Vegetation Succession and Disturbance on a Boreal Forest Floodplain, Susitna River, Alaska

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Vegetation development along the Susitna River floodplain exhibits multiple successional pathways in response to disturbances such as flooding, ice scour, wind, browsing, and logging. These can rejuvenate sites or slow vegetation development through surface erosion, deposition, and stem bending. Youngest vegetation types were dominated by Variegated Horsetail (*Equisetum variegatum*) on silty sites, Feltleaf Willow (*Salix alaxensis*) and Tall Blueberry Willow (*S. novae-angliae*) on medium-textured sites, Balsam Poplar (*Populus balsamifera*) on sandy sites, and Yellow Dryas (*Dryas drummondii*) on cobbly sites. Although Thinleaf Alder (*Alnus tenuifolia*) was sparse in early succession, it grew more rapidly than other species and created a closed overstory with poorly developed understory early in intermediate succession. Browsing disturbances temporarily limited height growth of willows and Balsam Poplar. After Balsam Poplar exceeded the reach of Moose (*Alces alces*), it grew taller than Thinleaf Alder to form Young Poplar Forests. As trees matured and natural thinning occurred, Old Poplar Forests formed with a woody understory including White Spruce (*Picea glauca*). Uprooted trees exposed mineral microsites for germination of Paper Birch (*Betula papyrifera*) seeds. These sites eventually developed into the Paper Birch - White Spruce Forests of late succession with a well-developed shrub understory.

Key Words: Moose, *Alces alces*, vegetation succession, disturbance, floodplain, browsing, riparian, Susitna River, Alaska.

Vegetation succession along floodplains of northern glacial rivers is affected by flooding, ice, wind, and wildlife interactions. The Susitna River drains over 2 million ha in southcentral Alaska near the population center of the state. It provides recreational opportunities as well as habitat for many species of wildlife. Concerns about potential hydroelectric development impacts in the Susitna basin prompted a study to examine present structure of the vegetation, its changes over time, causes of change, and wildlife interactions.

Many other northern rivers have been studied, including the Colville River (Bliss and Cantlon 1957), Chena (Viereck 1970), Tanana (Wolff 1976; Van Cleve et al. 1980; Walker and Chapin 1986; Walker et al. 1986; Viereck et al. 1993, Van Cleve et al. 1996), Stikine (Craighead et al. 1984), Exit Glacier Creek (Helm and Allen 1995) in Alaska and the Mackenzie (Gill 1972), Beatton (Nanson and Beach 1977), and Lillooet (Teversham and Slaymaker 1976) in Canada. The Susitna River differs from many northern river systems in that the (1) youngest stage of vegetation succession has four distinct communities based on substrate textures and (2) a well-developed Paper Birch (*Betula papyrifera*) - White Spruce (*Picea glauca*) Forest is present in later stages of succession. Browsing by Moose (*Alces alces*), Snowshoe Hare (*Lepus americana*), and Beaver (*Castor canadensis*) significantly alters vegetation structure as well as rates or pathways of succession (Bryant and Chapin 1986; Johnston and Naiman 1990; Moen et al. 1990; Naiman et al. 1994). Regeneration of Balsam Poplar (*Populus balsamifera*) on surface-disturbed soils following logging has been documented (Zasada et al. 1981). Prior Alaskan studies have focused on nutrient cycling (Van Cleve et al. 1980; Van Cleve et al. 1986; Van Cleve et al. 1993; Viereck et al. 1993) or biological controls during certain stages of vegetation succession (Bryant and Chapin 1986; Walker and Chapin 1986; Walker et al. 1986). Although effects of windthrow have been documented in southeastern Alaska (Deal et al. 1991; Bormann et al. 1995), ice effects have been largely ignored. Existing vegetation, differences on marked plots 3 and 14 years later, and aerial photographs from 1951 and 1980 were used to document the various successional stages along the Lower Susitna River and propose a conceptual model of effects of various disturbances on the successional pathways.

Site Description

The 500-km-long Susitna River drains the Alaska Range to the north and west, and the Talkeetna Mountains to the east, and flows into Cook Inlet to the south. This study focused on the lower part of the river from Chase (62.5° N 150.1° W) downstream to the mouth of the Deshka River (61.7° N 150.3° W) (Figure 1). Three distinct reaches had different channel structures which affected the amount of fluvial disturbance and the resultant vegetation and substrate structure. The Susitna River above its confluence with the Chulitna River contained armored channels and was subject to larger ice jams during

TABLE 1. Land covered (%) by each vegetation type in the Susitna River floodplain.[a]

Class	Alaska Vegetation Classification	Stands	Number of Transects	Lower[b]		Middle		Upper		Total	
Barren				15		26		4		14	
Early shrub				4		3		8		5	
Dryas	Dryas Dwarf Scrub	18	4								
Juvenile Poplar	"Open Low Scrub"[c]	5, 20, 21, 25	15		2		2		8		3
Willow	Open Low Scrub	6, 16, 22	9		1						<1
Horsetail	Mesic Forb Herbaceous	1, 8, 9, 13, 14, 15	18		1		1				1
Intermediate				18		17		6		15	
Alder	Closed Tall Shrub Scrub	2, 19, 23, 27	20		17		15		6		14
Young Poplar	Closed Broadleaf Forest	10, 12, 26	18		1		2		0		1
Late				51		47		73		55	
Old Poplar	Open Broadleaf Forest	3, 17, 24, 28	24		22		29		24		24
Birch - Spruce	Open Mixed Needleleaf - Broadleaf Forest	4, 11, 29	20		24		17		30		24
Paper Birch					2				19		5
White Spruce					3		1				2
Other				12		6		8		10	
Bog					5		5		0		4
Wet sedge-grass					7		1		2		5
Other forest									6		1

[a]Data are interpreted from aerial photograph of 24 August 1980, 1:48 000; taken at flow rates of 510 cms Gold Creek; 1840 cms Sunshine; 3370 cms Susitna Station. Percents for subtypes form a separate column to the right of the main types.
[b]Lower river is from Deshka River to Montana Creek, Middle is from Montana Creek to Chulitna River, and Upper is from Chulitna to Gold Creek.
[c]Closest Level III community in Alaska Vegetation Classification (Viereck et al. 1992) for sampled stages.

breakup compared to the more open reaches with braided and split channels. The section immediately below the Chulitna River had more cobbles than the other two reaches, but the finest materials were in the lowest reach. Reduced gradients and greater width below the confluence resulted in slower water velocities and more sand deposition in the lowest two stretches.

The Susitna River flow is frequently highest in July and August during summer rains when its contributory glaciers are also melting, but high flows also occur during breakup (personal observations). Lowest water levels occur during freezeup, but staging behind ice may cause river flows almost to summer levels. Additionally, overflow may refreeze and encase some plants in ice.

Methods

Vegetation was stratified into successional stages based on site visits in 1980 and early summer 1981 and on black-and-white aerial photographs of the river in 1951 and 1980 (1:48 000). These stages were identified as Early Shrub (Dryas, Juvenile Poplar, Willow, Horsetail), Intermediate (Alder, Young Poplar), and Late (Old Poplar, Birch - Spruce). Sample sites of relatively homogeneous vegetation were selected in each successional stage in the three reaches of the river and sampled in 1981 (Figure 1). Eleven (1, 5, 6, 8, 9, 13, 14, 16, 21, 22, 25) of the thirteen Early Shrub sites were resampled in 1984, one (20) had been completely or partially eroded between 1981 and 1984 and one (18, Yellow Dryas) was not resampled because it was a minor type. A former Birch - Spruce stand that had been logged was examined in 1981 and a Balsam Poplar - White Spruce Forest was examined in 1984 to understand the transition between Old Poplar Forest and Paper Birch - White Spruce Forest but the site was not sampled quantitatively. Sites were identified according to the Alaska Vegetation Classification System (Viereck et al. 1992), where possible, but that system was not designed for early successional plant communities (Table 1).

Most sites were sampled with four randomly-oriented, non-overlapping 30-m transects in June 1981, and two additional transects were measured in August to obtain adequate precision. End points were marked with 1-m lengths of electric conduit and labelled with metal tags. Phenological development had insignificant effect on plant cover between June and August because leaves had already expanded in June. Some Early Shrub sites were sampled with as few as two transects because of their small size.

Vegetation cover by species in each height category (0.0-0.4 m, 0.4-1 m, 1-2 m, 2-4 m, 4-8 m, 8-16 m, and >16 m) was recorded at points spaced 50 cm along each 30-m transect. These categories were selected to depict the height structure of overstory

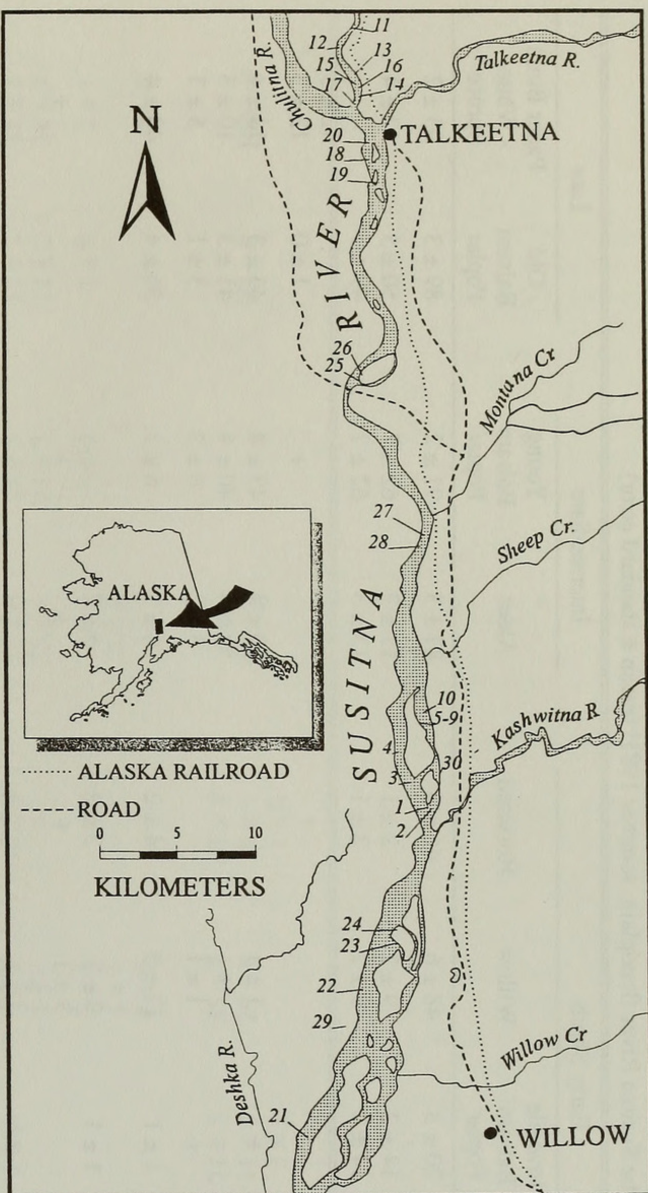

FIGURE 1. Location of study sites along the Susitna River, southcentral Alaska.

and understory and susceptibility to browsing disturbance. Leaf cover for any species at any point occurred within one height category. Hits on taller trees and shrubs were observed through an 8 × sighting scope mounted vertically on a pole placed over the point. The transect length and point spacing had been modified from prior vegetation sampling efficiency studies. Cover by life form categories was determined by counting points for the appropriate species within that life form, thus taking overlapping vegetation into account. Cover by mosses and lichens was minor because of flooding and litter deposition so they are only reported by category.

Ages and heights of dominant woody plants were measured on two randomly selected individuals per species along each transect in 1981. Heights of tall individuals were estimated using a range finder to focus on the tree top. The minimum age of each

TABLE 2. Cover (%) of vascular plants and life form categories along the Susitna River floodplain, summer 1981[a] (mean ± standard error).

	Early Shrub				Intermediate		Late	
	Dryas	Juvenile Balsam Poplar	Willow	Horsetail	Alder	Young Balsam Poplar	Old Balsam Poplar	Paper Birch - White Spruce
Total vegetation	9 ± 3	20 ± 3	48 ± 6	46 ± 6	87 ± 3	91 ± 2	89 ± 3	93 ± 2
Trees	6 ± 2	14 ± 2	9 ± 2	2 ± 1	13 ± 3	62 ± 7	50 ± 5	52 ± 4
Populus balsamifera, Balsam Poplar	6 ± 2	14 ± 2	9 ± 2	2 ± 1	13 ± 3	62 ± 7	49 ± 5	
Betula papyrifera, Paper Birch								42 ± 5
Picea glauca, White Spruce						+	1 ± 0	12 ± 3
Tall shrubs		+	1 ± 1		60 ± 4	47 ± 4	43 ± 3	14 ± 4
Alnus tenuifolia, Thinleaf Alder			+		59 ± 4	40 ± 4	41 ± 3	10 ± 3
Alnus sinuata, Sitka Alder		+	1 ± 1		3 ± 2	8 ± 2	3 ± 1	5 ± 3
Low shrubs	4 ± 1	1 ± 1	12 ± 3	4 ± 2	6 ± 2	6 ± 1	36 ± 4	40 ± 4
Dryas drummondii, Yellow Dryas	4 ± 1							
Salix alaxensis, Feltleaf Willow		1 ± 1	9 ± 2	3 ± 2	5 ± 2			
Salix novae-angliae, Tall Blueberry Willow			3 ± 1	+	+	+		+
Salix arbusculoides, Little Tree Willow			+					
Salix spp., willow			1 ± 0	1 ± 0	+			+
Viburnum edule, High Bushcranberry					+	3 ± 1	21 ± 3	19 ± 4
Rosa acicularis, Prickly Rose					+	3 ± 1	14 ± 2	20 ± 2
Rubus idaeus, American Red Raspberry					1 ± 0	+	4 ± 1	3 ± 1
Ribes triste, American Red Currant					+		3 ± 1	5 ± 1
Echinopanax horridum, Devil's Club							1 ± 1	4 ± 2
Perennial Forbs		5 ± 2	26 ± 6	41 ± 6	11 ± 3	9 ± 2	23 ± 4	44 ± 4
Equisetum variegatum, Variegated Horsetail		5 ± 2	25 ± 6	41 ± 6	1 ± 0		1 ± 1	8 ± 3
Equisetum arvense, Meadow Horsetail				+	1 ± 1	+	3 ± 1	19 ± 6
Equisetum sylvaticum, Woodland Horsetail		+					+	2 ± 1
Epilobium latifolium, Dwarf Fireweed		+			+	+		+
Epilobium angustifolium, Tall Fireweed					4 ± 2	1 ± 1		1 ± 0
Artemisia tilesii, Tilesy Sage			+		3 ± 1	3 ± 1		
Astragalus or *Oxytropis*		1 ± 0	+			+		
Hedysarum sp.			+		+			
Cornus canadensis, Bunchberry							+	1 ± 0
Heracleum lanatum, Cow Parsnip						+	+	
Mertensia paniculata, Tall Bluebell						1 ± 1	2 ± 1	2 ± 1
Pyrola spp., Wintergreen						+	+	
Rubus arcticus, Nagoon Berry						+		+
Streptopus amplexifolius, Clasping Twisted-Stalk						+	1± 0	1± 0

Continued

TABLE 2. (*Continued*).

	Early Shrub				Intermediate		Late	
	Dryas	Juvenile Balsam Poplar	Willow	Horsetail	Alder	Young Balsam Poplar	Old Balsam Poplar	Paper Birch - White Spruce
Sanguisorba stipulata, Sitka Burnet						+		
Trientalis europaea, Twin-Flower					+		+	+
Galium boreale, Northern Bedstraw					+	+	+	+
Dryopteris dilatata, Spinulose Shield- Fern							1 ± 0	7 ± 3
Gymnocarpium dryopteris, Oak-Fern							5 ± 2	4 ± 1
Matteuccia struthiopteris, Ostrich- Fern						+	7 ± 3	1 ± 1
Grass-likes		1 ± 0	2 ± 1	1 ± 0	38 ± 6	23 ± 5	12 ± 2	18 ± 3
Calamagrostis canadensis, Bluejoint Reedgrass			1 ± 1	+	38 ± 6	23 ± 5	12 ± 2	18 ± 3
Ground layer			2 ± 1		2 ± 2	1 ± 0	1 ± 0	2 ± 1
Lichens			1 ± 1		1 ± 0			
Moss			1 ± 0		1 ± 1	+	+	1 ± 0
Other Categories								
Bare Ground	50	71 ± 5	35 ± 7	47 ± 6	+			
Litter	16	11 ± 4	29 ± 8	8 ± 1	99 ± 1	+	92 ± 6	100 ± 0
Gravel, Cobbles	27	3 ± 1		1 ± 0				
Water				+				

[a] Number rounded to closest percent. '+' = <0.5% cover.

TABLE 3. Characteristics of low shrub-sized plants in different successional stages, summer 1981, Susitna River.[a]

	Early				Intermediate	
	Dryas	Juvenile Balsam Poplar	Willow	Horsetail	Alder	Young Balsam Poplar
Salix alaxensis						
Height (m)	0.33 ± 0.27	0.51 ± 0.5	0.79 ± 0.10	0.55 ± 0.07	1.55 ± 0.16	
Crown length (cm)	0.22 ± 0.13	0.3 ± 0.0	0.31 ± 0.03	0.16 ± 0.02	0.55 ± 0.08	
Age	5 ± 3	5 ± 1	6 ± 1	3 ± 0	8 ± 1	
Crown dominance[b]	2	2	2	2	6	
n	2	25	18	25	19	
Salix novae-angliae						
Height (m)		0.81 ± 0.0	0.83 ± 0.17	0.37 ± 0.04	1.12 ± 0.12	1.25 ± 0.14
Crown length (cm)		0.6 ± 0.0	0.30 ± 0.04	0.09 ± 0.01	0.51 ± 0.11	0.53 ± 0.07
Age		4	4 ± 0	2 ± 0	8 ± 2	9 ± 2
Crown dominance		2	2	2	6	6
n		1	7	16	4	8
Populus balsamifera						
Height (m)	0.19 ± 0.06	0.32 ± 0.06	0.49 ± 0.10	0.61 ± 0.15	2.48 ± 0.59	
Crown length (cm)	0.19 ± 0.02	0.22 ± 0.03	0.22 ± 0.03	0.32 ± 0.12	1.20 ± 0.37	
Age	5 ± 0	7 ± 1	7 ± 0	5 ± 1	16 ± 3	
Crown dominance	1	2	2	2	6	
n	8	30	18	15	7	
Alnus tenuifolia						
Height (m)			1.67 ± 0.92	0.54 ± 0.09	1.19 ± 0.18	1.39 ± 0.12
Crown length (cm)			0.62 ± 0.29	0.22 ± 0.03	0.43 ± 0.05	0.73 ± 0.09
Age			3 ± 0	3 ± 0	4 ± 1	6 ± 1
Crown dominance			3	2	6	6
n			2	2	7	32
Alnus sinuata						
Height (m)					2.46 ± 0.46	
Basal diameter (cm)					2.23 ± 0.66	
Age					7 ± 1	
Crown dominance					5	
n					4	
Picea glauca						
Height (m)					0.71	
Crown length (cm)					0.34	
Age					10	
Crown dominance					6	
n					1	

[a]Numbers are rounded to nearest unit of measurement. n=number of stems sampled.
[b]Crown dominance: 1=open grown, 2=dominant, 3=codominant, 4=intermediate, 5=overtopped, 6=subordinate, 7=ground.

measured tree or shrub was determined by counting growth rings on cross sectional cuttings or cores taken as near the ground as possible. Young woody stems were excavated on some sites to determine the total age of stem, part of which had been buried by sediment. Ages analyzed included only the above-ground age. Densities were also recorded by size class: < 0.4 m, 0.4-2 m, 2 m - 4 m tall and <4 cm DBH (diameter-at-breast-height),<4 m tall and >4 cm DBH, and > 4 m tall. Stems >0.4 m tall were considered available browse even though snow could reduce that availability in deep snow years. Moose could reach stems up to 4 m tall or > 4 m tall if DBH was < 4 cm. These categories are related to the amount of browsing disturbance possible and to the vegetation succession. Crown dominance was also reported for each species: 1 open grown, 2 dominant (received sunlight from above and sides), 3 codominant (received sunlight from above but not the sides), 4 intermediate (barely reaching main canopy), 5 overtopped (below general level of canopy), 6 subordinate (under overtopped), and 7 ground - lowest level. Two soil pits were dug in each site to evaluate depositional profiles.

To estimate the proportion of land area covered by each of the vegetation types at a given stream flow,

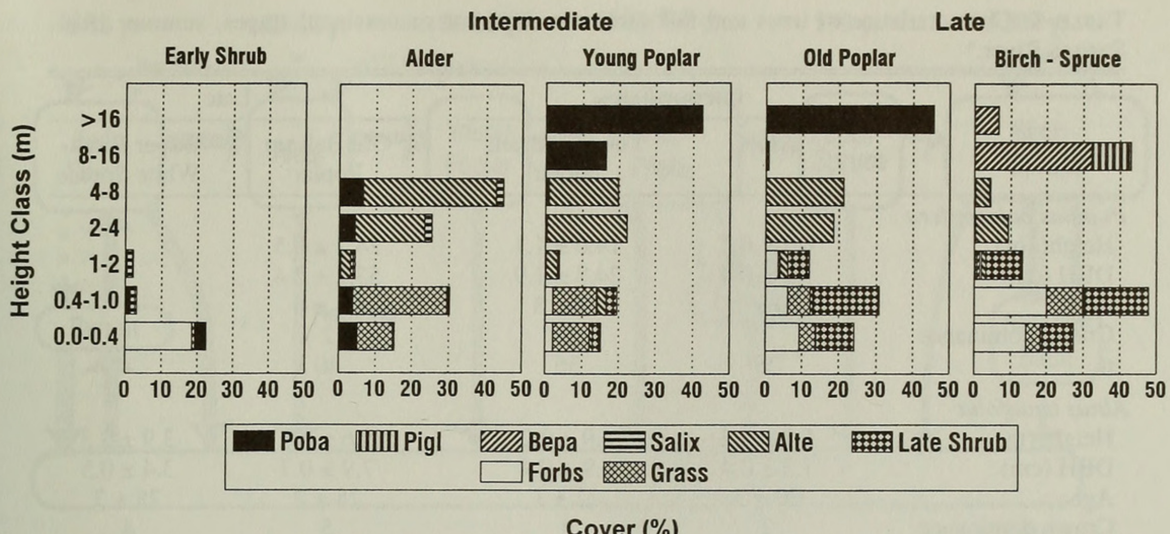

FIGURE 2. Scaled relative cover (%) (relative cover × total vascular plant cover) by major species or herbaceous life form and height class in each successional stage. Shrubs between 0.4 and 4 m tall are subject to Moose browsing disturbance. Poba = *Populus balsamifera*, Bepa = *Betula papyrifera*, Pigl = *Picea glauca*, Salix = *Salix alaxensis* + *Salix novae- angliae*, Alte = *Alnus tenuifolia*, Late shrub = *Rosa acicularis* + *Viburnum edule* + *Ribes triste*.

transects were plotted approximately every 4 cm (2 km) on aerial photographs (1:48 000 black- and-white taken in 1980). Points were systematically plotted approximately every 7 mm (350 m) along each transect from the base of slope on one side of the river to the base of first hill on the other side, which was considered the limit of the floodplain. The points were classified according to successional stage during a helicopter survey in June 1981.

Results

General

Early Shrub sites were most common on the two lower reaches where the floodplain was wide with split and braided channels. Approximately 20 to 30% of available land in this reach was occupied by Barren or Early Shrub stages (Table 1). Above the Chulitna River confluence, the river was narrower with well-defined channels. Here the mature forests predominated and occupied almost three-fourths of the available land area. Similarly the intermediate stage only occupied 6% of the area compared to >17% in the lower two reaches.

Some Early Shrub sites have remained in early succession from 1951 (aerial photographs) to 1995 although they are periodically flooded. While some Early Shrub sites eroded between 1981 and 1995, others advanced successionally. Part of a Birch -

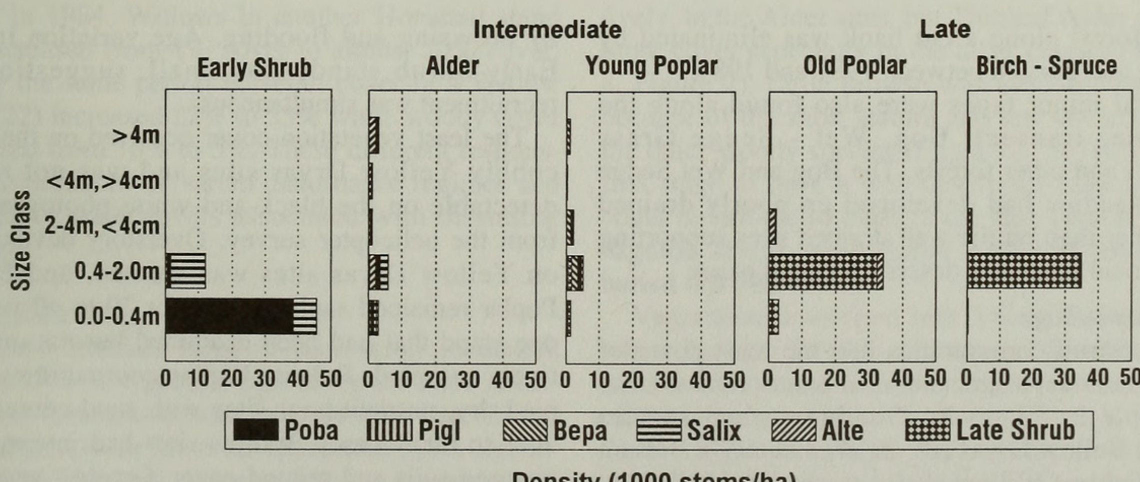

FIGURE 3. Density (stems ha^{-1}) of major woody species by size class in each successional stage. Size classes are by height (first number) and DBH (second number, if present). Stems sized 0.4 to 2.0 m tall and 2 to 4 m with DBH < 4 cm are subject to Moose browsing disturbance. Species codes are explained in Figure 2.

TABLE 4. Characteristics of trees and tall shrubs in different successional stages, summer 1981, Susitna River.[a]

	Intermediate		Late	
	Alder	Young Balsam Poplar	Old Balsam Poplar	Paper Birch-White Spruce
Populus balsamifera				
Height (m)	6.2 ± 0.3	14.0 ± 1.1	24.7 ± 0.5	
DBH (cm)	7.2 ± 0.4	24.8 ± 1.9	53.2 ± 2.4	
Age	19 ± 1	44 ± 3	98 ± 6	
Crown dominance	2	2	2	
n	28	36	40	
Alnus tenuifolia				
Height (m)	5.3 ± 0.2	4.9 ± 0.2	5.6 ± 0.3	3.9 ± 0.3
DBH (cm)	7.3 ± 0.4	6.9 ± 0.4	7.9 ± 0.7	3.4 ± 0.5
Age	20 ± 3	22 ± 1	28 ± 2	28 ± 3
Crown dominance	2	4	5	4
n	40	32	36	12
Alnus sinuata				
Height (m)	2.2 ± 0.5	3.5 ± 1.0	2.4	3.4 ± 0.8
DBH (cm)	3.4 ± 2.0	2.6 ± 0.4	2.1	7.3 ± 1.5
Age	17 ± 4	22 ± 3	38	50 ± 12
Crown dominance	4	5	5	5
n	4	3	1	3
Picea glauca				
Height (m)	2.2 ± 0.7	2.6	10.9 ± 1.0	13.8 ± 1.0
DBH (cm)	5.0 ± 0.7	-	21.4 ± 1.7	26.3 ± 1.8
Age	12 ± 2	13	100 ± 8	90 ± 5
Crown dominance	4	6	3	2
n	6	1	16	38
Betula papyrifera				
Height (m)	3.7 ± 0.8	4.6 ± 4.0		12.8 ± 0.6
DBH (cm)	-	-		28.1 ± 1.5
Age	12 ± 2	26 ± 17		70 ± 3
Crown dominance	4	4		2
n	7	2		35

[a]Numbers are rounded to nearest measurement unit. n=number of stems sampled.
[b]Crown dominance: 1=open grown, 2=dominant, 3=codominant, 4=intermediate, 5=overtopped, 6=subordinate, 7=ground.

Spruce forest along a cut bank was eliminated by flooding and erosion between 1981 and 1984.

Several minor types were also found along the helicopter transect: Bog, Wet - Sedge Grass Meadow, and other forests. The Bog and Wet Sedge Grass Meadow had developed on poorly drained soils rather than on the well-drained sites supporting successional pathways described in this paper.

Early Shrub Stage

Early Shrub communities had the least cover of any successional stage, and most plants were <0.4 m tall (Table 2, Figure 2). Dominant plant species included Yellow Dryas (*Dryas drummondii*), Balsam Poplar, Feltleaf Willow (*Salix alaxensis*), Variegated Horsetail (*Equisetum variegatum*), or combinations of these. Willows were the only species in this stage with mean height > 0.40 m (Table 3). Heights of Balsam Poplar and Feltleaf Willow were suppressed by browsing and flooding. Age variation in most Early Shrub stands was small, suggesting that recruitment was simultaneous.

The least vegetation cover occurred on the harsh, cobbly Yellow Dryas sites and was not readily detectable on the black-and-white photographs or from the helicopter survey. Overstory development on Yellow Dryas sites was stunted, and Balsam Poplar remained sapling sized for 20 to 40 years on one stand that had been examined but not quantitatively sampled. Balsam Poplar communities occupied dry, nutrient-poor sites with sand content near 90% in many cases. Willow sites had intermediate-textured soils and ground cover. Greatest vegetation cover and finest-textured soils, with silt >60%, among the Early Shrub sites occurred on Horsetail sites, which also included traces of sedges (*Carex* spp.) and cottongrasses (*Eriophorum* spp.).

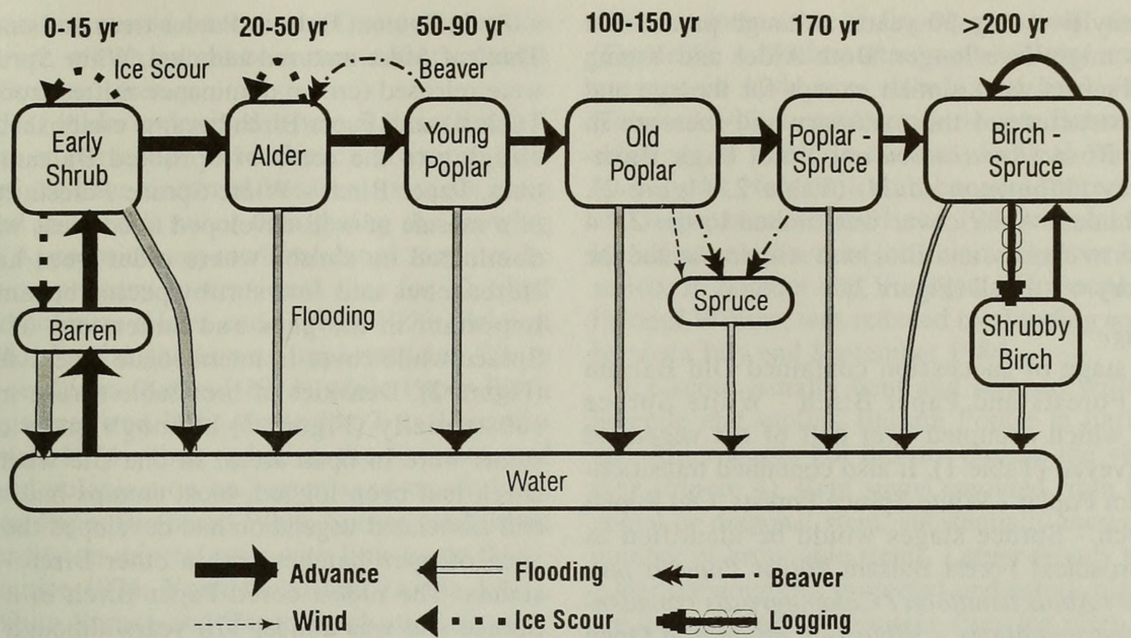

FIGURE 4. Conceptual model of successional pathways along the Susitna River and their controlling factors. Flooding includes erosion and sedimentation. Years above diagram represent generalizations of when types may dominate. Width of arrows represents relative importance of the pathway.

Thinleaf Alder grew more rapidly than other shrubs, 5-year-old alders being approximately 1.5 m tall while same-aged Balsam Poplars averaged approximately 0.5 m in height. Willow stands had the best-developed shrub community within the Early Shrub stage (Tables 2, 3). These shrubs formed the overstory (crown dominance = 2, Table 3).

Many Early Shrub sites changed considerably between 1981 and 1984. One stand (20) was sufficiently eroded that it could not be resampled. Two Juvenile Balsam Poplar stands (21 and 25) had almost identical cover values but stand 21 had more litter in 1984. One horsetail stand (16) had more horsetail and more bare ground in 1984 compared to 1981. Two horsetail stands (8, 9) had more Balsam Poplar in 1984. Willows in another Horsetail stand (13) increased from 1% cover to almost 20% cover. During the same period horsetail cover in a Willow stand (22) increased 22% to 53% while woody cover decreased from 18% to 5%. These different responses were functions of varied disturbance regimes and changes in water levels associated with dissimilar channels.

Intermediate Stage

The intermediate stage of succession accounted for 6 to 18% of vegetated land along the three reaches of the floodplain, and most of this was Closed Tall Scrub Alder (Table 1). These sites were characterized by Thinleaf Alder or Balsam Poplar which had developed into tall shrubs or trees. These would be classified as Open Tall Scrub *Alnus tenuifolia / Calamagrostis canadensis* and Closed Broadleaf Forest Balsam Poplar *Populus balsamifera / Alnus tenuifolia / Calamagrostis canadensis*, respectively at Level V of Viereck et al. (1992). Low shrub-sized plants (<1.5 m tall) were rare in the understory (crown dominance = 6) beneath a Thinleaf Alder or Balsam Poplar overstory (Figure 3, Tables 3, 4).

Total vegetation cover in Alder stands averaged 87% across all height classes (Table 2). Thinleaf Alder provided 59% cover, whereas Balsam Poplar provided only 13% cover, but was present in all stands. Bluejoint Reedgrass (*Calamagrostis canadensis*) produced a dense understory with 38% cover. Average ages of tall shrub-sized Thinleaf Alder and Balsam Poplar in Alder sites were approximately 20 years (Table 4). Mean Balsam Poplar and Thinleaf Alder heights were 6.2 and 5.3 m, respectively, in the Alder sites, but Thinleaf Alder provided more cover especially in the taller classes (Tables 2, 4, Figure 2). Little browse was available for Moose because of the short stature and low cover values of the other woody species (Figures 2, 3). This was the first stage to have a well-developed litter layer that could contribute to nutrient cycling. Multiple buried organic layers were found where sedimentation buried old litter layers.

Vegetation developed into Young Poplar Forests when Balsam Poplar overtopped Thinleaf Alder (crown dominance shifted from 2 to 4) and dominated the overstory with 62% cover (Figure 2, Tables 3, 4). These Balsam Poplar trees averaged 44 years of age and 14 m in height, which was more than double their height in the Alder stage and twice as tall as Thinleaf Alder in this stage. Thinleaf Alder stems had similar ages in both the Alder and Young Poplar Forests, suggesting that individual Thinleaf Alder stems may live only 20 years, although parent root systems might live longer. Both Alder and Young Poplar Forests were similar except for the age and species structure of the overstory and increase in Prickly Rose (*Rosa acicularis*) and High Bush-cranberry (*Viburnum edule*) (Table 2, Figure 2). Most Thinleaf Alder cover was limited to the 2 - 4 and 4 - 8 m classes, and Bluejoint still dominated the understory < 1 m tall (Figure 2).

Late Stage

Late stage of succession contained Old Balsam Poplar Forests and Paper Birch - White Spruce Forests which occupied over half of the vegetated land surveyed (Table 1). It also contained transitional Balsam Poplar - White Spruce Forests. Old Poplar and Birch - Spruce stages would be identified as Open Broadleaf Forest Balsam Poplar *Populus balsamifera / Alnus tenuifolia / Calamagrostis canadensis - Rosa acicularis - Viburnum edule* and Open Mixed Forest Spruce - Paper Birch *Picea glauca - Betula papyrifera / Calamagrostis canadensis - Rosa acicularis - Viburnum edule* types, respectively, at Level V of the Alaskan Vegetation Classification (Viereck et al. 1992). Old Balsam Poplar Forests characterized 25 to 40% of the vegetated floodplain while mixed stands of Paper Birch and White Spruce occupied 23 to 32% of the area (Table 1).

Although Old Balsam Poplar sites averaged 90% total vegetation cover, the overstory had thinned relative to the Young Poplar Forest (Figure 2). Shrub cover and density, especially of browse species, increased substantially (Figure 2). The oldest Balsam Poplar tree measured in 1984 was approximately 170 years, but many were 110 to 140 years of age. One (stand 3) was an Old Poplar site that had been flooded between 1981 and 1984, and litter was reduced from 100% to 50%. White Spruce was not detected along the sampling transects in 1981, but 9% cover was reported in 1984. In 1981 several minor forbs were found [Tall Bluebell (*Mertensia paniculata*), Pyrola (*Pyrola* spp.), American Red Currant (*Ribes triste*), Northern Bedstraw (*Galium boreale*), ferns], but these were negligible in 1984. The site had about twice as much Prickly Rose, High Bushcranberry, and Bluejoint Reedgrass in 1984 as it did in 1981. Similarly, another stand (17) went from 67% to 1% litter and many small forbs were no longer present. Prickly Rose and High Bushcranberry tripled between 1981 and 1984.

Flooding was still an important factor affecting understory species in Old Poplar Forests as evidenced by the preceding observations and numerous buried horizons, indicating that a forest floor was present during the flooding (Viereck et al. (1993). Changes in vegetation types occurred most often when banks were eroded or plants were physically removed, rather than from these depositional events that temporarily altered understories.

As individual Balsam Poplar trees and understory Thinleaf Alder matured and died, White Spruce trees were released (crown dominance shifted from 3 to 2, Table 4), and Paper Birch became established on soil clinging to the roots of uprooted Balsam Poplar trees. Paper Birch - White Spruce Forests consisted of a mosaic of well-developed treed areas with gaps dominated by shrubs where older trees had died. Herbaceous and low shrub species became more important in the gaps and understory of Birch - Spruce while cover in intermediate layers decreased (Figure 2). Densities of browsable shrubs increased substantially (Figure 3) although many of these stems were in open areas. In one site where Paper Birch had been logged, most stumps had sprouted and associated vegetation had developed the appearance of open patches within other Birch - Spruce stands. The oldest cored Paper Birch in a Birch - Spruce site was almost 170 years although ages of most mature trees were between 100 and 140 years while the oldest measured White Spruce tree was 124 years.

Some abandoned oxbows or otherwise poorly-drained sites developed into wetlands. These were dominated by Thinleaf Alder, Dwarf Arctic Birch (*Betula nana*), Buffaloberry (*Shepherdia canadensis*), Bluejoint Reedgrass, and sphagnum moss (*Sphagnum* spp.).

Discussion

Plant Species Establishment

The first plant species, such as Balsam Poplar and willows, to colonize a site had light, nondormant, wind- or water-dispersed seeds that germinated soon after landing on a moist, suitable substrate (Viereck 1970; Densmore and Zasada 1983; Walker et al. 1986; Helm and Allen 1995). Species that survived on these new surfaces had to survive flooding and sedimentation. Fall- and winter-dispersed seeds (Thinleaf Alder, Paper Birch, White Spruce) usually lagged summer dispersers by a year before they colonized.

Colonization appeared to be a stochastic event that did not occur each year (Walker et al. 1986). Survivability of new seedlings that germinated along high water lines depended on minimal flooding for the remainder of the summer (Sigafoos 1964; Fenner et al. 1985; Bradley and Smith 1986). Helm and Allen (1995) observed that Balsam Poplar seedling survival on a glacial floodplain may depend on dispersal close to summer rains, but early enough so that seedlings could survive flooding. Successful colonization along the Susitna might not occur each year since late summer flows were usually higher than spring flows. Two- to five-year old sites were rare both in 1981 and 1984 which suggested that new sites had not become available or were not colonized during the preceding few years. Bradley and Smith (1986) reported that suitable conditions for recruitment occurred once every five years on the Milk River, which would be a reasonable estimate for the Susitna River.

Thinleaf Alder colonized where Balsam Poplar, willows, or horsetails were already growing. This delay might have occurred because its seeds were dispersed in the fall rather than during the growing season. Appropriate mycorrhizal fungi may not be present on primary successional sites for Thinleaf Alder to colonize (Helm and Carling 1993; Helm et al. 1996). Partial shade was important for White Spruce seedlings (Safford 1974) while Paper Birch seedlings required light shade for 2 to 3 months (Brinkman 1974), thus reducing the likelihood of successful colonization on barren sand or silt bars. However, Paper Birch and White Spruce established more readily on mineral soils with little or no flooding (Clautice 1974; Youngblood and Zasada 1991). Most White Spruce and Paper Birch seed travel < 100 m (Zasada 1986), making distance from seed source a possible limiting factor.

Paper Birch generally became established after White Spruce, and seedlings occurred only on mineral soil on rootballs of trees uprooted by wind or gravity. This provided mineral soil and elevated the seedling above competition on the forest floor (Beatty and Stone 1986; Jonsson and Dynesius 1993). Old Paper Birch were primarily observed straddling rootballs from uprooted trees that were partially decomposed, indicating that the seedlings we observed on rootballs could indeed mature in those microsites. Gaps and windthrow microsites have been shown to be important for regeneration of other tree species at northern latitudes (Deal et al. 1991; Jonsson and Dynesius 1993).

Mechanisms of Successional Pathway Changes

Figure 4 depicts major successional pathways, relative importance (width of arrows) of each pathway, causes of changes, and approximate "time after stabilization" that various stages occurred. Burial of 5 to 10 years of plant growth with 0.5 m or more of sediment and rotten centers on older trees made aging only approximate. The Water compartment represented surface areas beneath water. Barren represented the first surfaces above water with little plant colonization (<2% cover). At any stage, erosion by flooding could cut banks, remove the substrate and vegetation, and return the location to Water. Older sites were found along cut banks while young sites were more often found on areas of recent deposition rather than along cut banks. Other disturbances usually prevented succession from advancing (arrow pointing to same cell) or regressed the site by removing the overstory.

The several phases within the Early Shrub stage could develop into each other (arrow cycling within that compartment), but substrate differences associated with the various phases likely resulted from different intensities of flooding and soil deposition (Figure 4). A Willow stand with willows and poplar present in 1981 was dominated by Variegated Horsetail with an understory of new Balsam Poplar seedlings in 1984. In contrast, Feltleaf Willow and Variegated Horsetail both became more abundant and larger between 1981 and 1984 on a hummocky, ice-affected site where the hummocks formed by ice action. In another site Variegated Horsetail, but not Feltleaf Willow, was reduced by flooding some time between July and September 1984.

Ice scour usually bent and scraped willows and juvenile and sapling Balsam Poplar in Early Shrub and Alder stages but did not change the vegetation type (Figure 4). Bent stems sprouted from the horizontal or diagonal stem, substantially increasing the number of browsable stems. Larger woody trunks of Alder communities protected understory plants from ice damage, but in younger sites ice often scraped the substrate, removing both the substrate and plants growing there. These became Barren sites. Ice also transported sediments to some sites.

Browsing by Moose and Arctic Hares slowed vegetation development by reducing heights on many shrubs in earlier stages. This allowed Thinleaf Alder to dominate more rapidly. Beavers were very active on some sites and removed most Balsam Poplar stems in a Young Poplar Forest, reverting it to an Alder site between 1981 and 1984 (Figure 4). Beavers also removed full-sized trees in Old Poplar Forests but did not alter the vegetation type. A hypothetical pathway exists for the formation of White Spruce stands if Beavers removed sufficient poplar from an Old Poplar Forest or Poplar-Spruce Forest. Shade and lack of mineral soil would probably preclude Paper Birch from growing on the site, thus favoring spruce establishment. Although other studies have noted substantial changes in vegetation as a result of tree-cutting by Beaver, the trees were Trembling Aspen (*Populus tremuloides*) (Johnston and Naiman 1990; Moen et al. 1990).

Disturbances could also slow vegetation development indefinitely. Some Juvenile Poplar sites appeared to be on 30-year old surfaces based on comparison of aerial photographs from 1951 and 1981, but above-ground ages were < 10 years. Underground portions of stems extended about 0.5 m below the present soil surface and accounted for 5 - 10 years of additional growth on deeply-sedimented sites. All of our Alder sites had Balsam Poplar as a codominant and would be expected to progress to Young Poplar, rather than remaining in Alder stage indefinitely.

One Old Poplar site had trunks broken 2 to 3 m above the ground, apparently by winter winds since no trees were uprooted from the frozen ground, and most trees fell in the same direction. Some White Spruce regeneration was evident, but the herbaceous understory was too dense and the soils too organic for hardwood seedlings, especially Paper Birch, to become established. We believe that this site may eventually become a White Spruce site, but could become an herbaceous, low or tall shrub site and remain in this stage indefinitely if other trees do not become established. This is indicated by wind arrow in Figure 4. Logging and firewood cutting in one Birch - Spruce site produced a community similar to the gap portion of the Birch - Spruce Forest although herbaceous competition could sometimes hinder woody regeneration from seed.

Comparisons with Other Northern Rivers

Vegetation succession along the Susitna River was similar to other boreal forest rivers in terms of the early shrub development (Feltleaf Willow, Balsam Poplar) and establishment of Old Poplar Forests, but differed primarily in the effects of substrate on initial community composition and in the importance of Birch - Spruce stage in late succession. Because of the greater presence of deciduous trees, mosses and lichens were only a minor component of the ground layer. Similarities to other northern rivers included the importance of Feltleaf Willow and the rareness of Balsam Poplar - White Spruce sites.

More Feltleaf Willow was found on gravelly alluvium than on sandy or silty materials on the Colville River on the Arctic slope (Bliss and Cantlon 1957) in contrast with the Susitna River. Gill (1972) also found Feltleaf Willow up to 6 m tall on the Mackenzie River delta. Feltleaf Willow almost never reaches these sizes in southcentral Alaska because of intense moose browsing and competition from tree species. These factors generally precluded Feltleaf Willow from reaching even 2 m height along the Susitna River. Observations of heavy browsing slowing growth of palatable species is consistent with observations on the Tanana River in interior Alaska (Wolff 1976; Bryant and Chapin 1986).

Vegetation along the Susitna River differed from other northern rivers in the greater variety of early seral communities resulting from variable river dynamics and substrate textures. The earliest stage described by Viereck (1970) along the Chena River in Interior Alaska was a 15-year-old Feltleaf Willow site. It established on coarser soils than Willow sites in the Susitna River floodplain, and it was much older than most of our Willow. However, Gill (1972) and Teversham and Slaymaker (1976) reported Balsam Poplar species on their coarser sites similar to the Susitna River. The greater variety of substrate textures on the Susitna River resulted from different fluvial dynamics. Sands were frequently deposited by intense summer floods, particularly below the Chulitna confluence, while silts and fine sands were deposited by milder floods and in backwaters behind ice jams (Helm et al. 1985).

Willow was reduced from Alder and later stages of succession by its shorter life span, browsing, and shade intolerance (Walker et al. 1986; Bryant 1987; Viereck et al. 1993). Van Cleve et al. (1980) observed that most willows died under closed canopy, although Feltleaf Willow and Thinleaf Alder survived in a state of reduced vigor. Prickly Rose and High Bushcranberry increased in understories because they were more shade tolerant (Van Cleve et al. 1980; Viereck et al. 1993).

Nanson and Beach (1977) observed that Balsam Poplar transitioned rapidly to White Spruce with no mixed stage in British Columbia. Their White Spruce seedlings were released when Balsam Poplar died on 100- to 150-year-old surfaces, similar to our transitional sites of Poplar - Spruce. White Spruce would normally be expected to follow Balsam Poplar in the successional sequence since it is longer lived and more shade tolerant than Paper Birch (Reed and Harms 1956). However, Paper Birch is able to reproduce on mineral soil in gaps left by fallen trees, and recruitment is sufficient to maintain the Paper Birch - White Spruce stage in the Anchorage - Matanuska Valley adjacent to our study area. This strong deciduous component with associated leaf fall probably limits the development of the moss and lichens in the ground layer. Along the Tanana River moss development did not exceed minor cover until the Balsam Poplar - White Spruce stage when White Spruce became codominant or dominant (Viereck et al. 1993).

Vegetation establishment appeared slower in the Susitna River floodplain compared to the Chena and Tanana Rivers in interior Alaska (Viereck 1970; Viereck et al. 1993). Early Shrub communities could persist in the Susitna River floodplain for 15 years or more while Alder tended to dominate 20 to 50 year old sites. In contrast Closed Alder and Willow stages dominated 5- to 10- year-old sites in the Tanana floodplain, and Young Balsam Poplar dominated 20- to 40-year-old sites (Viereck et al. 1993). Balsam Poplar dominated the canopy in Chena River sites that were approximately 50 years old, then White Spruce became dominant by 120 years (Viereck 1970). However, in the Tanana River floodplain, White Spruce was not dominant until about years 200-300 (Viereck et al. 1993). Our Old Balsam Poplar Forests were over 100 years old, and White Spruce was just becoming important in the understory, which was more similar to the Tanana River than to the Chena River. However, Birch - Spruce stage dominated sites over 200 years old in the Susitna River floodplain and appeared to be self-replacing.

Conclusion

Disturbances caused by flooding, including both sedimentation and erosion, and wildlife herbivory were major factors regulating vegetation succession along the Susitna River. Vegetation appeared to establish only in certain years, perhaps in response to rainfall and flood regimes. Most disturbances by flooding or ice caused sedimentation of the site and only caused a retrogression to bare ground or water if the substrate itself was eroded beneath the plants. Uprooted trees appeared necessary to produce safe sites with mineral soils and increased sunlight for Paper Birch establishment in forest understories. Small-scale disturbances caused by tree-falls created openings in the canopy and mineral soil for seedling establishment and development of shrub mosaics. Moose restricted the height growth of Balsam Poplar and willows in early stages. Beavers, however, could remove entire trees and force vegetation succession to an earlier stage. Vegetation patterns in the Susitna River floodplain thus resulted from disturbances by flooding, ice, wind, and browsing as well as stochastic events associated with seed dispersal and establishment.

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Literature Cited

Beatty, S. W., and **E. L. Stone.** 1986. The variety of soil microsites created by tree falls. Canadian Journal of Forest Research 16: 539–548.

Bliss, L. C., and **J. E. Cantlon.** 1957. Succession in river alluvium in Northern Alaska. American Midland Naturalist 58: 452–469.

Bormann, B. T., H. Spaltenstein, M. H. McClellan, F. C. Ugolini, K. Cromack, and **S. M. Nay.** 1995. Rapid soil development after windthrow disturbance in pristine forests. Journal of Ecology 83: 747–757.

Bradley, C. E., and **D. G. Smith.** 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. Canadian Journal of Botany 64: 1433–1442.

Brinkman, K. A. 1974. *Salix* L. Willow. Pages 746–750 *in* Seeds of woody plants in the United States. *Edited by* Schopmeyer, C. S. United States Department of Agriculture Forest Service, Washington, D.C.

Bryant, J. P. 1987. Feltleaf willow-snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. Ecology 68: 1319–1327.

Bryant, J. P., and **F. S. Chapin, III.** 1986. Browsing-woody plant interactions during boreal forest plant succession. Pages 213–225 *in* Forest ecosystems in the Alaskan taiga. *Edited by* K. Van Cleve, F. S. Chapin, III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness. Springer-Verlag, New York.

Clautice, S. F. 1974. Spruce and birch germination on different seedbeds and aspects after fire in interior Alaska. M.Sc. thesis, University of Alaska Fairbanks, Fairbanks, Alaska.

Collins, W. B., and **D. J. Helm.** 1997. Moose, *Alces alces*, habitat relative to riparian succession in the boreal forest, Susitna River, Alaska. Canadian Field-Naturalist 111: 567–574.

Craighead, F. L., E. L. Young, and **R. D. Boertje.** 1984. Stikine River moose study. Wildlife evaluation of Stikin-Iskut Dams. Alaska Department of Fish and Game, Juneau.

Deal, R. L., C. D. Oliver, and **B. T. Bormann.** 1991. Reconstruction of mixed hemlock-spruce stands in coastal southeast Alaska. Canadian Journal of Forest Research 21: 643–654.

Densmore, R., and **J. Zasada.** 1983. Seed dispersal and dormancy patterns in northern willows: ecological and evolutionary significance. Canadian Journal of Botany 61: 3207–3216.

Fenner, P., W. W. Brady, and **D. R. Patton.** 1985. Effects of regulated water flows on regeneration of Fremont cottonwood. Journal of Range Management 38: 135–138.

Gill, D. 1972a. Modification of northern alluvial habitats by river development. The Canadian Geographer 2: 139–153.

Gill, D. 1972b. The point bar environment in the Mackenzie River delta. Canadian Journal of Earth Science 9: 1382–1393.

Helm, D. J., and **E. B. Allen.** 1995. Vegetation chronosequence near Exit Glacier, Kenai Fjords National Park, Alaska, U.S.A. Arctic and Alpine Research 27: 246–257.

Helm, D. J., E. B. Allen, and **J. M. Trappe.** 1996. Mycorrhizal chronosequence near Exit Glacier, Alaska. Canadian Journal of Botany 74: 1496–1506.

Helm, D. J., and **D. E. Carling.** 1993. Use of soil transfer for reforestation on abandoned mined lands in Alaska. II. Effects of soil transfers from different successional stages on growth and mycorrhizal formation by *Populus balsamifera* and *Alnus crispa*. Mycorrhiza 3: 107–114.

Helm, D. J., W. B. Collins, and **J. C. LaBelle.** 1985. Riparian vegetation succession report. Draft Report. Alaska Power Authority, Susitna Hydroelectric Project. Prepared for Harza-Ebasco Susitna Joint Venture. 185 pages.

Johnston, C. A., and **R. J. Naiman.** 1990. Browse selection by beaver: effects on riparian forest composition. Canadian Journal of Forest Research 20: 1036–1043.

Jonsson, B. G., and **M. Dynesius.** 1993. Uprooting in boreal spruce forests: long-term variation in disturbance rate. Canadian Journal of Forest Research 23: 2383–2388.

Moen, R., J. Pastor, and **Y. Cohen.** 1990. Effects of beaver and moose on the vegetation of Isle Royale National Park. Alces 26: 51–63.

Naiman, R. J., G. Pinay, C. A. Johnston, and **J. Pastor.** 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75: 905–921.

Nanson, G. C., and **H. F. Beach.** 1977. Forest succession and sedimentation on a meandering river floodplain, northeast British Columbia, Canada. Journal of Biogeography 4: 229–251.

Reed, J. C., Jr., and **J. C. Harms.** 1956. Rates of tree growth and forest succession in the Anchorage - Matanuska Valley area, Alaska. Arctic 9: 238–248.

Safford, L. O. 1974. *Picea* A. Dietr. Spruce. Pages 587–597 *in* Seeds of woody plants in the United States. *Edited by* Schopmeyer, C. S. United States Department of Agriculture Forest Service, Washington, D.C.

Sigafoos, R. S. 1964. Botanical evidence of floods and flood-plain deposition. United States Geological Survey, Professional Paper 485–A.

Teversham, J. M., and **O. Slaymaker.** 1976. Vegetation composition in relation to flood frequency in Lillooet River Valley, British Columbia. Catena 3: 191–201.

Van Cleve, K., F. S. Chapin, III, P. W. Flanagan, L. A. Viereck, and **C. T. Dyrness.** *Editors.* 1986. Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function. Ecological Studies: Analysis and Synthesis. Springer-Verlag, New York. 230 pages.

Van Cleve, K., C. T. Dyrness, G. M. Marion, and **R. Erickson.** 1993. Control of soil development on the Tanana River floodplain, interior Alaska. Canadian Journal of Forest Research 23: 941–955.

Van Cleve, K., C. T. Dyrness, and **L. Viereck.** 1980. Nutrient cycling in interior Alaska flood plains and its relationship to regeneration and subsequent forest development. Pages 11–18 *in* Forest regeneration at high latitudes. *Edited by* M. Murray and R. M. Van Veldhuizen. United States Department of Agriculture Forest Service, PNW-107.

Van Cleve, K., L. A. Viereck, and **C. T. Dyrness.** 1996. State factor control of soils and forest succession along the Tanana River in Interior Alaska, U.S.A. Arctic and Alpine Research 28: 388–400.

Viereck, L. A. 1970. Forest succession and soil development adjacent to the Chena River in interior Alaska. Arctic and Alpine Research 2: 1–26.

Viereck, L. A., C. T. Dyrness, A. R. Batten, and **K. J. Wenzlick.** 1992. The Alaska Vegetation Classification. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, PNW-GTR-286. 278 pages.

Viereck, L. A., C. T. Dyrness, and **M. J. Foote.** 1993. An overview of the vegetation and soils of the floodplain ecosystems of the Tanana River, interior Alaska. Canadian Journal of Forest Research 23: 889–898.

Walker, L. R., and **F. S. Chapin, III.** 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology 67: 1508–1523.

Walker, L. R., J. C. Zasada, and **F. S. Chapin, III.** 1986. The role of life history processes in primary succession on an Alaskan floodplain. Ecology 67: 1243–1253.

Wolff, J. O. 1976. Utilization of hardwood browse by moose on the Tanana floodplain in interior Alaska. United States Department of Agriculture Forest Service, Pacific Northwest Forest and Range Experiment Station. 7 pages.

Youngblood, A. P., and **J. C. Zasada.** 1991. White spruce artificial regeneration options on river floodplains in interior Alaska. Canadian Journal of Forest Research 21: 423–433.

Zasada, J. 1986. Natural regeneration of trees and tall shrubs on forest sites in interior Alaska. Pages 44–73 *in* Forest ecosystems in the Alaskan taiga. *Edited by* K. Van Cleve, F. S. Chapin, III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness. Springer-Verlag, New York.

Zasada, J. C., L. A. Viereck, M. J. Foote, R. H. Parkenson, J. O. Wolff, and **L. A. Lankford, Jr.** 1981. Natural regeneration of balsam poplar following harvesting in the Susitna Valley, Alaska. The Forestry Chronicle 57: 57–65.

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