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Factors Affecting the Distribution of *Populus balsamifera* on the North Slope of Alaska, U.S.A.

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Abstract

Balsam poplar (*Populus balsamifera*) groves occur north of the Brooks Range and treeline in arctic Alaska in a region of continuous permafrost and tundra vegetation. A poplar grove near the Ivishak River (69°06'N, 147°53'W) that we studied in detail contains 11 clones within 350 m of the river. Individual clones range from 600 to 4500 m² in size and 90 to 200 yr in age. Poplar trees are larger in diameter in clones within 100 m of the river and less dense in clones away from the river. Unique soil thermal, moisture, and nutrient conditions may limit the expansion of poplar groves to only a few hundred meters from the river channel, including a "thaw bulb," or depression in the permafrost table; lithologic discontinuities that concentrate moisture in the rooting zone; and accumulation of Ca-enriched precipitates from aufeis deposits. We prepared a map showing the distribution of poplar groves on the North Slope from published reports, satellite images, topographic maps, and observations of a bush pilot. The groves occur within an area bounded by 68–69°N and 142–154°W. A preliminary model explaining the origin and distribution of balsam poplar groves was developed from the case study; unpublished data; and a review of the geologic, hydrologic, and ecologic literature. The groves preferentially occur in areas where there is a sharp change in relief from the Brooks Range to the Arctic Foothills, extensive river braiding accompanied by geothermal springs and aufeis deposits, and a regional groundwater flow system enriched in Ca that may be controlled by faulting.

Introduction

Balsam poplar (*Populus balsamifera*) groves occur on the North Slope of Alaska over 100 km from continuous populations in the taiga south of the Brooks Range (Spetzman, 1951; Wiggins and Thomas, 1962; Hultén, 1968; Viereck and Foote, 1970; Hettinger and Janz, 1974; Murray, 1980; Edwards and Dunwiddie, 1985). The North Slope is characterized by continuous permafrost and tundra vegetation; for this reason, the poplar stands are anomalous.

The distribution and factors affecting the distribution of balsam poplar in this region are poorly understood. Poplar groves on the North Slope appear to be limited to active or recently abandoned rivers. In this setting the seasonal thaw layer (active layer) tends to be thicker than in the surrounding tundra, and there is a continuous supply of sub-surface water (Hettinger and Janz, 1974; Murray, 1980). The groves are often associated with geothermal springs (Nava and Morrison, 1974; Zasada and Phipps, 1990).

The growth of balsam poplar along the North Slope is favored by a floodplain environment with ample moisture (Viereck and Foote, 1970; Hettinger and Janz, 1974; Murray, 1980), periodic flooding (Hettinger and Janz, 1974), a deep active layer within 50 m of the river (Nanson and Beach, 1977), and soils with a high pH (>7) and lithologic discontinuities (Nanson and Beach, 1977; Zasada and Phipps, 1990).

Balsam poplar stands on the North Slope are normally even-aged, less than 230 yr in age, and slow growing (Nanson and Beach, 1977; Edwards and Dunwiddie, 1985; Lev, 1987). The groves have an unusually high plant and animal diversity (Hettinger and Janz, 1974; Nanson and Beach, 1977; Edwards and Dunwiddie, 1985). There are several varieties of balsam poplar, including *P. balsamifera* var. *balsamifera* and *P. balsamifera* var. *subcordata*, which complicates taxonomic delineation. In addition, *P. balsamifera* readily hybridizes with *P. trichocarpa* (Viereck and Foote, 1970; Zasada and Phipps, 1990).

Balsam poplar groves may have originated from seeds carried over the Brooks Range, but the groves reproduce locally both from seed and asexually (Murray, 1980). The groves generally contain more than one clone (Edwards and Dunwiddie, 1985; Lev, 1987), with each clone containing from 10 to 150 or more individuals (ramets). The groves may be outliers along north-flowing rivers (Landhaeusser and Wein, 1993), or they may be relicts from a warmer period when balsam poplar was more widespread on the North Slope (Mott, 1978; Hopkins et al., 1981; Ritchie et al., 1983; Ritchie, 1984; Edwards and Dunwiddie, 1985).

There is considerable evidence of climate change in arctic Alaska, including increased winter and spring air temperatures since about 1970, negative mass balance of small arctic glaciers, warming of permafrost, increased plant growth accompanied by greater shrub abundance, and northward migration of treeline (Serreze et al., 2000). Therefore, the study of the distribution of balsam poplar on the Arctic Slope is of importance with regards to warming of the region.

The purposes of this study are three-fold: (1) to determine the site factors favoring the growth of a balsam poplar grove located along a tributary of the Ivishak River, (2) to summarize data regarding the distribution of balsam poplar along the North Slope, and (3) to prepare a descriptive model explaining the distribution of balsam poplar in arctic Alaska.

Study Area

The study area includes the eastern half of the North Slope of Alaska from 68° to 70°N latitude, bounded by the Colville River to the west (154°W) and the Kongakut River to the east (142°W) (Fig. 1). Although the study area includes the Arctic Coastal Plain, most of the balsam poplar stands occur in the Arctic Foothills physiographic province, as delineated by Wahrhaftig (1965).

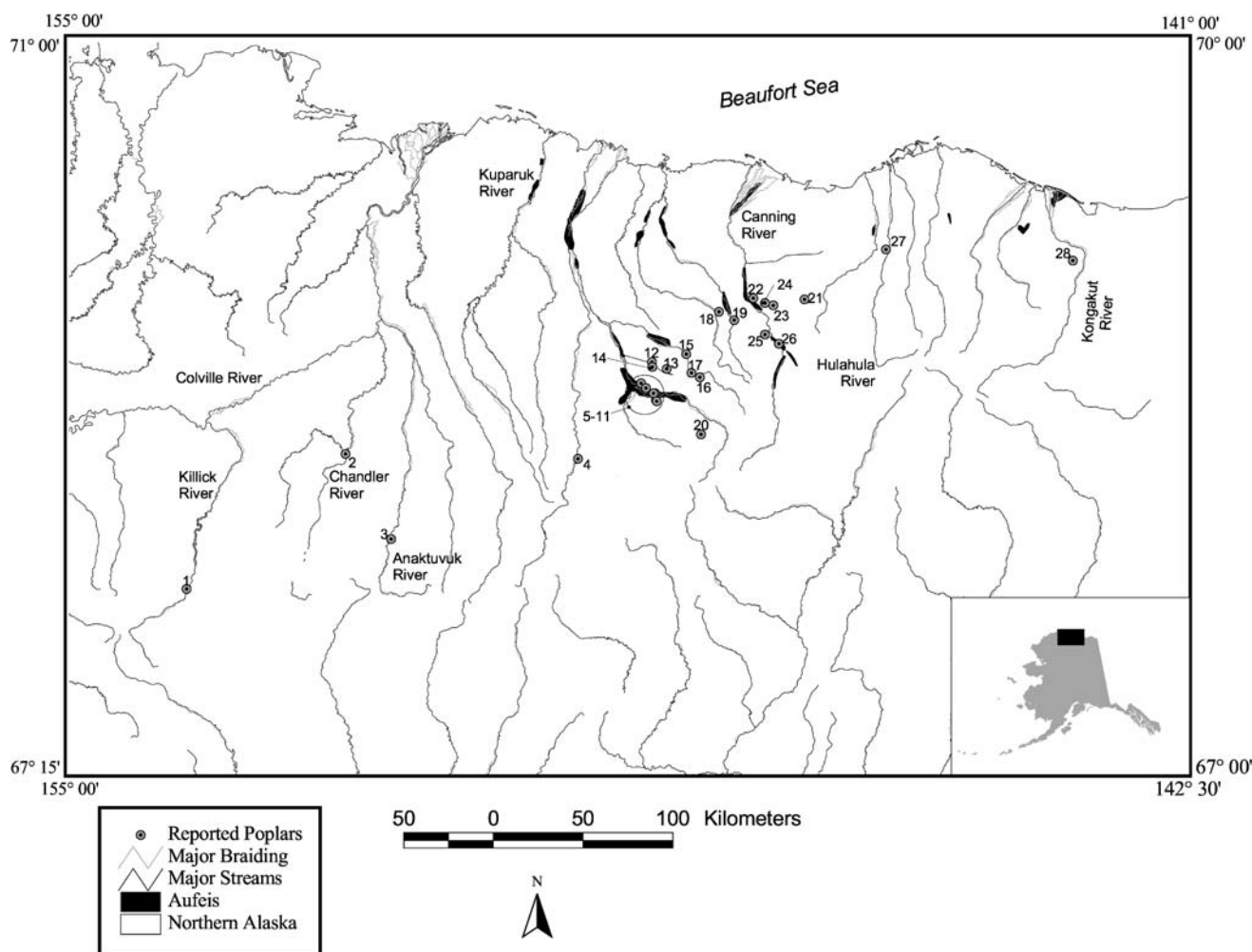


FIGURE 1. A map showing the location of balsam poplar groves in relation to braiding and aufeis development on major rivers on the North Slope of Alaska (numbered sites are described in Table 5).

The climate of the Arctic Foothills is harsh but warmer than that of the Coastal Plain to the north and the Brooks Range to the south. The average winter temperature is -20° to -24°C . Average summer temperature is 10° to 15°C , with freezing temperatures occurring during any month of the year (National Climatic Data Center, 1998). Annual precipitation is approximately 150 mm, with an additional 50 mm near the boundary of Brooks Range. Snowfall accumulation can vary from 750 to 1300 mm, with the highest amounts found near the Brooks Range.

Valleys in the southern part of the Arctic Foothills were glaciated repeatedly during the Pleistocene; the Ivishak River site described herein contains drift of the late Pleistocene Itkillik glaciation (Hamilton, 1986). Surface sediments in the Arctic Foothills also include alluvial and colluvial deposits overlying folded beds of chert, conglomerate, sandstone, and greywacke of Jurassic and early Cretaceous age.

The Arctic Foothills and Arctic Coastal Plain physiographic regions contain low-shrub and tussock tundra along with willow, birch shrub, and poplar (Wiggins and Thomas, 1962; Hultén, 1968; Hettinger and Janz, 1974; Gallant et al., 1995). The highest species diversity on the North Slope is associated with meadow vegetation on solifluction lobes and modern and abandoned river floodplains (Hettinger and Janz, 1974). The vegetation of these floodplains includes dwarf willow (*Salix reticulata*), mountain avens (*Dryas integrifolia* spp. *integrifolia*), cotton grass (*Eriophorum vaginatum*), sedge (*Carex bigelowii*), Labrador tea (*Ledum palustre* spp. *decum-*

bens), and moss (*Tomenthypnum nitens*). The understory vegetation of balsam poplar groves consists of arctic bearberry (*Arctostaphylos rubra*), felt-leaf willow (*Salix alaxensis* spp. *alaxensis*), other willows (*S. glauca* and *S. planifolia* spp. *pulchra*), and wintergreen (*Pyrola rotundifolia* spp. *grandiflora*) (Hettinger and Janz, 1974).

Poplar groves were identified from a review of vegetation surveys on the North Slope (Spetzman, 1951; Wiggins and Thomas, 1962; Hultén, 1968; Viereck and Foote, 1970; and Hettinger and Janz, 1974), personal communications with scientists and bush pilots, and a detailed examination of topographic maps and color-infrared satellite imagery. U.S. Geological Survey topographic maps, at a scale of 1:63,360, show trees or brush at least 2 m tall with densities sufficient to afford cover for troops but do not distinguish among forest cover types.

We used a digital database of the hydrographic system of the North Slope provided by the North Slope Borough Planning Department/GIS (D. Bevington, pers. comm.) to construct a base map. Major stream braiding and aufeis deposits identified by Sloan et al. (1976), Harden et al. (1977), Hall (1980a), Dean (1986), Sloan (1987), and Li et al. (1997) were digitized into ArcView 3.0 (Fig. 1). Aufeis deposits located along tributaries of principal north-flowing rivers are not shown in Figure 1, as they are too small to be represented at this scale. Similarly, major faults and geothermal springs identified by Hall and Roswell (1981) and Sloan (1987) were digitized in ArcView 3.0 (Fig. 2).

We examined a poplar grove along "Cottonwood Creek" (informal name), a tributary of the north-flowing Ivishak River

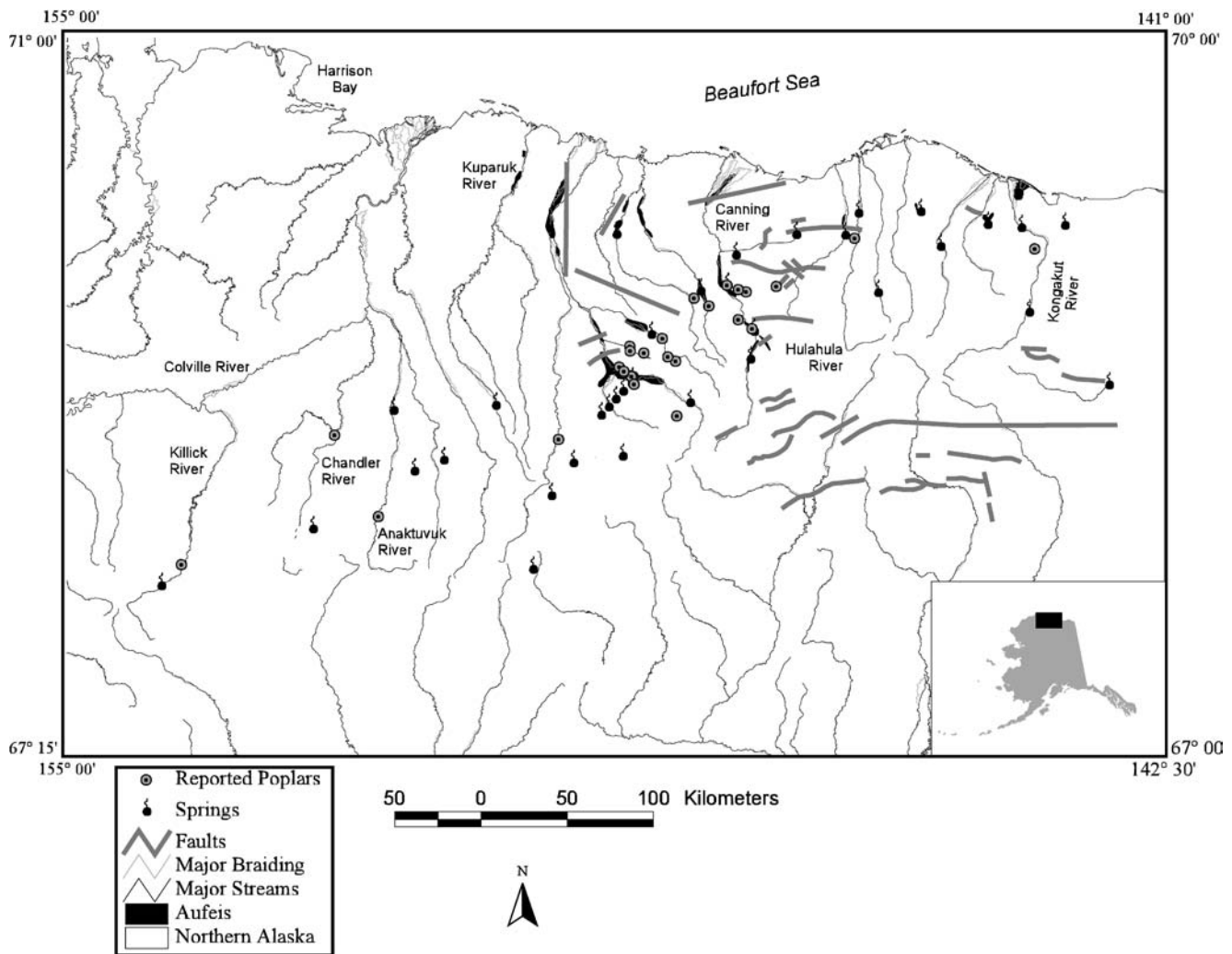


FIGURE 2. A map showing the location of balsam poplar groves in relation to faulting and geothermal springs on the North Slope of Alaska.

(69°06'N, 147°53'W) in the Arctic Foothills (site No. 5, Fig. 1). This grove was selected for comprehensive analysis because of its accessibility, comparatively large size (distributed over 40 ha), and information gathered by us and others during previous visits. The grove is located on the south side of the creek and contains 11 scattered stands on the banks of current and former braided channels.

Methods and Materials

SAMPLE COLLECTION

The Cottonwood Creek poplar grove contains 11 stands mapped from compass bearings and pacing; an uncorrected aerial photograph (approximately 1:1500 scale) was also used to adjust tree measurements to an aerial basis. After counting the total number of ramets in each stand, we randomly selected 2 trees from each of the 11 stands for measuring diameter at breast height (1.38 m) and total height (m). Although this sample is admittedly small (2% of all trees on the site), there was minimal variation in diameter (average difference = 3.6 cm, or 8%) and height (average difference = 1.3 m, or 5.6%) between the 2 trees within a stand, likely because they were ramets from the same parent. Increment cores were taken at 15 cm above the ground for the determination of radial increment and stand age.

Stembark conditions, including "cracked" (thin, vertical frost-induced cracks), scarred (broader abrasion from moose grazing and

flooding), and undamaged, were determined from a random survey of at least 20 trees per stand. Seedlings (including root suckers) were tallied in 5 randomly located, 4-m² plots in each stand. A stem analysis (Husch et al., 1972) was performed on a single tree in August 1997. Tissue samples of poplar branches, current twigs, current buds, and foliage were collected from the upper, middle, and lower crown. Disks were collected every 1 m along the stem for a total distance of 12 m, and the proportions of bark, sapwood, and heartwood were determined.

Variation in soil properties and soil temperature was examined along a north-south transect perpendicular to the river and along an east-west transect in forested and nonforested areas parallel to the channel. The north-south transect extended 200 m south from the river at 20-m intervals, passing through two of the largest stands. A 40-cm-deep soil pit was excavated at each sampling point.

Thirteen soil pits in alternating poplar stands and shrubby areas were excavated along the 1000-m-long east-west transect parallel to the river. Soils were described along both transects using the Soil Survey Division Staff (1993) protocol. Samples were taken from each horizon >2 cm in thickness. Soil temperature was measured at a depth of 40 cm with a digital thermometer.

Samples of bulk precipitation, poplar throughfall, and stream water were collected during a heavy precipitation event on 18 August 1998. An additional sample of stream water was collected on 14 August 1997.

Soil samples were returned to the University of Wisconsin–Madison for the determination of pH and gravimetric moisture content (dried at 70°C for 48 hr). Oven-dried soils were passed through a 2-mm sieve. Ninety-three soil samples were sent to the University of Missouri Soil Characterization Laboratory, where analyses were performed using methods established by the Soil Survey Staff (1996). These analyses include easily oxidizable organic C by dichromate digestion (6A1a); total N by semimicro Kjeldahl (6B2a); extractable P by the Olsen method (6S3); cation-exchange capacity by saturation with ammonium at pH 7 (5A8); exchangeable acidity (6Ha, 6H5); extractable Al (6G1); and particle-size distribution with sand and silt fractionation by sieving and pipette, respectively (3A, 3A1). Base cations were extracted with ammonium acetate (pH 8.2).

The University of Wisconsin Soil and Plant Analysis Laboratory (SPAL) (<http://riprock.soils.wisc.edu>) analyzed stream water, precipitation, and throughfall solutions for cations with an inductively coupled plasma optical-emission spectrometer (ICP-OES) and anions by ion chromatography. Bicarbonate was determined using the Gran titration method (Gran, 1952). Tissue samples were analyzed by SPAL for total nutrients (ICP-OES) and total Kjeldahl nitrogen following grinding in a laboratory mill.

Annual radial growth of poplar trees was determined from increment cores using a binocular zoom microscope (7–30×). Because *Armillaria mellea* (butt rot) and *Fomes ignarius* (heart rot) stem decay resulted in incomplete cores, the total age of 21 of the 22 sampled trees was estimated from the outermost 10 years of radial growth projected to the pith of the tree. Stand basal area was estimated stem density and basal area of the two sample trees. Finally, a wood fragment collected from a soil pit in stand 10 at the 52-cm depth was split; one subsample was sent to the U.S. Forest Products Laboratory for identification and another to the Lawrence Livermore Laboratory for radiocarbon dating.

STATISTICAL ANALYSES

Six of the stands were located within 100 m of the river and 5 of the stands more than 100 m away from the river. Differences in mean values between stands in proximity to the river were compared using an unpaired t-test, assuming equal variances.

Results

STAND CHARACTERISTICS

There were no significant differences in tree height, age, number of seedlings, the incidence of scarred and cracked trees, and basal area with distance from the river (Table 1). However, diameter was significantly greater ($p=0.01$) and density was significantly lower ($p=0.006$) within 100 m of the river.

Average radial increment was 1.1 mm yr⁻¹ and height increment was 7.6 cm yr⁻¹ (data not shown). Based on dendrochronological studies, a single tree experienced the greatest growth rates in 1940, 1970, 1959, 1885, 1887, and 1974, while poor growth occurred in 1875, 1889, and 1980 (data not shown). The radiocarbon date of the wood fragment found at a soil depth of 52 cm in stand 10 was 650 ± 50 BP. This date calibrates to between 550 and 670 cal yr BP at 2-σ (Stuiver et al., 2000).

TISSUE ANALYSES

Calcium, nitrogen, and potassium are the most abundant macronutrients in tissues of the sampled balsam poplar, followed by Mg, P, and S (Table 2). The micronutrients are arrayed Zn > Na > Fe > Mn > B > Al > Cu, except in sapwood, where Na was abundant,

TABLE 1

A comparison of vegetation and soil variables along a north-south transect with distance from the river^a

Variable	Mean (standard deviation)		Significance
	<100 m	>100 m	
Tree height (m)	10.3 (2.1)	8.1 (1.5)	0.08
Diameter at 1.37 m (cm)	28.5 (3.1)	20.7 (5.1)	0.01
Age (yr)	132 (28)	113 (30)	0.31
Stem density (stems ha ⁻¹)	237 (74)	551 (200)	0.0058
Seeding density (stems/4 m ²)	1.5 (0.8)	4.8 (3.6)	0.06
Cracked & scarred trees (%)	59 (19)	47 (10)	0.24
Basal area (m ² ha ⁻¹)	16.1 (8.7)	18.6 (11)	0.67
pH, topsoil (SU)	7.7 (0.2)	7.6 (0.5)	0.70
Soil temp., 40 cm (°C)	11.6 (0.8)	12.2 (0.5)	0.14
Silt, topsoil (%)	76 (2.5)	57 (22)	0.07

^a From unpaired, two-sample t-test, assuming equal variance.

followed by Al, Fe, Zn, Mn, B, and Cu. In perennial tissues, such as heartwood, sapwood, bole bark, live branches, and current twigs/buds, the mobile elements N, K, and P increased toward the apex of the tree. In contrast, the immobile element Ca was more concentrated toward the base of the tree or live crown.

SOIL PROPERTIES

Soils of the study area are poorly developed and contain a sequence of alluvium and buried organic horizons (Table 3). Lithologic discontinuities, consisting of overbank silts over river cobbles, were found at depths ranging from 40 to 43 cm in 5 of the 13 pits along the east-west transect and in 7 of the 11 pits along the north-south transect.

There were no trends in soil morphological or chemical properties with distance from the river or in relation to vegetation type (i.e., balsam poplar stand vs. shrubs) along the river. Silt concentration of the surface mineral horizon was lower away from the river, but the differences were not statistically significant (Table 1). In general, soils within 100 m of the river were silt loams with an average of 76% silt, 100% base saturation primarily by Ca, and a pH averaging 7.7.

SOLUTION ANALYSIS

The distribution of cations in precipitation, on a charge basis in descending order, was Ca > Al > Na > Mg > K > Mn; anions were distributed: NO₃ > Cl > SO₄ > HCO₃ (Table 4). Throughfall cations can be ranked K > Ca > Mg > Al > Na > Mn, and anions HCO₃ > Cl > NO₃ > SO₄. Streamwater cations can be ranked Ca > Mg > Na > Al > K > Mn and anions SO₄ > HCO₃ > NO₃ > Cl. All solutions were weakly acidic to neutral, with a pH ranging from 6.3 to 7.7.

Discussion

GROWTH AND ORIGIN OF THE COTTONWOOD CREEK BALSAM POPLAR STAND

The diameter and height growth rates of balsam poplar at Cottonwood Creek are comparable to those reported elsewhere in arctic Alaska and in areas immediately south of the Brooks Range. Radial increment ranged from 0.5 to 2.2 mm yr⁻¹ (data not shown), which is comparable to the 0.1 to 2.2 mm yr⁻¹ values reported by Edwards and Dunwiddie (1985) and Lev (1987).

Morphological features of the stands were examined using the criteria of Gom and Rood (1999). The 11 stands investigated at Cottonwood Creek likely represent individual clones in that they were

TABLE 2

Chemical composition of *Populus balsamifera* in arctic Alaska by tissue and crown/stem position

Tissue	Crown/ stem position	% by mass						mg/kg by mass						
		N	Ca	Mg	K	P	S	Zn	B	Mn	Fe	Cu	Al	Na
Heartwood	Lower stem	0.11	2.69	0.12	0.53	0.02	0.04	150	5.2	21	15	2.6	49	66
	Middle stem	0.12	1.06	0.08	0.59	0.03	0.05	100	4.3	11	14	2.4	43	66
	Upper stem	0.16	1.78	0.13	0.75	0.05	0.05	149	6.9	23	18	2.4	50	72
Sapwood	Lower stem	0.09	0.30	0.02	0.41	0.02	0.04	24	2.9	3.4	24	2.6	46	64
	Middle stem	0.10	0.13	0.02	0.40	0.02	0.04	24	2.9	3.0	18	2.6	39	62
	Upper stem	0.12	0.11	0.01	0.45	0.02	0.04	24	3.1	3.0	16	2.6	40	65
Bole bark	Lower stem	0.38	1.93	0.14	0.68	0.05	0.07	248	17	13	33	5.1	54	69
	Middle stem	0.53	1.52	0.14	0.69	0.08	0.08	354	20	15	38	3.8	51	65
	Upper stem	0.63	1.14	0.10	0.83	0.09	0.08	357	20	15	22	2.7	30	64
Live branches	Lower crown	0.30	1.89	0.13	0.64	0.04	0.03	223	12	19	33	4.1	<34	60
	Middle crown	0.42	0.98	0.08	0.65	0.05	0.04	159	12	14	15	4.2	<34	61
	Upper crown	0.74	1.41	0.10	0.71	0.09	0.06	200	14	15	26	5.6	<34	62
Current twigs/buds	Lower crown	1.04	2.21	0.15	0.83	0.13	0.08	191	19	21	58	9.3	41	69
	Middle crown	1.15	1.42	0.13	0.82	0.14	0.10	188	20	17	47	8.3	<34	67
	Upper crown	1.39	1.17	0.15	0.84	0.17	0.11	158	19	15	42	10.1	<34	64
Foliage	Lower crown	2.66	2.31	0.28	1.57	0.17	0.24	240	24	52	57	6.2	<34	72
	Middle crown	2.43	1.43	0.20	1.33	0.15	0.20	178	21	38	53	6.1	<34	68
	Upper crown	2.32	1.13	0.17	1.62	0.16	0.02	149	21	31	56	7.4	39	78

separated by distances ranging from 50 to 250 m, vary considerably in age, and contain distinct differences in phenological properties such as stem form, branching habit, bark color and texture, and leaf size and shape. The stands are of seed origin; the seeds may have been carried over the Brooks Range by wind and deposited throughout the southern Arctic Foothills. Because of the unique thermal and moisture conditions along the rivers draining the northern Brooks Range, balsam poplar becomes established only in specific localities. Alternatively, the seeds may be carried by water birds favoring riparian areas. The clones have persisted for at least 90 to 200 yr and possibly as long as 670 yr, based on a radiocarbon-dated wood fragment found at a depth of 52 cm in one of the stands.

There were no obvious differences in soil properties along the river or with distance from the river other than silt content, thus providing no distinct criteria for site selection for individual stands.

However, several factors appear to promote the establishment and growth of poplar groves: the soil thermal, moisture, and nutrient regimes all appear to be more favorable near the river. Soil temperatures taken at the 40-cm depth along both the north-south and east-west transects in mid-August 1998 were 10–12°C, in contrast with soil temperatures of 0–0.5°C reported at similar depths and time frame in arctic tundra (Nelson et al., 1997). The continuous subsurface flow of the river, even during the harsh winter months, depresses the permafrost table near and beneath stream channels (Corbin and Benson, 1983). A depression in the permafrost table results in higher near-surface soil temperatures; less heat energy is needed to thaw frozen ground and is, therefore, available to increase soil enthalpy.

A second factor that may influence the distribution of balsam poplar along Cottonwood Creek is the effect of lithologic discontinuities on soil moisture relations. Lithologic discontinuities strongly

TABLE 3

Soil properties of representative pedons at the "Cottonwood Creek" balsam poplar site, North Slope of Alaska

Horizon	Depth (cm)	Clay (%)	Silt (%)	Textural class	Exchangeable						Base saturation (%)	Organic C (%)	pH
					Ca	Mg	Na	K	Acidity	CEC			
					cmol(+)/kg								
Pedon A98-28; Clone 1													
Oi	0–1												
AC	1–4	9.9	66.3	sil	55.1	2.0	tr	0.4	3.2	60.7	100	7.8	7.4
Oeb	4–9	24.6	63.2	sil	146	8.5	tr	0.6	24.1	179	100	32.7	6.9
ACb	9–17	9.8	53.1	sil	44.9	1.6	tr	tr	4.3	47.2	100	2.2	7.9
Oab	17–20	17.4	48.0	l	87.0	3.1	tr	0.1	4.5	98.6	100	14.3	7.4
Cb	20–37	3.0	21.2	ls	38.2	1.2	tr	tr	9.8	39.4	100	0.8	8.1
2Cb1	37–94			vgls									
2Cb2	94–112												
Pedon A97-7; Clone 1													
Oi	0–4				51.7	4.0	tr	tr	26.9	146	100	50.3	6.4
C/Oa	4–16	20.2	65.8	sil	53.3	3.3	tr	tr	7.4	82.2	100	12.4	7.4
Oa1	16–19	32.7	49.4	sicl	69.1	4.8	tr	tr	17.6	121	86	34.2	7.2
Oa2	19–28	22.8	27.9	l	53.7	3.3	tr	tr	10.9	96.9	100	16.5	7.1
2Bw	28–32	5.3	15.9	vgls	63.9	3.3	tr	0.1	1.3	42.1	100	2.0	7.4
2Ck1	32–58	3.4	9.7	vgls	62.2	3.3	tr	0.1	0.7	35.9	100	0.5	7.7
2Ck2	58–70	4.0	9.5	vgls	41.6	2.4	0.1	0.1	0.2	36.6	100	0.5	7.9

TABLE 4
Chemical composition of natural waters along the North Slope of Alaska

Area	Solution type	Date	Latitude (N)	Longitude (W)	pH	mmol/L				Reference
						Ca	Mg	SO ₄	HCO ₃	
"Cottonwood" Creek	stream water	Aug. 1997	69°06'23"	147°53'79"	7.5	2.7	0.69	0.98	0.13	This study
"Cottonwood" Creek	stream water	Aug. 1998	69°06'23"	147°53'79"	7.7	4.1	1.5	3.5	1.9	This study
"Cottonwood" Creek	throughfall	Aug. 1998	69°06'23"	147°53'79"	6.3	0.19	0.059	0.02	0.41	This study
"Cottonwood" Creek	bulk precipitation	Aug. 1998	69°06'23"	147°53'79"	6.7	0.1	0.026	0.013	0.01	This study
Saviukviayak	spring	1974	68°56'20"	147°58'45"	8.0	2.3	0.6	0.22	2.3	Childers et al., 1975
Flood Creek	spring	1974	68°58'40"	147°51'30"	8.1	2.2	0.72	0.26	2.2	Childers et al., 1975
Ivishak River	spring	1974	69°01'50"	147°43'00"	7.8	2.1	0.75	0.23	2.2	Childers et al., 1975
Echooka River	spring	1974	69°15'35"	147°22'50"	7.9	1.8	3.0	0.50	2.2	Childers et al., 1975
Shublik River	spring	1974	69°28'20"	146°11'50"	8.0	1.9	0.91	0.77	2.1	Childers et al., 1975
Red Hill	spring	1974	69°37'37"	146°01'38"	7.5	2.7	1.7	1.5	5.3	Childers et al., 1975
Chandler River	precipitation	1979	68°15'	149°30'	6.4	0.075	0.016	0	0.33	Himes, 1980
Chandler River	precipitation	1979	68°15'	149°30'	5.9	0.070	0.015	0.021	0.24	Himes, 1980
Galbraith River	precipitation	1979	68°15'	149°30'	5.6	0.055	0.012	0	0.12	Himes, 1980
Atigun River	precipitation	1979	68°30'	149°30'	5.7	0.036	0.015	0	0.079	Himes, 1980
Atigun River	precipitation	1979	68°30'	149°30'	5.5	0.036	0.012	0	0.092	Himes, 1980

affect water retention and movement in soil parent materials (Kung, 1993). In the alluvial soils along Cottonwood Creek, silt-rich materials over cobbly loamy sand materials enhance water retention and availability for poplar roots by suspending water in the unsaturated zone. The widespread occurrence of lithologic discontinuities along transects, and their absence elsewhere on the arctic tundra, suggest that they provide a unique environment for rooting of balsam poplar. The effective rooting depth of balsam poplar ranged from 13 to 42 cm and averaged 29 cm.

A third factor investigated relative to the distribution of balsam poplar along Cottonwood Creek is the nutrient regime. Natural waters (bulk precipitation, throughfall, and streamwater), soils, and tree tissues at the Cottonwood Creek site are particularly enriched in calcium. Dissolved calcium in river water likely originates from the groundwater-fed stream system originating in the Brooks Range, which is supersaturated with respect to calcite (Table 4). The soils may be enriched in calcium from weathering of the calcareous alluvium or more likely from dry deposition of nearby aufeis deposits, which is discussed in the next section. The foliage, branch, and heartwood tissues of North Slope balsam poplar (Table 2) all contain as much as two times the concentration of calcium as *Populus* species outside Alaska (Bartos and Johnson, 1978; Pastor and Bockheim, 1984).

Although the tissues are enriched in calcium, it could be argued that the high level of calcium may not be essential for poplar growth. For example, crop and pasture plants grown in calcium-rich solutions showed little additional gain in biomass as calcium concentrations increased (Loneragan and Snowball, 1969). Moreover, calcareous parent materials occur elsewhere on the North Slope in the absence of balsam poplar (Bockheim et al., 1998). Therefore, Ca enrichment adjacent to the river may be a cofactor influencing the occurrence and growth of balsam poplar beyond its normal range.

Distribution of Balsam Poplar on the North Slope: A Descriptive Model

We identified 28 balsam poplar groves on the North Slope that occur from 68°N in the Brooks Range to 69°N latitude in the Arctic Foothills and from 142°W to 154°W longitude (Fig. 1; Table 5). Balsam poplar groves are found in areas with strong topographic gradients, typically where there is a $>200\text{-m km}^{-1}$ topographic gradient (Table 5). The stands occur in the foothills of the Brooks Range at elevations generally ranging from 245 to 638 m. The poplar groves

also are associated with spring-fed rivers, aufeis deposits, and areas of extensive river braiding (Figs. 1 and 2).

Three of the sites (Nos. 6, 20, and 28) occur at elevations >1000 m and are not associated with braiding and aufeis development on streams. These sites were identified from color-infrared photos and were not ground truthed. Therefore, they may represent tall *Salix* rather than *Populus balsamifera*. We also observed scattered trees along May Creek (68°40'N, 151°37'W) and low-scrub balsam poplar west of Toolik Lake (68°38'N, 149°38'W), but these occurrences are not listed in Table 5.

Therefore, balsam poplars are found adjacent to rivers where favorable thermal and moisture conditions exist, due to a unique combination of factors including areas of extensive river braiding accompanied by aufeis, faults that run parallel to the river, deeper thaw bulb, and warmer soil temperatures relative to the surrounding tundra (Figs. 1 and 2). These factors are illustrated in Figure 3 and are discussed separately below.

SUBSURFACE WATER FLOW

Springs emerging from the Brooks Range provide a continual source of water at temperatures around 0°C that inhibits permafrost beneath rivers and their adjacent floodplains (Corbin and Benson, 1983). The surface temperature of North Slope streams may be lower than the temperature of the surrounding ground because of surface reflectance and the high specific heat of water. The heat pulse penetrates deeper under the stream than in the adjacent floodplain due to the channel topography and higher thermal conductivity of saturated channel sediments. The net effect is to lower the permafrost table to depths of 6 m beneath the stream and about 4 m on the adjacent floodplain (Corbin and Benson, 1983). These findings have implications for the thermal regime of Cottonwood Creek.

AUFIS DEVELOPMENT

Aufeis or overflow deposits that form during the winter may cause a depression in the permafrost table. As the freezing front penetrates downward into the thaw bulb, aufeis (icings, naleds) can develop. Subsurface water flowing in the coarse alluvium beneath the stream channel is under increasing hydrostatic pressure due to the 9% volumetric expansion associated with the phase change (Hall, 1980a). During freezing of the water, ions are excluded from the ice crystal lattice, and at high concentrations they may further depress the freezing point. Eventually, the frozen overburden will deform upward and

TABLE 5
Physiographic features of sites containing balsam poplar

Grove number	Location	Latitude	Longitude	Elev. (m)	1:63,360 topo. map	Proximity to river (m)	Topo. Grad. (m/km)	Major braiding	Major aufels	Major faults	Springs nearby	Ca salts reported
1	Killik River	68°10'	154°10'	520	A2 Killik R.	yes	127	yes	no			
2	Ayiyak (Chandler) River	68°50'	152°00'	245	D4 Chandler Lk.	yes	170	no	no		yes	
3	Anaktuvuk River	68°24'	151°25'	585	B3 Chandler Lk.	yes	225	no	no			
4	Sagavanirktok River	68°45'	148°50'	500	C4-D4 Philip Smith Mtns.	yes	137	no	no	no	no	
5	"Cottonwood Creek"/ Ivishak River	69°06'	147°53'	338	A2 Sagavanirktok R.	yes	154	yes	yes	yes	yes	yes
6	Ivishak River	68°49'	147°08'	1385	D1 Philip Smith Mtns.	yes	—	no	no	yes	yes	
7	Ivishak River	69°05'	147°49'	385	A2 Sagavanirktok R.	yes	296	yes	yes	yes	yes	
8	Ivishak River	69°04'	147°49'	354	A2 Sagavanirktok R.	yes	315	yes	yes	yes	yes	
9	Ivishak River	69°03'	147°43'	362	A2 Sagavanirktok R.	yes	380	yes	yes	yes	yes	
10	Ivishak River	69°03'	147°42'	385	A2 Sagavanirktok R.	yes	231	yes	yes	yes	yes	
11	Ivishak River	69°01'	147°42'	615	A2 Sagavanirktok R.	yes	462	yes	yes	yes	yes	
12	Gilead Creek	69°12'	147°42'	415	A2 Sagavanirktok R.	yes	89	yes	no	yes	yes	
13	Echooka River	69°15'	147°21'	430	A1-B1 Sagavanirktok R.	yes	457	yes	no	yes	yes	
14	Gilead Creek	69°11'	147°42'	415	A2 Sagavanirktok R.	yes	292	yes	no	yes	yes	
15	Ivishak (Echooka) River	69°06'	147°42'	600	A2 Sagavanirktok R.	yes	355	yes	yes	yes	yes	
16	Echooka River	69°08'	147°10'	554	A1 Sagavanirktok R.	yes	461	yes	yes	yes	yes	
17	Echooka River	69°14'	147°13'	451	A1 Sagavanirktok R.	yes	367	yes	yes	yes	yes	
18	Juniper Creek	69°26'	146°46'	415	B5 Mt. Michelson	yes	88	yes	yes	yes	yes	yes
19	Kavik River	69°22'	146°30'	469	B5 Mt. Michelson	yes	39	yes	yes	yes	yes	yes
20	Porcupine Lake	68°45'	146°20'	1076	C4-D4 Arctic	no	—	no	no	yes	yes	
21	Canning River	69°28'	146°12'	338	A4 Mt. Michelson	yes	308	yes	yes	yes	yes	yes
22	Canning River	69°17'	146°06'	385	B4 Mt. Michelson	yes	237	yes	yes	yes	yes	yes
23	Canning River	69°25'	145°56'	431	B4 Mt. Michelson	yes	169	yes	yes	yes	yes	yes
24	Cache Creek	69°22'	146°00'	354	B4 Mt. Michelson	yes	355	yes	yes	yes	yes	yes
25	Ikiakpuk V./Cache Creek	69°25'	145°30'	638	B3 Mt. Michelson	yes	615	yes	yes	yes	yes	yes
26	Canning River/Marsh Fork	69°13'	145°54'	369	A4 Mt. Michelson	yes	537	yes	yes	yes	yes	yes
27	Hulahula River	69°21'	144°16'	508	B1 Mt. Michelson	yes	186	yes	no	yes	yes	
28	Egaksrak (Kongakut) River	69°12'	142°15'	1723	A3 Demarcation Point	yes	—	no	no	no	yes	

References on location: Spetzman, 1951; Hettinger and Janz, 1974; Murray, 1980; Larry Rivers, master guide #68, Alaska.

References on aufels: Sloan et al., 1976; Harden et al., 1977; Hall, 1980a; Hall and Roswell, 1981; Dean, 1986; Li et al., 1997.

References on faults: Hall, 1980b; Hall and Roswell, 1981.

References on springs: Childers et al., 1975; Sloan, 1987.

References on Ca salts: Hall, 1980b.

crack, allowing the water to rupture to the surface, where it quickly freezes. This process is repeated many times during the winter, and over time the aufeis aggrades upward. Ice at the top of the deposit is enriched in ions relative to the lower layers. The icings may reach sufficient thickness to prevent complete thermomechanical ablation in summer.

Aufeis remnants persisting well into the summer or year-round may contribute to river braiding by obstructing floodwater and causing channels to widen or new channels to form (Harden et al., 1977). Aufeis characteristically forms at the mountain front, where stream gradients decrease as rivers leave constricting valleys, pouring onto extensive outwash plains (Carey, 1973).

Corbin and Benson (1983) related soil temperature and stream water temperature along the North Slope to the latent heat of fusion of icing deposits during the winter and penetration of the summer heat pulse. Although icings enhance heat loss by removal of the insulating snow cover, their net thermal effect is the addition of heat to the system through the release of latent heat during freezing. The heat available from freezing a 20-cm-thick aufeis overflow is more than twice the amount required to bring thick accumulations of aufeis to their melting point (Corbin and Benson, 1983). The percolation of water downward along ice fractures advects heat more efficiently than conduction, which is the only other mechanism for transporting heat to the soil surface.

INFLUENCE OF FAULTS

A system of faults across the Brooks Range–Arctic Foothills contact contributes to the groundwater flow network and may indirectly influence the distribution of balsam poplar (Fig. 2). Whereas faults running perpendicular to the generally north-flowing rivers have limited aufeis development and are not associated with known poplar groves, faults parallel to the rivers have aufeis and according to our map are often accompanied by balsam poplar.

Spring water emerging from the north flank of the Brooks Range carries a large dissolved load of calcium carbonate and calcium sulfate (Childers et al., 1977; Hall, 1980b; Himes, 1980). The bedrock of the Brooks Range is composed of a complex sequence of calcareous limestone, sandstone, and shale (Sloan, 1987; Moore et al., 1994). The Lisburne Limestone, Endicott Sandstone, and Sadlerochit Sandy Limestone aquifers direct groundwater from recharge areas high in the Brooks Range along faults and solution cavities to discharge areas in the Arctic Foothills and Coastal Plain (Carey, 1973; Childers et al., 1977; Hall, 1980b; Sloan, 1987; Moore et al., 1994). Freezing of streamwater during the winter forces precipitation of this dissolved load, providing a continually renewed source of base cations to soils along reaches with aufeis.

The impact of faults on the groundwater flow system is not completely understood, but the transport time and distance traveled

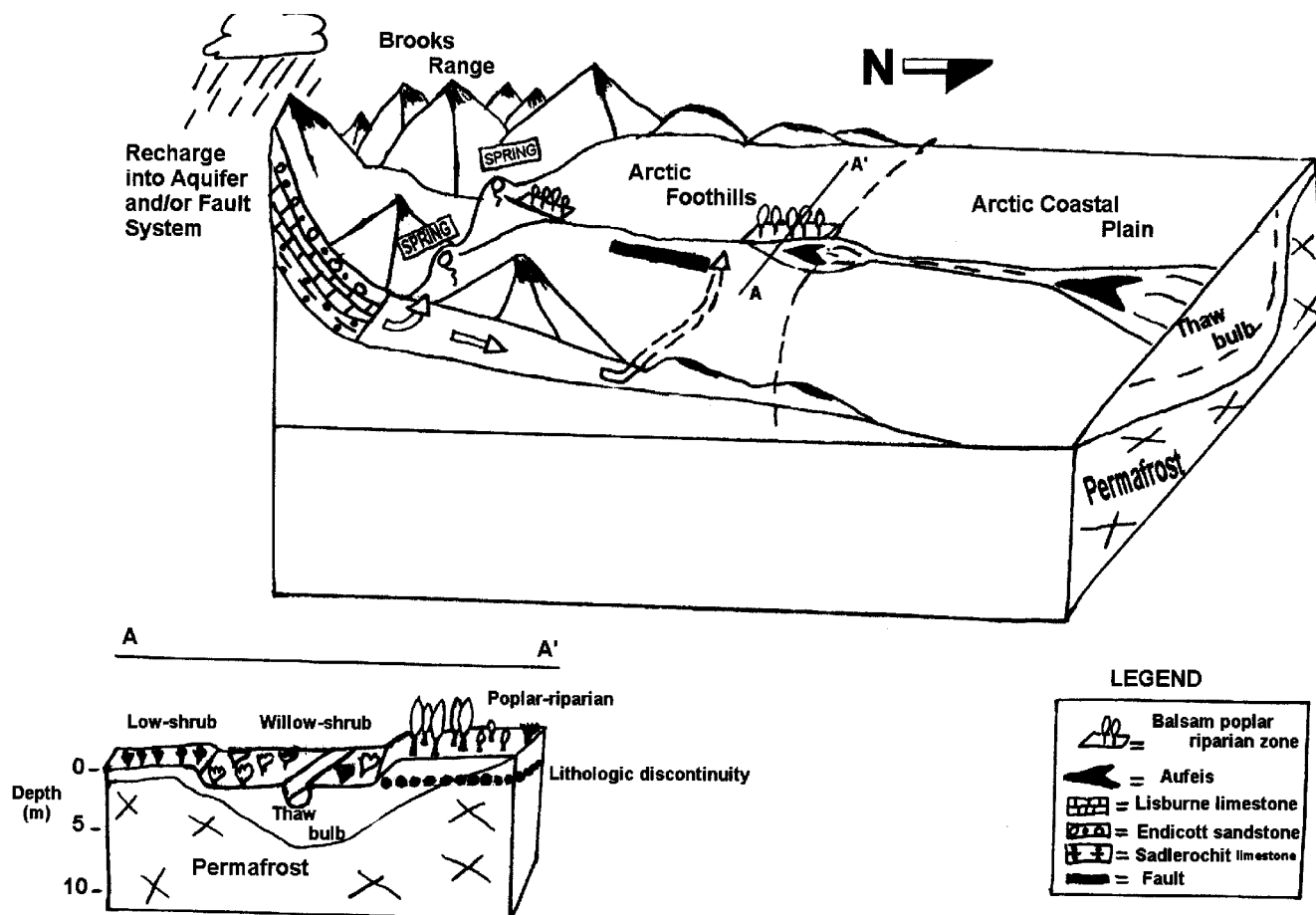


FIGURE 3. A preliminary model showing conditions favoring balsam poplar on the North Slope of Alaska.

from the recharge area appear to be important (Carey, 1973; Childers et al., 1977). The groundwater residence time may increase due to impeded flow through pervasive permafrost, enhancing dissolution of the calcareous bedrock (Childers et al., 1975; Himes, 1980; Sloan, 1987). The presence of a thaw bulb adjacent to the river increases drainage of water through the soil profile, reduces moisture, increases soil temperatures, and provides a deeper rooting zone than in areas away from the thaw bulb (Carey, 1973; Corbin and Benson, 1983).

The estimated annual precipitation of 150 mm and an average of 25 mm during the summer months (June–August) would appear to be insufficient to support poplar growth, particularly considering that the seasonal thaw layer as determined from this study is more than 2 m thick. However, lithologic discontinuities in stratified fluvial sediments may suspend water in the unsaturated zone, which plants can readily use.

QUATERNARY HISTORY OF POPLARS ON THE NORTH SLOPE

It is not known when balsam poplar first appeared on the North Slope. The poplar grove examined at Cottonwood Creek contained clones ranging from 90 to 200 yr in age; a wood fragment from 52 cm below the modern soil surface was radiocarbon dated at 650 ± 50 BP. These data suggest that balsam poplar may have been on the North Slope for at least the past 650 yr. However, poplars may have existed at specific locations on the North Slope for thousands of years. Buried poplar logs along the north-flowing Sagavanirktok River and the Nigu River in the Brooks Range and in the floodplain of the Putuligayuk River near Prudhoe Bay were radiocarbon dated at 8400 ± 300 yr BP (Detterman, 1970), 11,100 BP (Hopkins et al., 1981), and $35,600 \pm 550$ BP (Hopkins et al., 1981), respectively, suggesting that poplar may even have been present during the mid-Wisconsin.

Therefore, it is likely that poplars on the North Slope of Alaska and in northwest Canada have occurred as groves or clumps on suitable sites throughout the Holocene (Mott, 1978; Hopkins et al., 1981). The natural pioneering characteristics of *Populus* and its ability to withstand severe climatic conditions make it adaptable to the harsh climatic conditions of the region (Ritchie and Hare, 1971). Whether or not the modern stands are relicts cannot be determined from this study. However, warm summers in Beringia during the early Holocene may have permitted poplar expansion (Hopkins et al., 1981). These warmer climatic conditions were associated with greater amounts of exposed land from marine regressions, creating a more continental climate.

The warming of arctic Alaska during the past three decades has resulted in increased shrub abundance (Sturm et al., 2001). This increase in shrub cover will alter the partitioning of energy in the summer, trapping of snow cover in the winter, and ecosystem carbon distribution. A major question is whether warming of arctic Alaska has affected the growth and distribution of balsam poplar.

Conclusions

A balsam poplar grove near the Ivishak River is composed of 11 clones that range from 90 to 200 yr in age and are spaced at distances of 50 to 250 m. The clones have slow radial and height growth rates that are similar to other clones studied on the North Slope. The clones originated from seeds carried over the Brooks Range either by wind or birds. Soil thermal, moisture, and nutrient regimes all appear to be most favorable within 100 m of the river. We prepared a map (Fig. 1) showing the distribution of 28 balsam poplar groves on the North

Slope that is based on published reports, Land-Sat images, topographic maps, and observations of scientists and a bush pilot. The groves are invariably in areas of braided streams and aufeis deposits. In addition, the groves commonly are in areas of faulting and geothermal springs (Fig. 2). We developed a preliminary model (Fig. 3) showing that the distribution of balsam poplar in arctic Alaska is due to a unique combination of factors, including a steep topographic gradient, braided streams and aufeis deposits, the lack of near-surface permafrost within several hundred meters of the river, and stratified sediments that enhance retention of soil moisture in the rooting zone.

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