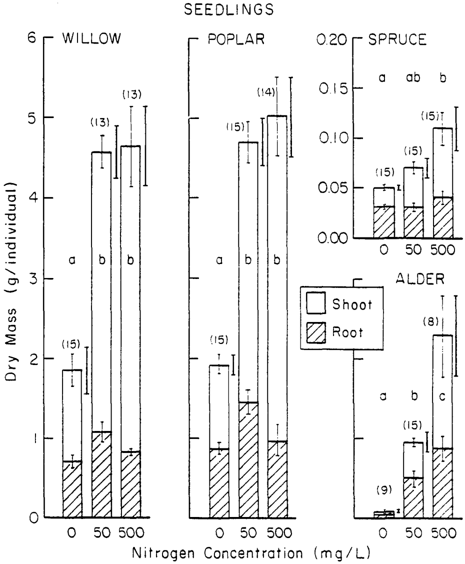


Fig. 3-12. Dry mass of seedlings of major flood plain species grown in pots with mineral soil from the vegetated-silt stage at three levels of nitrogen, mean ± SE. All other nutrients were supplied weekly in a complete Hoaglands solution. Sample sizes are in parentheses. Heavy bars are standard errors for total plant mass.

DISCUSSION

Nutrients

This study was designed to answer two questions: (1) Does alder facilitate or inhibit the establishment and growth of tree seedlings? and (2) Do the physiological responses to changes in light, moisture, and nutrient regimes of seedlings of the four study species determine the course of successional replacements?

The results of this study provide evidence that alder does inhibit seedling establishment on an Alaskan flood plain succession. Physiological responses of seedlings appear to be important in determining the rate of succession but not the overall pattern of species replacements, which is governed more by life spans of the principal species (chapter two). Despite demonstrated nutrient limitations on early successional silt bars, the positive effects of nutrient addition by alder appear to be offset in the short term by increased root competition, shading, and herbivory (chapter two) in the alder-dominated stage. Additionally, few species can establish with alder present (chapter two). These inhibitory interactions, and the fact that all species can establish before alder becomes dominant (chapter two), suggest that the presence of alder is not necessary for establishment of any of the species studied. In the absence of alder, the general successional pattern would probably remain the same.

Aboveground growth of transplanted and natural seedlings was limited by N and P on the early successional silt bars, as demonstrated by strong positive fertilizer responses. Applications of N and P fertilizer in this study were similar to the levels contributed by alder to the flood plain system (Van Cleve et al. 1971, Van Cleve and Viereck 1972). Therefore, the strong seedling responses to fertilization in pre-alder stages served as an approximate guide to potential seedling responses in the alder stage without the additional influences of litter, shade, root competition, and herbivory. Willow, alder, and poplar seedlings had higher fertilized to control dry mass ratios than spruce, suggesting higher growth rates and a greater likelihood of capturing early successional resources. Biomass of fertilized plots on the vegetated-silt bars was almost eight times greater than unfertilized plots after three growing seasons with fertilization (NPK: 20-20-20 fertilizer applied at 50 g/m^2). I know of no comparable experiments for a primary succession. Mellinger and McNaughton (1975) found average net productivity in a 6-year-old field doubled one year after NPK:10-10-10 was applied at 5.6 g/m^2. Less response to fertilization was found in total vegetation when they fertilized a 17-year-old field. I found the least response to fertilization in understory vegetation of the alder stage. Willow and herbaceous plants were responsible for most of the increased production on the Tanana River.

Belowground responses of seedlings were only measured in greenhouse experiments in my study. Different patterns of root growth may have successional consequences for seedlings on the flood plain. Willow and poplar generally had higher shoot to root ratios than alder and spruce. These differences between species increased with fertilization of greenhouse seedlings and fit the pattern of rapid growth and resource dominance by willow and poplar in the field. Root suckers may increase the distribution of poplar (Zasada et al. 1981), especially in years unfavorable to seedling establishment. Slow root growth in spruce may limit its establishment on frequently silted river bars (Krasny et al. 1984) and favor establishment of the faster-growing, more flood tolerant willow and poplar (chapter two).

Soils of primary successional sequences typically have low initial nutrient availability (Johnson et al. 1976, Robertson and Vitousek 1981, Vitousek et al. 1984, chapter one) and plant growth is presumably nutrient-limited (Van Cleve et al. 1980, Finegan 1984). Few studies, however, have tested this assumption experimentally. Several studies conducted in Glacier Bay, Alaska (Schoenike 1958, Lawrence et al. 1967) provide some evidence that N limits growth of poplar (see chapter four). It is not clear if alder is always the source of the N (Cooper 1923). Bradshaw (1983) showed that grasses grew better in the presence of an N-fixer. In the present study, seedlings grown in the alder-dominated stage had the highest N and P concentrations of all stages, yet seedling growth was generally least in this stage. Krasny et al. (1984) also found lower root and shoot biomass of Picea glauca in alder communities on the Tanana River flood plain than in more open, pre-alder communities. These results suggest that some resource other than nutrients is limiting growth in this stage.

Nutrient availability in terrestrial secondary succession depends (among other things) on the nutrient status of the site prior to disturbance (Vitousek et al. 1981, Vitousek et al. 1982) and on the nature of the disturbance (Vitousek and Melillo 1979, White 1979). Nutrient availability may (Marks 1974, Bormann and Likens 1979) or may not (Harcombe 1977) be important in determining the pattern of vegetation development in secondary succession.

Nitrogen fixation by alder has long been used in forestry (Wilson 1920, Kohnke 1941, Lawrence 1958, Gordon et al. 1979) to improve soil conditions. However, the effects of fast-growing alder on conifer regeneration may be detrimental in managed forest ecosystems (Binkley 1981), and species such as Sitka alder (Alnus sinuata), with a more shrub-like growth form than red alder, are being planted. Binkley et al. (1984) found no increase in Douglas-fir (Pseudotsuga menziesii) basal area, average diameter or height when Sitka alder and red alder was introduced, though N concentrations in Douglas-fir foliage and alder site soils increased. The closed canopy on the the alder sites may cause pruning of the lower Douglas-fir branches. Further, Douglas-fir foliage from alder sites was lower in P and S (Binkley et al. 1984), suggesting that alder may be a superior competitor for a limited pool of available P (Ho 1979). Thus, alder may have short-term detrimental effects on adjacent vegetation despite beneficial N additions.

Nitrogen fixation by alder is presumably more important to soil development in primary rather than in secondary succession, as initial N levels are usually lower in the former (Van Cleve and Viereck 1971, Bradshaw 1983). However, long term removal experiments will help to determine the direct influence of alder on other species. The present study demonstrated that the net effect of dense alder stands on understory seedling growth was negative. Furthermore, N additions, presumably from continued silt deposition, can occur in primary succession in the absence of alder (Viereck 1970). Alder appears to promote long-term soil development but may be a successful competitor for resources in the short term.

Light

Growth of seedlings transplanted under alder canopies appeared to be inhibited by shading. A 70% reduction in light from the early successional vegetated-silt stage to the alder stage corresponded with decreases in photosynthesis among all four study species. However, artificial shade treatments had no effect on transplant photosynthetic potential (shade cloth removed), suggesting competition for light may not be too severe in the alder, poplar, and spruce stages.

Willow, alder, and poplar seedlings on early successional sites along the Tanana River had photosynthetic rates five to eight fold greater than spruce seedlings. Species differences in shade tolerance may be a factor in determining species replacements in old field (Bormann 1953) or forest succession (Kozlowski 1949, Bazzaz 1979, Runkle 1982). Early successional sun-adapted plants may have higher light-saturated rates of photosynthesis than later successional shade-adapted plants (Boardman 1977). Bazzaz (1979) includes poplar in his list of early successional trees with relatively high photosynthetic rates, while Lawrence and Oechel (1983) report maximum photosynthetic rates for Populus tremuloides and P. balsamifera at warm soil and air temperatures, conditions typical of early succession. Alder and willow are also early successional colonizers (Viereck and Little 1972, Densmore 1979) with moderately high photosynthetic rates (Lawrence and Oechel 1983), whereas spruce photosynthetic rates are much lower (Clark 1961). These differences among the photosynthetic rates of the four study species may affect patterns of successional replacement.

The present study confirms the general conclusion (Grime 1979) that plant dry matter production generally declines in response to shade. However, responses can vary among species (Grime 1979), as shown here when dry mass of transplanted willow, alder and poplar seedlings declined from the vegetated-silt to the alder stage but transplanted spruce seedling growth did not change significantly. Fertilization responses indicated nutrients were not limiting spruce growth in the alder stage, so the relatively high shade tolerance of spruce may account for the observed lack of a growth response. Reduced growth did occur in all species when grown in shade in the comparatively low light regime of a greenhouse. The high shade tolerance of spruce supports the well-established idea (Harper 1977, Bazzaz 1979) that changes in successional dominance may in part be determined by the relative shade tolerance of the species. Spruce may be able to survive in the dense alder thickets whereas the other, less shade tolerant species cannot.

Water

Drought stress may be a factor in limiting seedling growth on early successional silt bars of the Tanana River. When willow and poplar seedlings were shaded, stomatal resistance decreased and transpiration increased. Water stress can be severe on flood plains in early successional stages (Gill 1970, Johnson et al. 1976) during periods of low water tables. Terrace development is often associated with both increased water retention in forest floors (Johnson et al. 1976) and increased water stress from increased distances to the water table (Lindsey et al. 1961, Franz and Bazzaz 1977, Menges and Waller 1983). Declining water availability with terrace development has been suggested as the cause of succession on the Yellowstone River in Montana (Weaver and Boggs 1983). River sorting and periodic deposition of soil particles of different sizes results in heterogeneous soil profiles, with layers of different bulk densities and water retention. Resultant variations in soil moisture may affect germination (Pickett and Bazzaz 1978, Krasny et al. 1984, chapter two), or rooting patterns and competitive interactions (Pickett and Bazzaz 1976, Bazzaz 1979) of successional species. For example, moisture requirments for germination have been shown to restrict the distribution of Salix nigra (McLeod and McPherson 1973).

Root competition

Alder and poplar canopies on the Tanana River flood plain appear to inhibit seedling growth in the understory. Canopy removal resulted in increases in KCl extractable soil N (chapter one) and increased growth of transplanted seedlings. Canopy removal is known to increase extractable N (Williams and Cooper 1979, Matson and Vitousek 1981, Gordon and Van Cleve 1983), but its effects on understory plant growth are compounded by the parallel increases in light, soil, and air temperatures, and decline in litterfall (Gregory 1966). Removal of root competition by trenching also resulted in increased extractable N in this study (chapter one) and has been documented elsewhere (Vitousek et al. 1982). Naturally occurring spruce seedlings responded with increased growth in most of the trenched plots in the present study. Similar competition between roots of late successional tree seedlings and early successional forests has been demonstrated in earlier trenching experiments (Korstian and Coile 1938, Lutz 1945, Shirley 1945). These positive responses to canopy removal and trenching indicate that both root competition (for nutrients, moisture, or other factors) and light competition inhibit understory growth on the Tanana River flood plain.

The present study provides experimental evidence indicating that alder does not facilitate establishment and growth of tree seedlings.

It also suggests that different physiological responses of seedlings to environmental changes is important in determining the rate at which succession occurs. Using transplants and controlled greenhouse experiments, the interactions between soil development and successional plant growth were experimentally investigated. Initially, allogenic factors such as terrace development and water availability controlled plant growth. Subsequently, autogenic processes (N fixation, competitive interactions) assumed importance. Alder contributed significantly to soil development in this system (Van Cleve et al. 1971, chapter one). Yet examination of the interactions of N-fixing alder with seedlings of other species demonstrated that alder competitively inhibits establishment and growth of other species. Facilitation by alder, if it occurs, must be considered facultative (Dean and Hurd 1980) rather than obligatory.

Different physiological responses of seedlings to changes in nutrient availability and light affect this successional pattern. Spruce grows more slowly, is less responsive to fertilization, and is more shade tolerant than willow, alder, and poplar. In addition, it is less palatable to hares. These characteristics may allow spruce to continue to establish after the initial wave of colonization, provided there is a mineral soil surface on which to germinate (chapter two). Further understanding of the processes controlling successional replacements (chapter four) will come from such comparative ecophysiological studies.

CHAPTER FOUR: Successional Processes

Plant ecologists recognize many processes that are responsible for successional changes in species composition. These processes include facilitative or competitive interactions between species, and interactions determined by the life history traits of the species involved. Current controversies focus on models which combine several of these processes, making it difficult to determine the relative importance of each process. The evidence for each process as a determinant of successional change is reviewed here, and the circumstances identified wherein each process is likely to be important. The example of an Alaskan flood plain succession is used to show how each of these processes interacts through both successional time and the developmental phases of a plant's life-time.

FACILITATIVE PROCESSES

Facilitation is the process whereby the presence of an early successional species makes the environment more favorable for growth of a later successional species (Connell and Slatyer 1977). Facilitation can be obligatory (Horn 1976) in the sense that species B cannot establish without the prior presence of species A, or it can be facultative (Dean and Hurd 1980) in the sense that species A increases the probability of establishment or increases the growth rate of species B. Facilitative interactions are expected to be particularly important in primary succession and in stressful environments where a few successful colonizers can ameliorate the environment for later successional species. Facilitative interactions (or at least obligatory ones) are less likely to occur in secondary successional environments which are generally more favorable to plant growth.

Facilitative interactions between species can be distinguished from facilitation due to biogeochemical processes (McIntosh 1981). The former occurs within the developmental phases of a single plant's life-time, particularly during the colonization and maturation phases (Connell and Slatyer 1977, Table 4-1). It involves more or less direct interactions of two species. The latter type of facilitation is less direct and involves responses of species to soil development (Olson 1958, Lawrence 1979, Van Cleve and Viereck 1981). The numerous connotations of the term facilitation help to explain why the existence of facilitative processes is currently being debated (McIntosh 1981, Finegan 1984). Studies emphasizing short-term interactions of species may not find evidence of facilitation when facilitation is defined only in terms of biogeochemical processes. Likewise, studies concerned with long-term ecosystem development are not likely to find evidence for facilitative processes that only involve short-term interactions of species. In this discussion, a broad interpretation of facilitation will be used, including any environmental change of biotic origin that favors the establishment or growth of a species.

Table 4-1. Successional mechanisms determining species replacements. Modified from Connell and Slatyer (1977).

Model	Developmental Phase		
	Colonization	Maturation	Senescence
Facilitation	life history (arrival time) facilitation	facilitation	life history (longevity) competition (elimination)
Tolerance	life history (arrival time)	life history (growth rate)	competition (elimination)
Inhibition	life history (arrival time) competition (inhibition)	competition (inhibition)	life history (longevity)

Plant responses to the presence of nitrogen-fixing species are frequently cited as evidence of facilitation in primary succession. One example of facilitation comes from china clay waste, a man-made, primary successional surface in England, where Bradshaw (1983) found grasses grew better in the presence of *Lupinus arboreus*, a nitrogen-fixer. There are, however, very few such straightforward examples of facilitation in terrestrial succession. Alder is well known for its association with nitrogen-fixing bacteria (Bond 1956, Daly 1966, Van Cleve et al. 1971) but its effect on the growth of other species is not always as obvious as in the case of *Lupinus arboreus*. Studies have shown both low nutrient availability (Johnson et al. 1976, Robertson and Vitousek 1981, Vitousek et al. 1983, chapter three) and nutrient-limitations to plant growth (Schoenike 1958, Lawrence et al. 1967) in primary succession. Artificial fertilization with alder litter improved growth of poplar trees on a glacial moraine (Lawrence et al. 1967) in Alaska. However, Cooper (1923) noted that spruce colonizing moraines grew equally well in willow and alder-dominated stands. An Alaskan flood plain study (chapter three) documented inhibition of seedling growth in alder stands, and indicated that competitive interactions for light and soil resources outweighed the benefits of nitrogen additions by alder. Thus, growth of plants in the early stages of primary succession is generally nutrient-limited, but the response to nutrient additions (such as by nitrogen-fixers) may depend upon an interaction of competitive and facilitative processes.

Species in early succession can provide shade that improves soil moisture in dry environments, thereby facilitating the establishment of species in later succession. This is an example of a direct facilitative interaction between species. For example, in the black spruce forests of interior Alaska, feather mosses establish only following development of a full canopy by black spruce (Foote 1983), presumably because the increased shading reduces the drought stress, which is a major limitation on the growth of these species (Skre et al. 1983). Similarly, on volcanic disturbances in Hawaii (Smathers and Gardner 1979), bird-dispersed Myrica faya seeds can germinate and survive better under the shade of Metrosideros polymorpha canopies than in the open. Facilitation can also occur when early successional species improve conditions for germination and seedling growth of later successional species by the accumulation of water-retaining soil organic matter. This is an example of a less direct facilitative effect from soil development that has been shown to influence successional replacements on granite outcroppings in Georgia (Lugo and McCormick 1981). Again, this mode of facilitation is most likely to be important in early succession in severe environments.

Stabilization of the substrate is another process by which early colonizers may directly facilitate establishment of later successional species, particularly in the harsh environments of primary succession. Extensive development of lateral roots of willow on river banks or grasses on dunes (Olson 1958) can stabilize the substrate, allowing species with less rapid root growth to establish.

Facilitation can also occur via more complex and less direct interactions between species. Trees and shrubs of early succession can serve as perches for birds and increase the probability of establishment of bird-dispersed seeds in abandoned fields (Pickett 1982, McDonnell and Stiles 1983), on volcanic ash (Smathers and Gardner 1979), in orchards, or in chalk quarries (Finegan 1984). Facilitation can also involve interactions with herbivores or pathogens. For example, seed predators or pathogens can preclude establishment of seedlings of a given species beneath parent trees, whereas seedlings of other species may not be so affected (Janzen 1970). Thickets of alder on the Tanana River flood plain provide cover for snowshoe hares which eliminate palatable species in early succession, thereby reducing competition for less palatable species such as spruce. Dense Juniperus communis shrubs may provide protection from cattle grazing for the establishment of Sorbus aucuparia (Miles 1979). These more complex examples clearly involve competitive processes in addition to facilitation.

There is evidence for interspecific facilitation in aquatic primary succession where successional consequences of species interactions are more easily interpreted due to shorter life cycles. Aquatic primary succession is analogous to primary succession in terrestrial systems because previously uncolonized sites can be sequentially invaded by species whose colonization abilities differ.

Competition for recruitment space (see below) is also important to both systems. Nutrients are generally more evenly distributed in aquatic than in terrestrial systems.

Several studies show the importance of substrate preparation in aquatic systems. Turner (1983) found that recruitment of barbed surfgrass seeds (Phyllospadix scouleri) in the intertidal zone was only possible with the prior establishment of a red alga (obligatory facilitation). Dean and Hurd (1980) demonstrated facultative facilitation occurred when settlement by mussels in an estuarine fouling community was greater on surfaces previously occupied by tunicates and hydroids than on bare surfaces. Menge (1976) and Standing (1976) also report faster colonization of previously vegetated surfaces, though colonization occurred on bare surfaces as well. These studies are examples of direct facilitation between two species. However, Sousa (1979) found early colonizing algae inhibited later arrivals, and Dean and Hurd (1980) found evidence of competitive as well as facilitative processes.

Grazing can affect species replacements in aquatic primary succession. Establishment of a later successional (Fucus vesciculosus) was facilitated by snails grazing preferentially on early successional algae in one rocky intertidal community (Lubchenco 1983). Alternatively, Harris et al. (1984) found an example of refuge facilitation on a storm-denuded marine reef habitat in California. Fast-growing, early successional algae protected newly settled kelp from excessive damage by grazing fish. As with the studies involving terrestrial herbivores, these examples of facilitation are indirect, involving complex interactions of species.

Facilitation is likely to be more important in certain severe primary successional environments than in less severe environments. However, several studies suggest that there are secondary successional sequences in old fields (McCormick 1968, Hils and Vankat 1982) and forests (Niering and Goodwin 1974) where facilitation is of little importance in directing changes in species composition.

COMPETITIVE PROCESSES

In contrast to facilitation are those competitive interactions among species, whereby early colonizers inhibit the growth and/or establishment of later arrivals. This process can be demonstrated by removing the early colonizers, which increases the growth of the later-arriving species. Initially, competition is likely to be for space in which to colonize. Resources may also be pre-empted (Werner 1976) at an early stage, but are more likely to be contested later in succession as resource availability declines. Competitive processes are expected to be most important in favorable environments. In some cases, competition appears to be primarily for soil resources (nutrients or water), or for light. Plants probably compete for several of these resources simultaneously.

Competition for soil resources has been demonstrated by trenching experiments that remove root competition between early successional forests and late successional seedlings (Korstian and Coile 1938, Lutz 1945, Shirley 1945). Increased growth of hardwood seedlings in trenched plots in these mesic forests is probably from reduced competition for nutrients rather than from reduced competition for water (Miles 1979). However, such competitive inhibition may be only temporary. McIntosh (1980) noted that in the Korstian-Coile plots the early successional pines were declining in cover while the previously suppressed hardwoods were increasing. The relative importance of competitive processes in determining successional changes in species composition can, like facilitative processes, vary with successional time.

Inhibition of one species by another due to competition for water is most likely under severe drought conditions. Competition for water in early succession can affect spatial patterning (Pickett and Bazzaz 1976, Bazzaz 1979). As organic matter (and consequently moisture retention capacity) increases, competition for water may decrease. Competition for light may then become more important.

Competition for light is often considered to influence species replacements in forest succession (see Bazzaz 1979). Shade tolerance, light saturation curves, and foliage arrangement can differ, however, between early and late successional species (Bazzaz 1979). Thus, shade-adapted late successional species with lower light-saturated phyotosynthetic rates may not be strongly inhibited by the shade of early successional forests. Then the late successional species could either gain dominance by living longer than the early successional species or by outcompeting them for other resources such as nutrients. Alternatively, late successional species could gain dominance by preventing regeneration of the early successional overstory species. For example, Burton and Mueller-Dombois (1984) found that dense tree fern subcanopies in Hawaii inhibit regeneration of the canopy species Metrosideros polymorpha. Again, the relative importance of competition for light is expected to change through successional time.

Pre-emption of colonizable surfaces is another way in which early successional species can inhibit the establishment of later successional species. This occurs when green algae colonize intertidal rocks and inhibit colonization by perennial red algae (Sousa 1979). Preemption of space by annuals can inhibit colonization by perennials in old field succession (Keever 1950, McCormick 1968, Parenti and Rice 1969, Abul-Fatih and Bazzaz 1979, Hils and Vankat 1982). Dense swards of grass presumably offer little potential as seed beds to other species (Connell and Slatyer 1977). A similarly unfavorable seed bed for colonization can occur when trees in early succession produce a dense litter. This has been shown to inhibit germination of tree seeds in alder thickets in Alaska (chapter two), and moss growth in taiga forests (Foote 1983). Acid duff can provide an unfavorable seed bed for tree regeneration in dense stands of ericaceous shrubs (Niering and Goodwin 1974). Establishment under such conditions is often possible only when a disturbance creates a colonizable surface.

Competitive inhibition of later successional species by early colonizers may happen through allelopathy. Rice (1979, 1984) suggested that pioneer species in old-field succession can delay the establishment of later successional species that require higher levels of nitrogen by allelopathic inhibition of nitrogen-fixing bacteria. At present, it is unclear to what extent allelopathic chemicals are generally toxic to all plants (including the one that produced them) and to what extent they affect certain competing species (Stowe 1979).

Competition for space, soil resources, and/or light is likely to influence patterns of successional replacement. However, species may respond to competition by niche differentiation (Parrish and Bazzaz 1982), which would reduce competitive interactions. The evidence discussed above suggests that competition is partly responsible for structuring successional plant communities, particularly in favorable environments and in later successional stages. Both competitive and facilitative interactions, however, may be more important in altering the rate at which succession occurs than in determining the overall pattern. Life history processes may ultimately establish the pattern of successional replacements.

LIFE HISTORY PROCESSES

Establishment and Regeneration

Establishment and regeneration are key control points in the life cycle of any plant (Harper 1977) and are therefore likely to be a critical influence in successional change. Early successional species often have abundant mobile seeds that result in a heavy seed rain over broad areas (e.g. Harper 1977, Grubb 1977, Grime 1979). Later successional species tend to produce fewer, heavier seeds that are less mobile but which contain sufficient storage reserves to provide resources for early growth of seedlings, particularly in the face of competition from adult plants during the establishment phase (Cook 1980). Dispersal ability can be of particular importance in the colonization of newly disturbed surfaces that are far from the seed source, such as volcanic islands, or in large-scale disturbances such as glacial moraines, lava flows, or forest fires. Dispersal ability can also be important in gap succession in deciduous or tropical forests (Noble and Slatyer 1980). However, when gaps are colonized by vegetative reproduction, as in the encroachment of prairie vegetation on a previously grazed area (Glenn-Lewin 1980), colonization depends more on the composition of adjacent vegetation, than on the arrival times of propagules.

Longevity of propagules is another life history characteristic that can be important in determining the pattern of colonization. Many early successional species have persistent seeds buried in the soil, which germinate only under conditions characteristic of disturbance (e.g. increased light, temperature fluctuations, and sometimes presence of nitrate). Species in later succession are less likely to have a persistent buried seed pool (Livingstone and Alessio

1968). Thus, early successional species have a higher probability than later successional species of being present at the time of disturbance, a factor that can be an important influence on a successional sequence.

Regeneration may depend on the time of year in which a disturbance occurs. Keever (1950, 1979) found that the presence of early successional, old-field dominants was largely determined by the time of year a field was last cultivated, because of seasonal differences in seed dispersal of the colonizing species. For similar reasons, the seasonal timing of storms also strongly influenced patterns of algal colonization and intertidal succession (Sousa 1979).

The differences in propagule dispersability and longevity between early and late successional species ensure initial dominance by early successional species. Subsequent life history processes that distinguish successional species are growth rates and life spans.

Growth rate

Typically, colonizing species have higher maximum potential growth rates than do later successional species (Grime 1979, Chapin 1980). (Realized growth rates depend highly upon competitive interactions and are covered in the preceding section on competition.) Thus, even if all species were to arrive simultaneously, the early successional species would be more prominent in terms of biomass and cover during the initial stages of succession (Egler 1954). Hosner and Minckler (1963) reported that willows grew faster and were taller than cottonwoods when both colonized Illinois flood plains simultaneously. In a New England hardwood stand Oliver and Stephens (1977) found mid-successional red maple grew taller than late-successional red oak for 20 yr but by age 40 their relative heights were reversed. Uhl and Jordan (1984) found that fast-growing pioneers dominated the initial colonization phase in a burned tropical clearing. Later successional species were also on the site but grew more slowly, forming a subcanopy.

Differences in maximum potential growth rate are important in explaining species change through succession in high resource environments. In low resource environments as in early successional nitrogen-deficient sites, slow growth rates are more likely, and differences among species growth rates may be less important.

Longevity

Late successional species are typically more long-lived than early successional species. In the absence of regeneration following initial establishment, differential longevity of species is an important factor determining the disappearance of early successional species and the persistance of late successional species. Hibbs (1983) concluded that different life spans were a factor in driving forest succession in New England. Van der Valk (1981) considered life spans important in explaining wetland succession and distinguished between annuals, perennials, and vegetatively propogated species with no definite life span. On an Alaskan flood plain, the longevities of four principal woody species determined the overall successional pattern (chapter two). Differential longevity of species may be particularly important in explaining successional change in situations where disturbances are infrequent and catastrophic. In frequently disturbed areas, mortality may be more dependent on allogenic factors than on life spans.

Species differences in the life history processes of establishment and regeneration, growth rates, and longevity are often adequate to explain overall successional patterns. Modification of this basic pattern occurs from the biotic interactions of competition and facilitation and from external perturbations, as described below.

ALLOGENIC PROCESSES

Changes in physical environment that are more or less independent of the vegetation can be important determinants of succession. For example, flooding of a river may provide a seed bed of mineral soil that enables spruce to establish (chapter two), whereas absence of such flooding might delay or prevent establishment on these sites. Wind-thrown trees may provide similar seed beds of mineral soil in late successional forests.

White (1979) has suggested that there are few truly allogenic disturbances not in some way affected by the biotic community. If the periodicity of the disturbance is shorter than the life span of the species involved, adaptation to the disturbance will occur, with the eventual dominance of species more tolerant of flooding or wind storms. These adaptations lend an autogenic component to the successional processes (White 1979). Only disturbances that occur at such low frequencies that they do not affect such adaptations would then be truly allogenic. Therefore it is appropriate to consider successional change as being driven by a combination of processes ranging from autogenic to allogenic.

STOCHASTIC PROCESSES

Succession is not a completely deterministic process. Each process described above has a stochastic component to it which influences succession. For example, competitive balances between species are influenced by the climate in a given year. The effects of a facilitator can be dampened by annual fluctuations in herbivore pressure. Allogenic processes are largely stochastic factors that are less interwoven with biological phenomena. Life history processes have a strong stochastic element. For example, succession depends on (1) effects of climate on seed production, seedling establishment and growth, (2) coincidence of a good seed year and favorable conditions for germination, (3) localized distribution of seed sources and microhabitats, and (4) the stochastic nature of mortality of individuals and the species composition of the seed or seedling pools in the understory.

PROCESS INTERACTIONS

No one of the processes outlined in the previous sections is likely to individually explain successional change, and many are likely to be important simultaneously in the interaction between any two species through succession. This is seen clearly in the interaction of alder and spruce on an Alaskan flood plain (chapters one, two, and three).

Flooding is an allogenic factor that is essential to provide a seed bed of mineral soil for establishment of either species. Flooding interacts with the stochastic factors listed above. If the flooding occurs in spring following winter dispersal of alder and spruce seeds, conditions may be favorable for establishment, provided late season droughts or floods do not kill the seedlings. Spruce and alder can establish in mineral soils on the early successional silt bars. Only spruce can establish following major floods which deposit silt in the understory of alder, poplar, or spruce stands. Spruce establishment following these major floods depends upon a large seed crop which occurs in approximately 11 year cycles.

Competitive and facilitative processes are also important. The inability of alder to establish in later stages may be related to shade intolerance or its vulnerability to hare predation. Spruce seedlings are slow-growing and apparently more tolerant of shade, browsing, and root competition (chapter three). Alder increases soil nitrogen (chapter one), which reduces nutrient stress (chapter three) for spruce seedlings growing in alder stands. These nutrient additions may facilitate the growth of spruce at some later point in its life cycle. Alder, however, inhibits establishment of spruce seedlings by its dense litter layer and inhibits growth of seedlings by shading and competition for water (or some other unidentified soil resource). All of these effects of alder upon spruce have been demonstrated experimentally.

Alder seedlings grow more rapidly than spruce seedlings (Chapin et al. 1983), which may explain why alder becomes an important forest dominant before spruce, even where the two establish simultaneously. The greater life span of spruce (at least 300 yr) than alder (perhaps 50-100 yr) assures later dominance of spruce. In summary, allogenic, stochastic, competitive, life history, and perhaps facilitative processes simultaneously affect the interaction of alder and spruce during succession and no single successional model (sensu Connell and Slatyer 1977; Table 4-1) adequately describes successional change on the Tanana River.

RELATIVE IMPORTANCE OF SUCCESSIONAL PROCESSES

Given that many successional processes may operate simultaneously in any given situation (see above discussion and Hils and Vankat 1982), the next step is to evaluate the relative importance of each successional process. One way to do this is to attempt to remove the effects of each process individually and evaluate changes that occur to the system. The successional processes outlined above may be combined into four major groups: (1) life history processes (establishment and regeneration, potential growth rate, and longevity) which imply no species interaction, (2) competitive inhibition which implies negative interactions among species, (3) facilitation which implies positive interactions among species, and (4) stochastic and allogenic processes which might account for deviations from the deterministic predictions of a successional model. The life history processes together serve as a null model for biological interactions in succession (Botkin 1981). Life history traits alone may be sufficient to explain a given successional sequence. Note that this grouping of processes differs from that of Connell and Slatyer (1977) who combined several processes into three likely, yet mutually exclusive, scenarios (Table 4-1). They assume life history processes and competitive interactions are a component of all the models and that facilitative processes are limited to one model.

Perhaps the first step in evaluating the importance of different successional processes is the documentation of the life history traits of the major successional species, to determine whether these might be sufficient to explain a given successional pattern. Here the most difficult aspect is the estimation of arrival time, growth rate, and longevity of each species in the absence of other successional species, particularly those species hypothesized to be "facilitators" or "competitors." With the help of simulation models such as JABOWA (Botkin 1981), life history data could be used to predict a successional sequence assuming no interactions among species. The simplest example might assume that all species in the present study colonize the Tanana River silt bars simultaneously and that growth rates and longevities were, in descending order, willow > alder > poplar > spruce. Then relative dominance would also follow the same pattern. Deviations from this prediction are then presumably due to processes of facilitation, competitive inhibition, or stochastic/allogenic factors.

To determine whether facilitative or competitive interactions exist, data can be collected on the ecophysiology of the successional species. Responses to experimental perturbations and removal of critical species can explain, for example, whether alder facilitates or inhibits growth of spruce. Such removal experiments have been done (cf. McCormick 1968, Keever 1979) with annuals and short-lived perennials but are obviously more difficult to do with trees. To appropriately evaluate the growth of spruce with and without alder, for example, would take several decades. Yet shorter-term experiments (cf. Binkley et al. 1984, chapter three) do provide preliminary information on species interactions. With such physiological data, deviations from predicted successional patterns based on life history traits can then be explained in terms of competitive or facilitative processes. If physiological responses are not sufficient to explain deviations from the null model, stochastic or allogenic processes are important in determining the successional sequence.

These processes may not be constant but may vary during the life span of each species and throughout the duration of the entire successional sequence. For example, on the Tanana River flood plain, alder inhibits establishment of spruce seedlings (chapters two, three) but may facilitate later growth of spruce trees. Allogenic processes such as flooding and silt deposition become less influential with successional time as biotic controls over soil development and species survival increase. Changes in the relative importance of each process can affect rates or types of species replacements. Successional change is the result of the interaction of all of these processes.

SUMMARY

There are many questions that remain unanswered in the study of plant succession (McIntosh 1981). Perhaps the most basic of these is whether succession follows a predictable pattern of ecosystem development with properties emerging that are greater than the sum of the parts (Odum 1969), or whether succession is merely a result of interacting plant life histories (Miles 1979). There has been an historical failure of unifying generalities applied to the succession process (McIntosh 1981). Whittaker and Levin (1977) suggest attention should be centered more on analyzing, modeling and comparing individual cases than on attempting generalizations from every study. Alternatively, certain basic processes may be common to many successional sequences (chapter four). Consequently, whereas the conclusions from the present study are based on detailed field experiments, their contribution to successional theory is dependent not only on their repeatibility in this and similar ecosystems, but also on the validity of current generalizations about succession.

Most studies of forest succession can examine only a short interval of the whole successional sequence. Consequently, the present study focused on seed dispersal, seedling establishment, and seedling physiology. These factors are of particular importance on the Tanana River flood plain where only spruce seedlings establish after the initial stages of succession and where initial colonization patterns largely determine the first 200 yr of succession.

Transplanted seedlings provided a comparison of seedlings responses to each successional stage. However, conclusions based on these transplants must consider the effects of transplant shock. Longer-term studies and studies of species interactions at later stages of development will complement the present study. Studies of the causes of senescence and mortality will be particularly helpful in understanding the mechanisms of species replacements.

This study will contribute to the development of management plans for timber stands on interior Alaska flood plains. Flood plain forests have traditionally been the most accessible forests of the interior. Renewed interests in firewood for heating and local sources for lumber have again focused attention on these highly productive forests. A knowledge of seed rain, natural regeneration potential, facilitative and competitive interactions of commercial species are necessary to promote economically and ecologically sound forestry practices. The negative effects of alder trees on white spruce seedlings suggest caution be used in planting alder for soil improvement. Yet moderate responses to fertilization by spruce seedlings in all stages not dominated by alder indicate some soil-improvement procedures would be useful. The rapid growth rates and abundant natural regeneration of poplar suggest its use in fast-rotation forestry practices. Mineral seed beds are necessary for all species, so some seed bed preparation would be necessary to obtain stand regeneration.

The pattern of soil development on the Tanana River flood plain in central Alaska is initially controlled by the abiotic factors of flooding and silt deposition (Van Cleve et al. 1981, chapter one). Soil particle size and moisture retention affected nutrient availability but did not have a direct effect on germination or seedling survival. Other factors such as water table, flooding, silt deposition, and forest litter were more important (chapter two). Within 30 years of silt bar stabilization, biotic factors were an important influence in soil development. The nitrogen-fixing alder had the greatest impact on soil development, increasing Kjeldahl and KCl extractable nitrogen pools and decreasing pH (chapter one).

Seeds of all four study species arrived and germinated on early successional silt bars (chapter two). However, willow and poplar seeds and seedlings were more numerous than alder and spruce, probably because their lighter seeds are more readily dispersed. The absence of forest stand regeneration and the failure of all seedlings except spruce to establish in later successional stages suggests the applicability of a modified initial floristic composition (IFC) model (Egler 1954): after initial silt bar colonization by all species, the seral communities were dominated first by the short-lived willow and alder, then by poplar and finally by the long-lived spruce.

Seedling growth was limited by low nutrients in early succession (chapter three). However, despite increases in nitrogen availability from alder, seedling growth then became limited by root and light competition from overstory alder and poplar and by increased herbivory from hares. Photosynthetic rates were lower in the shade of alder thickets than on the more open bars. The physiological responses of seedlings may alter the relative abundance of species in each stage but relative longevities appear to be more important in determining the overall successional pattern.

Although no one of the models adequately explains the Tanana River flood plain succession, the models that seem most appropriate are the tolerance model (Connell and Slatyer 1977) and the initial floristic composition (IFC) model (Egler 1954). All species colonize very early in the sequence (IFC) and, once established, do not appear to affect the general pattern of sequential dominance. The approximately 30-year-old alder thickets appear to competitively inhibit new seedling establishment but by then poplar and sometimes spruce are well established and willow is dying. The causes of senescence and death have not been studied for this sequence so it is not known if mortality is due primarily to competitive interactions or inherent longevities. The relevance of the facilitation model (Connell and Slatyer 1977) to primary succession is discussed below.

Terrestrial primary succession is commonly considered the last bastion where Clementsian facilitation still seems to apply (Connell and Slatyer 1977, Noble 1981, Finegan 1984). Scanty experimental data (see chapter three) shows early successional plants may be nutrient limited but the successional consequences of this are still speculative. To show that poplar grows better on glacial moraines when fertilized with alder litter (Lawrence et al. 1967) suggests alder may facilitate poplar but this assumption needs further experimental verification. Alder may have detrimental effects on poplar growth as well (chapter three).

Observations of rates of growth of trees on glacial moraines in Alaska (Cooper 1923, 1931, Crocker and Major 1955, Lawrence 1958, 1979) are not substantial enough to support a particular successional theory (Finegan 1984, chapter three). Interestingly, work by Cooper (1923, 1931, 1939) has been interpreted as supportive of both life history based models (Miles 1979) and facilitation (Finegan 1984). Both interpretations are possible. Cooper states (1923) that the spruce that are present before alder thickets develop are stunted. Yet he also says (Cooper 1923) alder is not necessary for good spruce growth.

The debate about the existence of facilitation is complicated by the broad connotations the term has acquired. Besides the original meaning applied to plant interactions (Connell and Slatyer 1977) and the application to seed dispersal (Finegan 1984), autogenic soil development has been thought to facilitate species growth in primary succession (Olson 1958, Lawrence 1979, Van Cleve and Viereck 1981).

Facilitation due to species attributes must be distinguished from facilitation due to biogeochemical processes (McIntosh 1981, chapter four). Are the microsite changes in nutrient availability, soil texture, soil profile development, and soil chemistry that a nitrogen fixer such as alder causes (chapter one) actually facilitating growth of other species? Aboveground microclimatic changes need to be considered too. Physiological responses of seedlings in this study (chapter three) suggest the net short-term effect is negative, but the effects of alder on poplar or spruce trees may be positive in the long term. The role of facilitation in primary terrestrial succession will be clarified as more experimental work is undertaken.

A new framework for a general theory of succession will probably contain elements of each of the Connell and Slatyer models (1977) and IFC (Egler 1954). It will likely be reductionistic in its approach but flexible enough to retain obvious merits of the holistic approach to ecosystems (Finegan 1984), especially as these emergent properties are more carefully defined. It will need to account for developmental phases of plant life histories, the dynamics of species invasions by both asexual and sexual reproduction, the role of nutrient limitations and the influence of recurring disturbances, none of which is adequately addressed in current models (Loucks 1981). It may even need to be ecosystem specific. There is no a priori reason to assume that colonization of silt bars is guided by the same principles as colonization of clearcut woodlands or tropical lava flows or arctic vehicle tracks. Ultimately, understanding of the natural cycling of vegetation patterns will guide us in managing and reclaiming disturbed systems. Basic principles of succession will be particularly helpful if they are the result of actual experimental study.

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