Height and growth rings of *Salix lanata* ssp. *richardsonii* along the coastal temperature gradient of northern Alaska

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Salix lanata ssp. *richardsonii* from open-tundra and streamside populations were studied at seven sites along a 100-km north–south transect following the Sagavanirktok River from the Alaskan arctic coast to the foothills of the Brooks Range. Mean July temperatures along this transect vary from 2.6 at the coast to 10°C at the base of the foothills. Mean maximum heights of the sampled open-tundra willows increased from 10 ± 2 at the coast to 37 ± 8 cm at the southern end of the transect. Mean maximum heights of sampled streamside willows increased from 0 at the coast to 147 ± 25 cm. The mean maximum height of willows in both habitats showed very strong correlations with thawing degree-days. Mean growth-ring widths increased from 92 ± 20 at the coast to 188 ± 57 μm at the southern end of the transect and were also highly correlated with the temperature gradient. The results are discussed in light of other arctic studies of willow growth rings and Cantlon's system of vegetation subdivisions within the Alaskan arctic.

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Le *Salix lanata* ssp. *richardsonii*, provenant des tundras exposées et des populations situées près des ruisseaux, a été étudié à sept sites le long d'un transecte nord–sud de 100 km longeant la Rivière Sagavanirktok, de la côte arctique de l'Alaska aux contreforts de la chaîne de montagne Brooks. Les températures moyennes de juillet le long de ce transecte varient de 2.6 à la côte à 10°C à la base des contreforts. La moyenne des hauteurs maximums des saules des tundras exposées augmente de 10 ± 2 à la côte à 37 ± 8 cm à l'extrémité sud du transecte. La moyenne des hauteurs maximums des saules riverains augmente de 0 à la côte à 147 ± 25 cm. La moyenne des hauteurs maximums des saules des deux habitats montre de très fortes corrélations avec des degrés-jours de dégel. La largeur moyenne des anneaux de croissance passe de 92 ± 20 à la côte à 188 ± 57 μm à l'extrémité sud du transecte et était également en étroite corrélation avec le gradient de température. Ces résultats sont discutés à la lumière d'autres études arctiques sur les anneaux de croissance du saule et du système de Cantlon sur les subdivisions de la végétation à l'intérieur de l'arctique de l'Alaska.

[Traduit par la revue]

Introduction

The stature and productivity of shrubs are worldwide criteria for dividing the Arctic into vegetation subzones (Sørenson 1941; Polunin 1951; Böcher 1954; Andreev 1966; Alexandrova 1970; Bliss 1981). For example, Nicolas Polunin (1951) commented that "...the vegetable productivity on land increases more markedly than the totality of species as we travel further south..." He further stated that this increased productivity is due to the greater importance of shrubs and dwarf shrubs. Although biogeographers have long emphasized the importance of shrub physiognomy for defining arctic vegetation zones, there are few data that quantitatively show how the shrub heights and growth rings respond to temperature along continuous latitudinal transects.

The central arctic coastal plain of northern Alaska (Fig. 1) is a good area to examine the vegetation effects of a steep coastal temperature gradient because the vegetation zonation is highly compressed in this region. Three of Young's (1971) four arctic floristic zones occur within 50 km of the Beaufort Sea coast in the vicinity of Prudhoe Bay. The only other area of the Arctic where Young (1971) shows this to occur is a region east of the Kolyma River in the USSR. The central Alaskan arctic coastal plain near the Sagavanirktok River is extraordinarily flat with most environmental factors other than temperature varying narrowly so that it is possible to study the vegetation effects of a steep coastal temperature gradient with minimal confounding effects from other variables.

Along the gradient, inland from the coast there is an increase in the total number of plant species and subtle changes to the overall tundra vegetation physiognomy (Clebsch 1957; Cantlon 1961; Wiggins and Thomas 1962; Clebsch and Shanks 1968; Young 1971). Most of the growth-form changes along this north–south transect are on a scale of a few centimetres. The major exception to this is the height of riparian willows, which increase from prostrate forms at the coast to nearly tree-sized shrubs at the northern edge of the foothills. Less pronounced changes to shrub physiognomy occur on the open tundra.

In this study, I examine the height and growth rings of the most common erect willos, *Salix lanata* L. ssp. *richardsonii* (Hook.) A. Skvortz., along the coastal temperature gradient and relate the results to recognizable vegetation zones on the coastal plain. The study transect follows the Dalton Highway along the Sagavanirktok River for 100 km southward from the arctic coast (70°15′ N, 148°20′ W) to the base of the arctic foothills of the Brooks Range (69°25′ N, 148°35′ W) (Fig. 1).

I chose *Salix lanata* for three principal reasons: (*i*) it is a woody species with a multiyear growth record; (*ii*) it occurs abundantly along the entire transect; and (*iii*) it exhibits nearly its full range of height growth potential along the Sagavanirktok River transect.

Methods

Fieldwork

I measured the heights and growth rings of *S. lanata* at eight locations along the Sagavanirktok River (Fig. 1). Five of these locations "East Dock," "Drill Site 9," "Deadhorse," "Mile 350," and "Pipeline Intersection," were selected within 40 km of the coast to measure willow growth in the steepest part of the temperature gradient. The two stations at the southern end of the transect, "Pump 2, Coastal Plain," and "Pump 2, Foothills," were established within 2 km of each other to determine whether the better drained environment on the upland affects the height of open-tundra willows.

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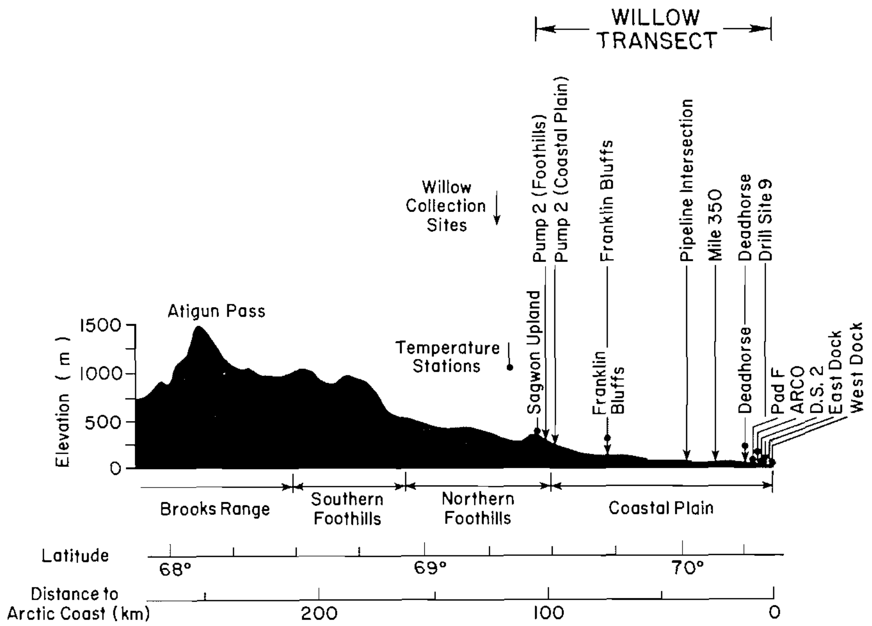

FIG. 1. Location of temperature stations and willow collection sites.

At each location the heights of 50 of the tallest willows were measured in a streamside site and 50 on a nearby open-tundra site. I selected the tallest willows because I wanted representatives of the willow's full growth potential at a given site. I also haphazardly collected 50 willows without their roots from each open-tundra location (except the East Dock) for analysis of growth rings. The willows were cut at ground level with a pocket knife.

Growth-ring analysis

The willows were sectioned and mounted according to procedures outlined by Jensen (1962). The stems were dehydrated for 2 weeks in alcohol. They were then sectioned in 10 μm thick slices, mounted, fixed by Mayer's albumin, and allowed to dry for 24 h. They were stained with safranin and fast green, cleared in clove oil, and mounted in Permount medium.

The slides were studied by projecting them on a wall, using a Leitz microscope-slide projector. The annual rings were marked on long strips of paper along two radii for each section. The two radii were compared to locate rings that were missing on one or the other sample. Mean ring width of an individual willow was calculated by dividing the mean radius by the number of growth rings. The 25 willows with the clearest growth records were selected from each station for the final analysis.

Most of the sectioned willows, 107 of 175, were in the 16- to 30-year age-class (Fig. 2). This subset was used for regression analysis of mean increment widths to compare roughly equivalent age groups. The mean ring widths were calculated at each station for all 25 willows and for the willows in the 16- to 30-year age-class. The data were divided into two subsets. The first consisted of data from all 175 willows, and the second consisted of data from the 107 willows in the 16- to 30-year age-class.

Data analysis

Height and growth-ring widths were regressed against distance from the coast, predicted mean July temperature, and predicted thawing degree-days (TDDs), using linear and exponential regression equations. Best-fit equations are presented in this paper. Temperature data were available for seven stations along the transect for 1976 and 1977 (Fig. 1 and Table 1). The predicted mean July temperatures and TDDs at each collection site were obtained from the best-fit regression equations of 1976 and 1977 temperatures versus distance from the coast. For mean July temperature, $Y = 3.63X^{0.22}$, $r = 0.90$; and for TDDs, $Y = 308X^{0.23}$, $r = 0.90$ (Fig. 4). These equations are based on the shortest distance to the coast. Haugen and Brown (1980) have shown that the best-fit equations are obtained by measuring the distance to the coast along the primary wind vector (N 75° E). Both distances were tried in these correlation analyses, and there were only slight differences in the results; therefore, for clarity of presentation, only the results using the shortest distance to the coast are presented here.

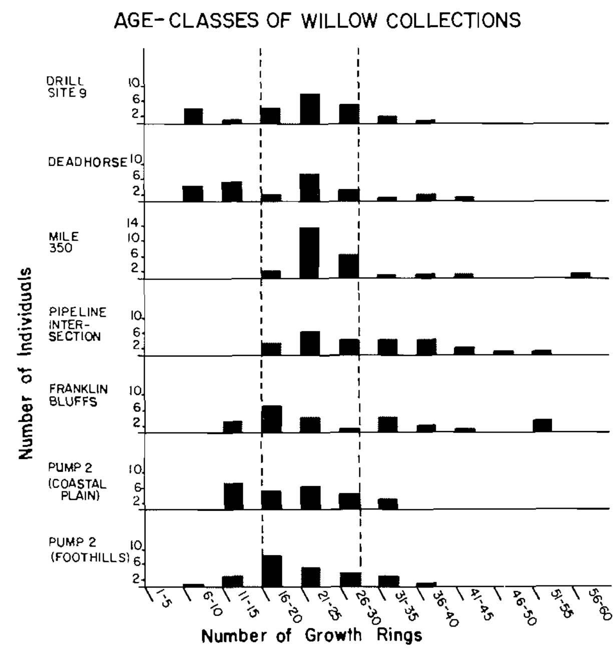

FIG. 2. Age-class of willow collections. The 107 willows between the ages of 16 and 30 (broken lines) were used for one portion of the regression analysis.

Results

Willow heights

Open-tundra willows have a linear response to TDDs ($r = 0.82$), while streamside willows respond exponentially ($r = 0.96$) (Table 2, Fig. 4). Near the coast, maximum height of sampled open-tundra willows averaged 10 $\pm$ 2 and at the

TABLE 1. Summary of summer temperature data for several stations along the Sagavanirktok River, Alaska

Station	Distance to coast (km): Shortest	Distance to coast (km): In wind direction	Year	Temperature (°C): June	Temperature (°C): July	Temperature (°C): August	Temperature (°C): September	Summer warmth index	TDD	Floristic zone
West Dock	0.7	0.7	1976	—	4.1	4.2	0.3	—	—	
			1977	−1.5	2.6	4.2	1.6	8.4	318	2
*Drill Site 9	4.0	18.0								
Drill Site 2	4.6	20.1	1977	0.1	4.2	7.1	2.2	12.2	438	3
Pad F	7.1	11.3	1976	—	5.4	4.1	1.1	—	—	3
			1977	4.0	4.2	6.2	1.7	16.1	491	
ARCO	6.0	21.0	1976	3.2	6.8	6.6	1.7	18.3	571	3
			1977	3.7	5.5	8.2	2.5	19.9	643	
			8-year mean	3.0	6.7	6.0	0.2	16.0	526	
*Deadhorse	12.0	26.0	1976	4.3	7.3	5.8	—	—	—	3
			1977	5.7	7.6	9.8	5.8	28.9	—	
*Mile 350	25.0	43.0								
*Pipeline Intersection	37.0	62.0								
*Franklin Bluffs	70.0	125.0	1976	3.2	9.8	9.4	2.7	25.1	793	4
			1977	5.7	7.5	12.1	3.2	28.5	884	
*Pump 2 (Coastal Plain)	98.0	235.0								
*Pump 2 (Foothills)	100.0	235.0								
Sagwon Upland	102.0	240.0	1976	5.0	10.8	10.0	2.7	29.0	913	4
			1977	6.5	10.0	12.9	3.3	32.7	1040	

NOTE: Thawing degree-days (TDD) are the sum of all mean daily temperatures above 0°C. Data are from the U.S. Army Cold Regions Research and Engineering Laboratory.
*Willow collection locations.

TABLE 2. Summary of growth-ring data (mean ring width, μm)

Station	All 175 Willows: N	All 175 Willows: $\bar{X}$	All 175 Willows: SD	Willows in 16- to 30-year age-class (107 Willows): N	$\bar{X}$	SD
Drill Site 9	25	92	20	17	90	15
Deadhorse	25	138	55	12	108	29
Mile 350	25	102	19	21	105	19
Pipeline Intersection	25	92	19	13	108	15
Franklin Bluffs	25	155	65	12	150	20
Pump 2, Coastal Plain	25	150	50	15	131	33
Pump 2, Foothills	25	188	57	17	182	35
Total	175	131	57	107	124	40

TABLE 3. Correlation coefficients (r) for ring width versus distance to coast and TDD

Data set	Distance to coast	TDD
All 175 willows		
All rings	0.485	0.438
Inner 10 rings	0.634	0.593
Middle 10 rings	0.343	0.301
Outer 10 rings	0.210	0.192
107 willows in 16- to 30-year age-class		
All rings	0.686	0.652
Inner 10 rings	0.713	0.669
Middle 10 rings	0.378	0.349
Outer 10 rings	0.273	0.285

NOTE: All correlations were significant at the $p < 0.01$ level.

northern edge of the foothills, averaged 37 ± 8 cm high. In contrast, streamside willows varied from 10 ± 2 at Drill Site 9 to 147 ± 25 cm at the edge of the foothills. Areas with fewer than 400 TDD had taller willows in open-tundra areas than in streamside sites, possibly because of delayed growing seasons in stream channels due to late-lying snowbanks.

The height of open-tundra willows leveled off at about 50 cm. At the southern end of the transect, there was no statistical difference between the height of open-tundra willows on the wet coastal plain and those on the upland.

Growth rings

The growth-ring data are summarized in Table 2. Mean ring width of sampled willows increased from 90 ± 20 at the Drill Site 9 to 188 ± 57 μm at the Pump 2, Foothills, location. The mean ring width for all 175 willows was 131 ± 57 μm. The oldest willow had 60 growth rings and the youngest had 8. Mean ring width of the 16- to 30-year age-class was not significantly different from that of the entire data set, although the standard deviations are consistently lower (Table 2).

The growth-ring widths were strongly correlated with the coastal temperature gradient (Fig. 5). The strongest correlation occurred with distance to the coast and the inner 10 rings of willows in the 16- to 30-year age-class ($r = 0.71$) (Table 3). There was virtually no difference between the correlations using mean July temperature and total thawing degree-days, so only the TDDs correlations are presented in Table 3.

Discussion

Effects of summer temperature on willow height

The effects of the coastal temperature gradient are maximized because temperatures at the northern end of the gradient are close to freezing for most of the summer, and the accumulation of thawing degree-days is often less than 300°C (Fig. 3). At the southern end of the coastal plain, the mean July temperature is near 10°C, and the number of total thawing degree-days is over three times that at the coast.

The heights of streamside willows should level off at the southern end of the transect, but this does not occur in the

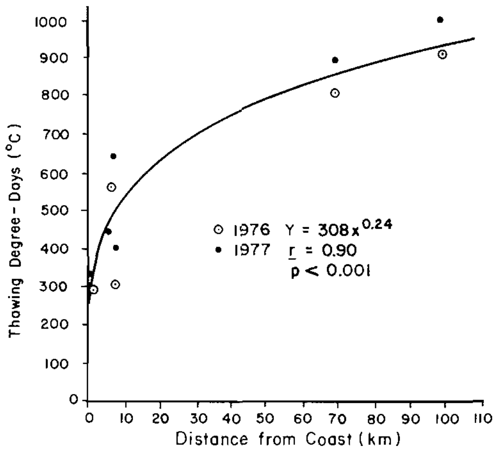

FIG. 3. Thawing degree-days gradient along the coastal plain section of the trans-Alaskan pipeline. Points represent 1976 and 1977 TDDs at stations shown in Fig. 1. Data are from Haugen (1979).

available data. Argus (1973) listed the height of *S. lanata* as varying between 60 and 300 cm, with a record height of 700 cm, and Viereck and Little (1972) stated that the upper limit is usually 200 cm. At the base of the foothills (100 km from the coast), where there are approximately 900 TDDs annually, numerous individuals exceed the 200-cm value.

Effects of summer temperature on willow growth rings

Although there is a heritage of willow growth-ring studies in the Arctic (Polunin 1951; Beschel and Webb 1962; Warren Wilson 1964), there is apparently none using *S. lanata*. The results of this study show a strong correlation between summer temperature regime and growth-ring widths in open-tundra environments and are, thus, encouraging for dendrochronological studies using *S. lanata*. Mean growth-ring widths of open-tundra willows in the 16- to 30-year age-class doubled over the length of the transect. The ring widths of *S. lanata* at the Prudhoe Bay Coast (92 $\pm$ 0.15 mm) are comparable with those reported for *S. arctica* on Cornwallis Island (Warren Wilson 1964).

Without detailed response functions, one must be cautious in ascribing growth-ring variations to any single factor. Many woody plants exhibit smaller, more irregular annual growth rings at lower temperatures; however, other environmental factors, including elevation, moisture, wind, and nutrients, can also influence the size of radial increments (Fritts 1976). However, most of these other variables do not vary greatly along this transect. For example, the total elevation gain in over 100 km is only about 150 m. The willows were all collected from nearly equivalent wet peaty sites. The soils are consistently alkaline along the floodplain of the Sagavanirktok River (pH = 7.5 $\pm$ 0.18 with a range of only 0.7 (Webber et al. 1978)). Furthermore, the available climatic data (Benson et al. 1975; Gamara and Nunes 1976; Everett 1980; Haugen and Brown 1980) show only small differences in precipitation, wind, and snow along the transect, although fog is more common at the coast (Conover 1960).

The correlations between ring width and TDDs are not as strong as those between willow height and TDDs (compare Table 3 and Fig. 4), but this is to be expected because only the tallest willows were measured for height, whereas growth rings were measured on haphazardly collected willows from several size classes and age-classes. The r values are consistently higher when willows of a common age class are correlated. (For example, compare r values for willows in the 16- to 30-year age-class with willows from the entire data set (Table 3). The outer rings of older willows are smaller and show relatively poor correlations with the temperature gradient (Table 3). The strongest correlations between temperature and growth rings occur during the first 10 years of growth ($r = 0.71$ for the inner 10 rings of willows in the 16- to 30-year age-class). The weakest correlations occur with the outer 10 rings ($r = 0.27$), and the middle 10 rings have an intermediate correlation ($r = 0.38$).

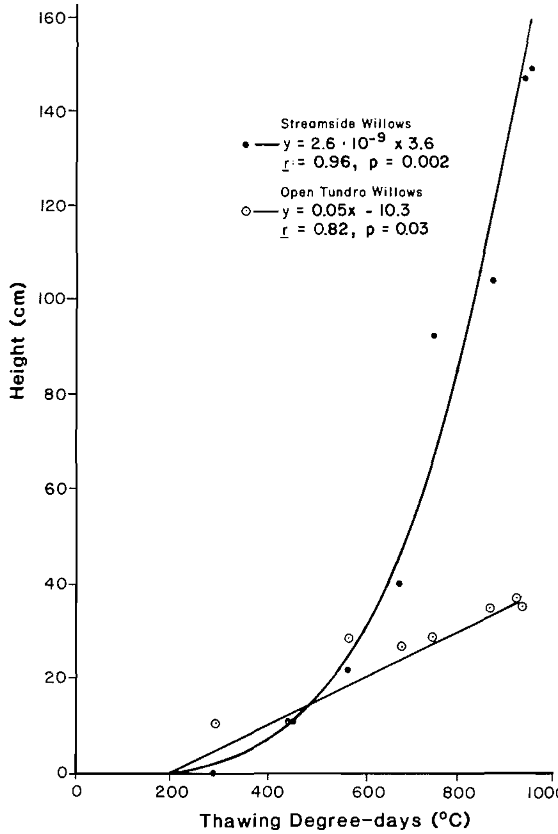

FIG. 4. Willow height versus thawing degree-days. Temperatures at each willow collection site are predicted values based on 1976 and 1977 data (Haugen 1979).

Relevance to concepts of arctic vegetation zonation

The results support the concept that the willows are an important key to general vegetation zonation on the arctic coastal plain. In northern Alaska, Cantlon (1961) and Young (1971) have divided the coastal plain into vegetation zones. Both systems use temperature as a major criterion for zonation. Young's is a floristic system and Cantlon's is based primarily on the physiognomy of the vegetation and is thus more directly relevant to this study.

Cantlon recognized two principal vegetation regions on the coastal plain, a coastal region that he termed the "littoral subzone" and an inland area that he called the "typical tundra subzone." He also recognized a "shrub tundra subzone" that occurs mainly in the warm interior valleys of the arctic foothills and also extends onto the coastal plain along the Colville River but does not occur along the transect of this study.

The littoral subzone is defined as the area north of the 7°C mean July isotherm. This zone is based on a similarly named subzone in the USSR (Sheludiakova 1938). This boundary was also used by Alexandrova (1970) to separate the northern sub-

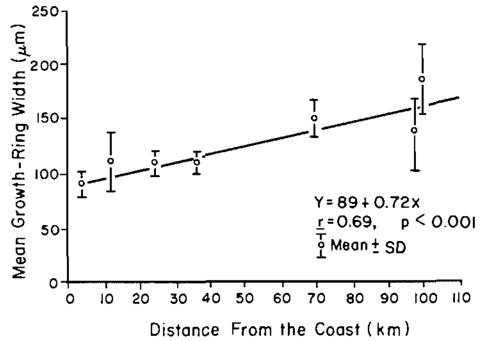

FIG. 5. Open-tundra willow growth-ring width versus distance from the coast. Data represent only the age-class of 16–30 years.

arctic subzones. The littoral subzone is characterized by (*i*) a small total flora with approximately 150 total species, (*ii*) minor importance of dwarf shrubs and the rarity or absence of many shrub taxa, (*iii*) essential absence of true shrub vegetation even along rivers, (*iv*) wide occurrence of wet meadows, dominated by *Dupontia fisheri*, (*vi*) relatively little *Sphagnum*, and (*vii*) marked reduction in the number of vegetation types compared with inland areas.

"Typical tundra" covers most of the coastal plain south of the 7°C mean July isotherm and has the following characteristics: (*i*) considerable dwarf-shrub cover in most vegetation types, (*ii*) true shrub vegetation in areas with deep but early-melting snow cover, (*iii*) well-developed *Salix alaxensis* shrub vegetation along the rivers, (*iv*) vast areas of *Eriophorum vaginatum* tussock tundra, (*v*) abundance of mosses, particularly *Sphagnum*, (*vi*) presence of several aquatic vascular plant species, and (*vii*) absence of numerous taxa associated with the shrub tundra subzone (most notably *Alnus crispa*) and the littoral subzone.

The location of Cantlon's littoral and typical tundra subzones can be roughly delineated along the transect by using the available climate data. The 1976 July mean temperatures were near the 8-year mean at the ARCO station (Table 1) and can be used to approximate the width of Cantlon's subzone along the transect.

Immediately adjacent to the coast, where mean July temperatures are 4°C or less and there are less than 400 total TDDs, *S. lanata* does not generally occur in streamside sites, although as Cantlon (1961) notes, occasional clumps of erect shrubs such as *S. glauca* and *S. alaxensis* can be found even at the coast. *Salix lanata* does occur on the open tundra at the coast but generally not where there is any influence from salt spray, and even in protected sites it is extremely stunted. Near the coast, *S. lanata* is the only common erect deciduous shrub. Most other shrubs have creeping or matted growth forms.

At 10 km from the coast, streamside *S. lanata* exceeds dwarf-shrub stature. (Note that according to the Alaska statewide vegetation classification scheme, dwarf shrubs are less than 20 cm tall; low shrubs are 20–150 cm tall; and tall shrubs are greater than 150 cm (Viereck and Dyrness 1980)). It is also interesting that the curves for streamside and open-tundra willow heights cross at about 10 km from the coast (about 525 TDDs) (Fig. 4). This is indicative of the lack of or relative unimportance of erect willows in streamside habitats near the coast and their presence in open-tundra habitats. The width of the littoral subzone (i.e., the area north of 7°C isotherm) is about 25 km measured in the direction of the prevailing winds from the east-northeast (Haugen 1979). This is equivalent to about 15 km directly south of the coast in the region of the Sagavanirktok River. North of this boundary there were less than 600 TDDs in both 1976 and 1977 (Fig. 4), and *S. lanata* is generally less than 20 cm tall even in protected streamside environments (Fig. 4).

South of Deadhorse (or about 15 km from the coast), Cantlon's typical tundra subzone begins, and the abundance, diversity, and stature of streamside willows increase dramatically. At 30 km from the coast, streamside *S. lanata* exceeds 50 cm, other erect willows, including *S. alaxensis*, *S. glauca*, and *S. niphoclada*, become common, and extensive lush riparian willow communities begin appearing. The willows continue to increase in size until at 100 km from the coast the mean maximum height of streamside *S. lanata* exceeds 150 cm.

This small study illustrates the overriding control of temperature on the stature of coastal plain willows especially in streamside environments, where nutrients are likely to be nonlimiting. In open-tundra environments, cold soil temperatures and low nutrient fluxes are likely limiting factors for willow growth as they are for other tundra species (e.g., Bliss 1956; McCown 1978; Chapin 1983; Shaver et al. 1986). The size of streamside *S. lanata* is a good indicator of local temperature regimes along the Sagavanirktok River. Dendrochronological studies with streamside willows could prove especially useful for examining the effects on shrub biomass (and vegetation zonation) of predicted climatic warming in the Arctic.

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