Performance of Indigenous and Introduced Slender Wheatgrass in Alaska, and Presumed Evidence of Ecotypic Evolution

Leslie J. Klebesadel

Emeritus Professor of Agronomy
Agricultural and Forestry Experiment Station
Palmer, Alaska

UNIVERSITY OF ALASKA FAIRBANKS

Agricultural and Forestry Experiment Station
School of Agriculture and Land Resources Management

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Summary

Objectives of this study were to evaluate forage and seed production, winter hardiness, and stand longevity of several collections of native Alaskan slender wheatgrass (*Agropyron trachycaulum* (Link) *Malte*), and to compare their performance with introduced cultivars of slender wheatgrass and standard Alaska forage grasses in other species. Eight experiments at the Matanuska Research Farm (61.6° N. Lat.) near Palmer, Alaska demonstrated the superior winter hardiness and forage productivity of indigenous Alaskan slender wheatgrass lines (collected from 62° to 67° N. Lat.) over introduced cultivars 'Revenue' (originating at 52° to 53° N) from Saskatchewan and 'Primar' (adapted at 46° to 48° N) from the Pacific Northwest.

Forage yields of indigenous lines were lower in the seeding year with only basal leaves produced; seeding-year plants of local strain 'Alaska-44S' and introduced Revenue and Primar produced higher forage yields from numerous elongated culms per plant. In first-cut harvests in the second and later years, indigenous Alaskan lines produced heavy forage yields, but these were followed by generally much lower second-cutting yields, than introduced slender wheatgrass cultivars, 'Polar' or 'Manchar' bromegrass (*Bromus inermis Leyss*), or 'Engmo' timothy (*Phleum pratense L.*). Indigenous slender wheatgrass was more adversely affected by drought stress than were Alaska-44S, Revenue, or Primar. When not under drought stress, indigenous lines produced high seed yields.

The cumulative weight of evidence in these experiments strongly indicates that the Matanuska Valley roadside population of slender wheatgrass, included in these experiments as Alaska-44S, represents an early introduction (about 1930?) to Alaska from a more southern source, a population that has undergone evolutionary, selective modification toward adaptation to the subarctic environment. Alaska 44-S resembled cultivars introduced from more southern latitudes in: (a) producing elongated culms during the seeding year, (b) retaining green (non-yellowing) foliage prior to freeze-up, (c) better foliar tolerance to severe moisture stress, and (d) high seed yield during moisture stress.

In contrast, it differed from introduced cultivars and was more similar to indigenous Alaskan slender wheatgrass in higher levels of autumn food-reserve storage and superior winter hardiness. These characteristics are important to survival and persistence in this area and indicative of adaptive change. The normally short life span of slender wheatgrass plants would tend to accelerate generational cycling, gene sorting, and rate of natural selection toward adaptation in a new environment.

These results confirm the desirability of using northern-adapted strains (cultivars, ecotypes) of perennial grasses for optimum winter survival in southcentral Alaska. The superior performance of the indigenous Alaskan slender wheatgrass collections underscores the desirability of further collections of native Alaskan ecotypes and species for evaluation for various uses in northern latitudes.

Introduction

Slender wheatgrass (*Agropyron trachycaulum* (Link) *Malte*) is a relatively short-lived, tall-growing, perennial, cool-season bunchgrass (Figure 1), and represents one of the few grasses native in North America that has become a cultivated crop (Asay and Knowles 1985; Crowle 1968; Hanson 1972). Only two cultivars currently are in use in North America: Primar, released in 1946, originated from a collection near Beebe (46.1° N) in Montana (Schwendiman and Law 1946), and Revenue, released in 1970, derived from a single plant collected near Revenue (52.2° N) in Saskatchewan (Crowle 1970).

The native range of slender wheatgrass extends from above the Arctic Circle in Alaska and Canada (Hulten 1968) southward to the mountains of California, Arizona, and New Mexico (Hitchcock 1951). Within that considerable north-south range, exceeding 30 degrees of latitude and 2000 miles, there undoubtedly exists a clinal gradient of genetic and physiologic variability (Cornelius 1947; Larsen 1947; Rogler 1943; Wilsie 1962). Such a gradient in plant variability would parallel a general north-south gradient in environmental conditions (differences in annual photoperiodic pattern, length of growing season, winter stresses, etc.). Accordingly, an ecotype at any location would possess physiologic characteristics in harmony with locally prevailing climatic condi-

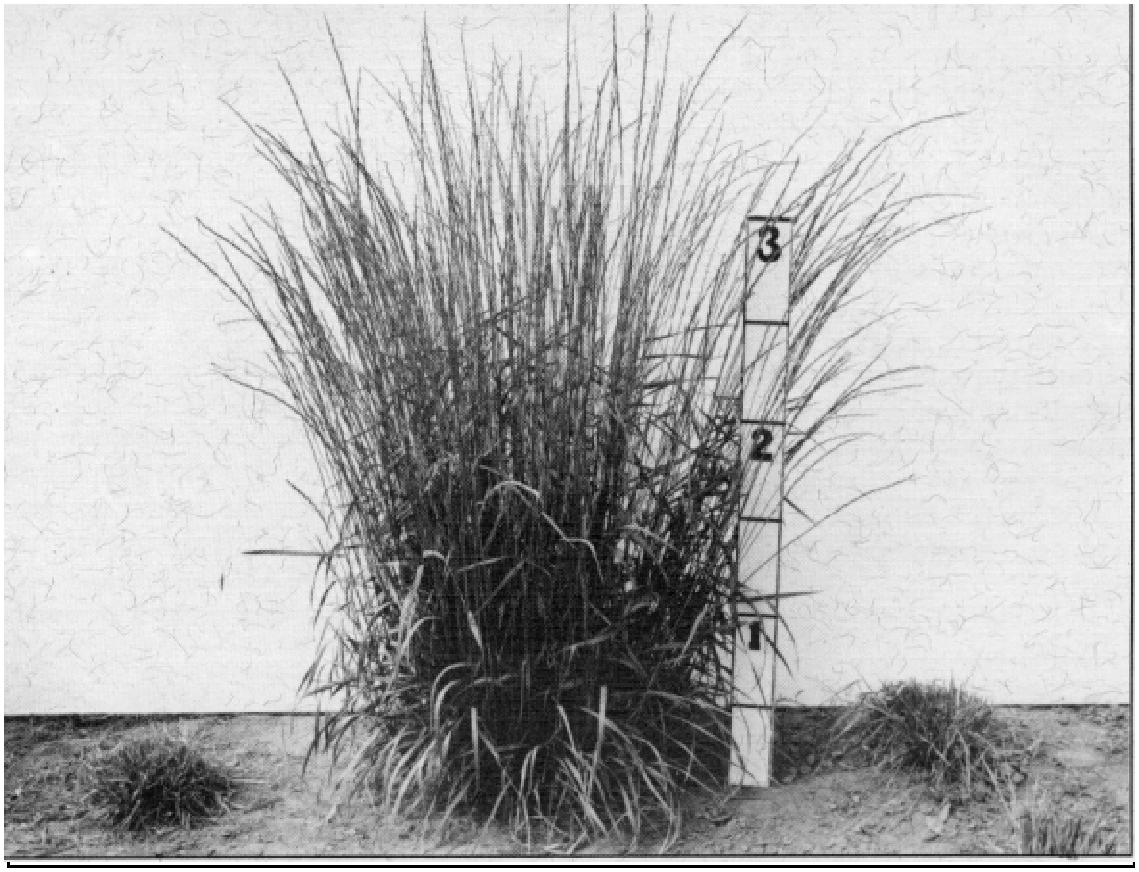

Figure 1. *A two-year-old individual plant of indigenous Alaskan slender wheatgrass. Numbered stake is three feet tall; photo taken 1 July.*

tions. Yet an ecotype taken from one area and grown at a latitudinally distant location within that same species' range could fare poorly in response to unaccustomed climatological conditions (Klebesadel 1971a, 1971b, 1985; Klebesadel et al 1964, Klebesadel and Helm 1986; Newell and Keim 1943; Rogler 1943).

Pringle et al. (1975) at Beaverlodge, Alberta (55° N Lat.), compared slender wheatgrass collections from four latitudinal zones between 53° and 68° N in Canada. They found marked differences among latitudinal ecotypes in responses to diurnal photoperiodic effects, a climatic variable linked to latitude.

Slender wheatgrass was first seeded in experimental trials in Alaska in 1905 at the Copper Center Station (Irwin 1945). The earliest plantings at the Matanuska Station, the site of the present study, were made in six different years between 1922 and 1941. In those early trials, slender wheatgrass was "one of the hardiest grasses tried," produced "good growth year after year" (Irwin 1945). It was recommended for use locally (Alberts 1933). Despite those relatively favorable early reports on slender wheatgrass performance, it is currently not grown as a forage crop in Alaska.

For about a decade, beginning in 1956, numerous seed collections of indigenous slender wheatgrass were gathered from various geographic locations throughout Alaska (Figure 2). These were evaluated in spaced-plant nurseries and, following seed increase, in rows and in broadcast-seeded plots to determine seed and forage production potential, winter hardiness, and other agronomic characteristics.

The objectives of experiments reported here were to compare slender wheatgrasses from various latitudinal origins in North America for performance and suitability for use in subarctic Alaska, to assess agronomic merit of indigenous collections of slender wheatgrass, and to derive a better understanding of factors influencing winter hardiness of strains within the species at this latitude. Results reported are from eight individual experi-

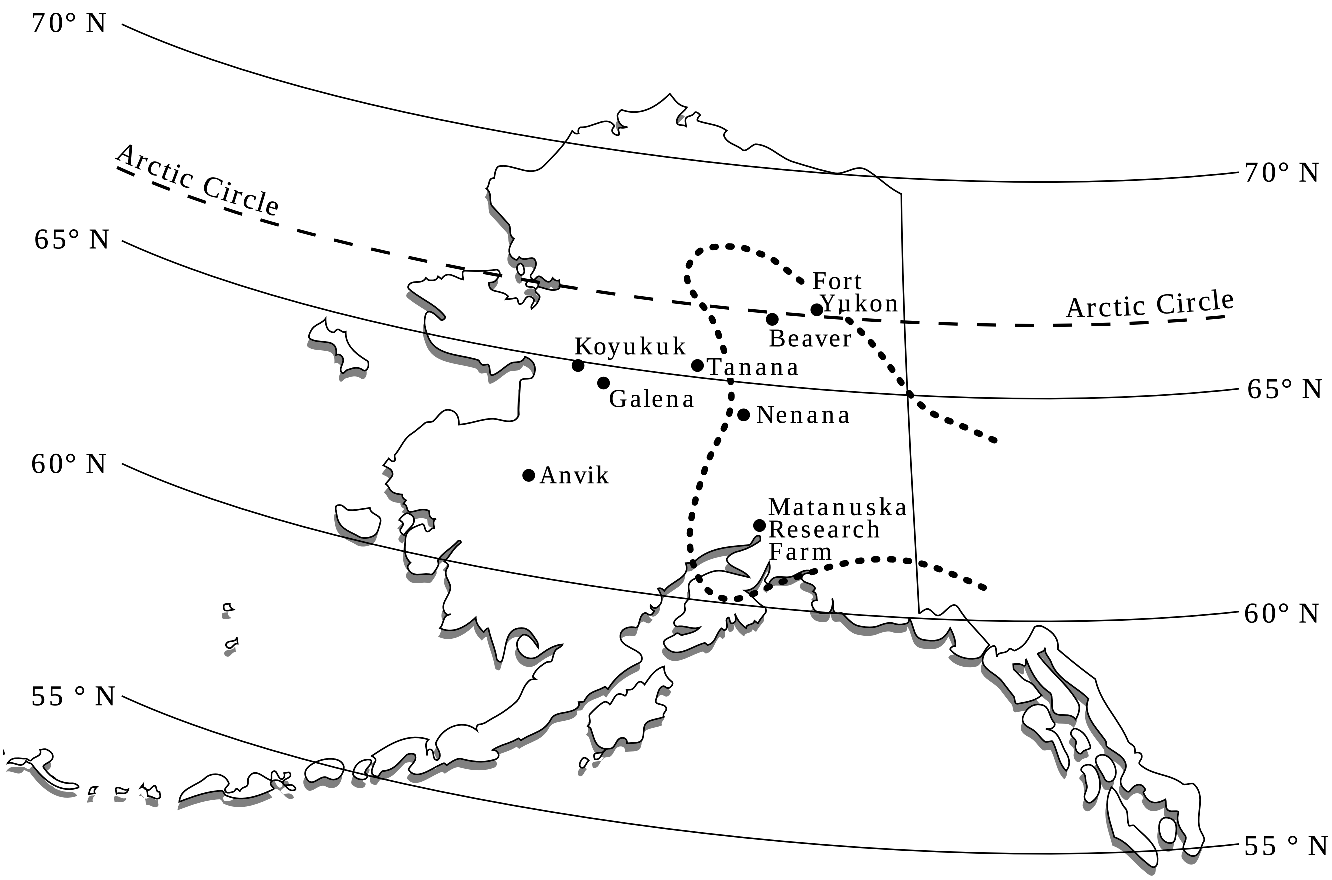

Figure 2. *Locations in Alaska of seed collections of indigenous slender wheatgrass used in this study, and the Matanuska Research Farm where collections were evaluated. The three westernmost collection sites (Anvik, Koyukuk, Galena) serve to extend the previously known native range of slender wheatgrass in Alaska a considerable distance beyond the limits set forth by Hulten (1968) reproduced here as dotted line.*

ments conducted over a 10-year period at the University of Alaska's Matanuska Research Farm (61.6° N) near Palmer in subarctic, southcentral Alaska.

Materials and Methods

All field experiments were conducted on Knik silt loam (coarse-silty over sandy or sandy-skeletal, mixed, non-acid Typic Cryorthent). Commercial fertilizer, disked into plowed seedbeds before planting each experiment, supplied nitrogen (N), phosphorus (P), and potassium (K) at 32, 56, and 54 lb/A, respectively. All experimental sites were selected for good surface drainage. No companion crops were planted.

Numerous individual collections of indigenous Alaskan slender wheatgrass are identified by number and locality of collection in Tables 1 and 5. Following early evaluations, a composite line of indigenous Alaskan slender wheatgrass was formulated consisting of a bulk of several individual collections; this line was included in all experiments except I and V and is identified in tables and figures as Alaska composite or Native Alaskan. A collection from a slender wheatgrass stand along a Matanuska Valley roadside near Palmer was included in all experiments as Alaska-44S.

Non-Agropyron check cultivars included in all forage and seed-production experiments were Polar bromegrass (predominantly *Bromus inermis Leyss.* x *B. pumpellianus Scribn.*), Manchar smooth bromegrass (*B. inermis*), and Engmo timothy (*Phleum pratense L.*). With all broadcast-seeded plots, planting rates were adjusted on the basis of germination trials to plant grasses at the following rates in lb/A: slender wheatgrass 18, bromegrass 22, and timothy 8. Individual broadcast-seeded plots measured 5 x 20 feet. All row and broadcast-plot field plantings utilized randomized complete block experimental designs; four replications were used in all experiments except Experiments III, IV, and VII which utilized three replications. All forage harvests from broadcast-seeded plots were conducted as described earlier (Klebesadel 1985). All forage yields are reported on the oven-dry basis (140°F).

Each spring following establishment, commercial fertilizer, top-dressed in late March or early April before visible spring growth of grasses, supplied N, P, and K on broadcast-seeded plots at 126, 42, and 40 lb / A, respectively. Ammonium nitrate was top dressed one to three days after the first-cutting forage harvest in all broadcast-seeded plot tests to supply N at 85 lb / A. On seed-production rows, N, P, and K were top-dressed in spring at 126, 42, and 40 lb / A in 1967; at 85, 28, and 26 lb / A in 1968; and at 64, 33, and 50 lb / A in 1969 and 1970.

Experiments I through IV — Four separate broadcast-seeded plot tests were planted to compare slender wheatgrass strains from different latitudinal origins for winter hardiness and forage yields. Planting dates, grasses compared, harvest dates, and yields for Experiments I through IV appear in Tables 1 through 4, respectively.

Experiment V — To evaluate seed production, 14 slender wheatgrass strains and three non-Agropyron forage grasses were seeded in rows 18 feet long and 24 inches apart on 20 June 1966; strains included appear in Table 5. In August of 1967 and 1968, a 12-foot segment was harvested from the mid-portion of each row. Seed was threshed and cleaned and yields were calculated.

Experiment VI — A second planting for seed-production comparisons was made with rows 18 feet long and 18 inches apart on 14 June 1968. Four slender wheatgrass strains and three non-*Agropyron* forage grasses were included as listed in Table 6. Seed harvests were made the two subsequent years as in the previous experiment.

Experiment VII — Four slender wheatgrass strains (Alaska composite, Alaska-44S, Revenue, and Primar) were seeded in rows on seven dates at about 10-day intervals, starting near 20 May in both 1970 and 1971. Rows were 22 feet long and 18 inches apart. Seedlings were thinned when 2-to-3 inches tall to leave individual plants 6-to-8 inches apart. On 12 October of both years, when grass growth had ceased, the number of jointed culms exceeding 6 inches in height were counted per plant. In 1970, counts were made on all plants per row (mean = 32); in 1971, counts were made on 10 typical plants in each row.

Experiment VIII — Three slender wheatgrass strains, Alaska composite, Alaska-44S, and Primar were seeded in rows 12 inches apart and 50 feet long on 22 June 1966 and 20 June 1967. When seedlings were 2-to-3 inches tall, rows were thinned to leave individual seedlings 6-to-8 inches apart.

Seedlings were withdrawn from the field on 10 October of both years to determine levels of stored food reserves crowns achieved prior to onset of winter in overwintering plants. Plant preparation was as described in Experiment IV of an earlier report (Klebesadel 1985). All etiolated regrowth was harvested (severed at the point where it emerged from the tiller stubble) at successive two-week intervals after pots containing prepared plant crowns were placed in a warm, dark chamber. Harvests continued until exhaustion of food reserves and death of plants. Harvested etiolated growth was dried at 140°F. Stored food reserves were calculated as milligrams (mg) oven-dry regrowth per oven-dry gram (g) of plant crown tissue potted.

On 25 October 1966 and 20 October 1967, after killing frost, aerial growth of plants remaining in the field was clipped and removed leaving a 2-inch stubble to prevent differential snow retention on rows during winter. In mid-May of 1967 and 1968, after spring growth had started, living and dead plants were counted in all rows planted the previous year and winter survival percentages were calculated. Over both years and all three strains, winter survival data were determined on a mean of 86 plants per row.

Results and Discussion

Forage Yields

Experiments I through IV — Tables 1 through 4 present forage yields from broadcast plots in four separate experiments; duration of tests ranged from three to six years. In general, the native Alaska lines produced relatively meager seeding-year forage yields (Tables 1, 2, and 3). In contrast to introduced cultivars which produced elongated culms, seeding-year growth of indigenous lines consisted almost exclusively of basal leaves with few or no elongated culms (Figure 3). Seeding year growth differences are discussed in greater detail in Experiment VII.

Strain	Latitude of origin (°N.)	Forage yield 1966 29 Sept	1967 10 July	1967 25 Sept	1968 27 June	1968 11 Sept	Total
		Oven-dry tons per acre					
Slender wheatgrasses:							
Native AK-60-140 (Ft. Yukon)[1]	66.6	0.07 d[2]	3.38 abc	0.41 d	2.80 ab	0.95 bc	7.61 e-j
Native AK-60-134 (Ft. Yukon)	66.6	0.01 d	3.00 a-d	0.37 d	2.81 ab	0.78 bc	6.97 f-j
Native AK-60-167 (Ft. Yukon)	66.6	Tr[3]	2.85 bcd	0.35 d	2.96 a	0.77 bc	6.93 f-j
Native AK-60-154 (Ft. Yukon)	66.6	0.05 d	2.76 b-f	0.44 d	2.78 ab	0.84 bc	6.87 g-j
Native AK-60-156 (Ft. Yukon)	66.6	Tr	3.12 a-d	0.31 d	2.73 ab	0.53 c	6.69 g-j
Native AK-60-139 (Beaver)	66.3	Tr	2.83 b-e	0.47 d	2.39 b	0.87 bc	6.56 hij
Native AK-60-137 (Tanana)	65.2	Tr	2.46 def	0.52 d	2.37 b	0.95 bc	6.30 ij
Native AK-60-168 (Tanana)	65.2	0.02 d	2.60 c-f	0.34 d	2.35 b	0.91 bc	6.22 ij
Native AK-60-161 (Galena)	64.7	0.16 d	3.50 ab	0.39 d	3.11 a	1.19 b	8.35 b-f
Native AK-60-164 (Koyukuk)	64.7	0.02 d	3.70 a	0.40 d	2.75 ab	0.99 bc	7.86 d-h
Native AK-60-175 (Nenana)	64.5	Tr	2.58 c-f	0.35 d	2.39 b	0.84 bc	6.16 j
Native AK-60-149 (Anvik)	62.7	Tr	2.39 def	0.37 d	2.76 ab	1.05 bc	6.57 hij
Means		0.03	2.93	0.39	2.68	0.89	6.92
Alaska-44S	61.5	0.81 b	2.70 b-f	1.32 b	1.28 c	1.88 a	7.99 c-h
Primar	46-48	1.08 a	0.64 g	1.26 b	Tr	Tr	2.98 k
Checks:							
Polar bromegrass	61.6	0.94 ab	2.76 b-f	1.44 b	3.11 a	1.74 a	9.99 a
Manchar bromegrass	43-47	1.12 a	2.03 ef	1.69 a	2.90 ab	2.03 a	9.77 ab
Engmo timothy	69-70	0.47 c	1.99 f	0.76 c	1.47 c	1.96 a	6.65 g-j

[1] Alaskan community nearest to original seed collection site.

[2] Within each column, means not followed by a common letter are significantly different (5% level) using Duncan's Multiple Range Test.

[3] Trace amount of herbage, insufficient for harvestable yield.

Table 1. *Seeding-year and subsequent forage yields from broadcast-seeded plots of 14 slender wheatgrass strains from diverse latitudinal origins, and three standard forage grass cultivars, at the Matanuska Research Farm (61.6° N). (Experiment I, planted 20 June 1966.)*

Strain	1968	1969		1970		1971		1972		Total
	2 Oct	10 July	24 Sept	16 July	30 Sept	8 July	15 Sept	11 July	25 Sept	
Slender wheatgrasses:	Oven-dry tons per acre									
Alaska composite	0.27 d[1]	0.29 c	0.20 e	3.37 a	0.33 c	1.92 a	0.74 c	3.53 a	0.02 c	10.67 b
Alaska-44S	0.48 d	0.94 a	0.30 de	2.84 ab	0.63 bc	0.79 c	1.21 b	3.04 a	0.26 bc	10.49 b
Revenue	1.66 ab	0.46 bc	0.55 bc	2.42 bc	1.10 ab	0.03 d	1.04 b	1.40 b	0.28 bc	8.94 c
Primar	0.82 cd	0.80 ab	0.40 cd	1.91 c	1.07 ab(WK)[2]	—	—	—	—	5.00 e
Checks:										
Polar bromegrass	1.15 bc	0.66 ab	0.68 ab	2.81 ab	1.46 a	1.07 b	1.64 a	3.08 a	0.97 a	13.52 a
Manchar bromegrass	1.13 bc	0.47 bc	0.79 a	2.65 abc	1.54 a	0.56 c	1.28 b	1.66 b	1.01 a	11.09 b
Engmo timothy	1.83 a	0.13 c	0.19 e	1.95 c	1.58 a	0.01 d	0.50 c	0.82 c	0.57 b	7.58 d

[1] Within each column, means not followed by a common letter are significantly different (5% level) using Duncan's Multiple Range Test.

[2] No further yields; stand winter killed completely.

Table 2. *Seeding-year and subsequent forage yields from broadcast-seeded plots of slender wheatgrass strains from diverse latitudinal origins, and three standard forage grass cultivars, at the Matanuska Research Farm. (Experiment II, planted 13 June 1968.)*

	1969	1970		1971		1972		1973		1974		
Strain	7 Oct	9 July	16 Sept	7 July	27 Sept	5 July	2 Oct	10 July	10 Sept	21 June	17 Sept	Total
Slender wheatgrasses:	Oven-dry tons per acre											
Alaska composite	Tr[1]	2.72 a	0.45 b	1.77 a	1.07 c	3.23 a	Tr[2]	2.60 b	Tr	1.54 ab	Tr	13.38 b
Alaska-44S	0.26 b	3.30 a	1.13 a	1.36 b	2.04 ab	2.41 bc	Tr (WK)[3]	—	—	—	—	10.50 bc
Revenue	0.78 a	3.12 a	1.37 a	0.26 d	1.58 abc(WK)	—	—	—	—	—	—	7.11 c
Primar	0.11 b	0.38 b	0.25 b(WK)	—	—	—	—	—	—	—	—	0.74 d
Checks:												
Polar bromegrass	0.22 b	2.98 a	1.57 a	0.83 c	2.20 a	3.12 ab	0.80 a	3.53 a	1.01 b	2.25 a	0.54 a	19.05 a
Manchar bromegrass	0.83 a	2.59 a	1.47 a	0.19 d	1.84 ab	2.16 c	1.25 a	3.46 ab	1.38 a	2.00 ab	0.86 a	18.03 a
Engmo timothy	0.07 b	3.23 a	1.34 a	0.01 d	1.42 bc	Tr	Tr	0.85 c	Tr	1.27 b	Tr	8.19 c

[1] Within each column, means not followed by a common letter are significantly different (5% level) using Duncan's Multiple Range Test.
[2] Trace amount of herbage insufficient for harvestable yield.
[3] No further yields; stands winter killed completely.

Table 3. *Seeding-year and subsequent forage yields from broadcast-seeded plots of slender wheatgrass strains from diverse latitudinal origins, and three standard forage grass cultivars, at the Matanuska Research Farm. (Experiment III, planted 6 June 1969, three replications.)*

Strain	1970 22 Sept	1971 8 July	1971 7 Oct	1972 5 July	1972 18 Oct	1973 11 July	1973 12 Sept	1974 27 June	1974 10 Sept	1975 26 June	1975 19 Sept	Total
Slender wheatgrasses:	— — — — — —	— — —	— — —	— — —	— — —	Oven-dry tons per acre	— — —	— — —	— — —	— — —	— — —	— — —
Alaska composite	0.47 ab[1]	1.07 a	1.51 b	3.02 a	0.30 ab	1.75 bc	Tr[2]	Tr	Tr	Tr	Tr	8.12 b
Alaska-44S	0.48 ab	0.63 b	2.40 a	2.78 ab	0.13 b	1.60 bc	0.02 b	1.36 b	Tr	0.37 b	0.48 b	10.25 b
Revenue	0.76 a(WK)[3]	—	—	—	—	—	—	—	—	—	—	0.76 c
Primar	0.72 a(WK)	—	—	—	—	—	—	—	—	—	—	0.72 c
Checks:												
Polar bromegrass	0.11 b	0.12 c	1.13 b	2.22 b	0.62 a	2.94 a	0.62 a	2.96 a	0.17 a	2.10 a	1.95 a	14.94 a
Engmo timothy	0.21 b	0.10 c	1.65 b	1.07 c	0.47 ab	0.95 c	0.49 a	2.20 a	0.19 a	0.31 b	1.42 a	9.06 b

[1] Within each column, means not followed by a common letter are significantly different (5% level) using Duncan's Multiple Range Test.

[2] Trace amount of herbage insufficient for harvestable yield.

[3] No further yields; stands winter killed completely.

Table 4. *Seeding-year and subsequent forage yields from broadcast-seeded plots of slender wheatgrass strains from diverse latitudinal origins, and two standard forage grass cultivars, at the Matanuska Research Farm. (Experiment IV, planted 25 June 1970, three replications.)*

Strain	Latitude of origin (°N)	Seed yield 1967		Seed yield 1968	
Slender wheatgrasses:		— — Pounds/acre — —			
Native AK-60-140 (Ft. Yukon)[1]	66.6	1350	a-d[2]	908	ab
Native AK-60-134 (Ft. Yukon)	66.6	1587	ab	799	abc
Native AK-60-167 (Ft. Yukon)	66.6	987	d	451	cd
Native AK-60-154 (Ft. Yukon)	66.6	1217	a-d	784	abc
Native AK-60-156 (Ft. Yukon)	66.6	1387	a-d	877	ab
Native AK-60-139 (Beaver)	66.3	1321	a-d	867	ab
Native AK-60-137 (Tanana)	65.2	1152	bcd	986	a
Native AK-60-168 (Tanana)	65.2	1368	a-d	822	abc
Native AK-60-161 (Galena)	64.7	1502	abc	844	abc
Native AK-60-164 (Koyukuk)	64.7	1690	a	780	abc
Native AK-60-175 (Nenana)	64.5	1067	cd	860	ab
Native AK-60-149 (Anvik)	62.7	1170	bcd	1175	a
Means		1317		846	
Alaska-44S	61.5	991	d	520	bc
Primar	46-48	81	e	105	de
Checks:					
Polar bromegrass	61.6	169	e	129	de
Manchar bromegrass	43-47	30	e	28	e
Engmo timothy	69-70	141	e	93	de

1 Alaskan community nearest to original seed collection site.

2 Within each column, means not followed by a common letter are significantly different (5% level) using Duncan's Multiple Range Test.

Table 5. *Seed yields of indigenous slender wheatgrass collections from various sources in Alaska, strain Alaska-44S, the cultivar Primar from the Pacific Northwest, and three non-Agropyron forage cultivars, during two years at the Matanuska Research Farm (61.6° N). (Exp. V, planted 20 June 1966).*

First-cutting yields of native slender wheatgrass in the years after establishment usually exceeded those of introduced Primar due to winter injury of Primar (Tables 1, 2, and 3). However, first-cutting yields of the native slender wheatgrass were markedly lower than Primar when the latter showed good winter survival and below-normal precipitation (Figure 4) led to inadequate moisture supply (1969, Table 2). Similarly, Newell and Keim (1943) in Nebraska found northern strains of smooth bromegrass to be more susceptible to drought stress than strains from southern origins.

During the time of sub-normal precipitation, the indigenous Alaska composite strain showed strikingly more severe symptoms of moisture stress (curled, dried leaves) than introduced Revenue and Primar, or than the Alaska-44S strain of uncertain original derivation. Alaska-44S resembled Primar and Revenue more than the indigenous Alaska strain in tolerance to moisture stress, suggesting that this strain may represent an introduction. This observed differential response among strains to moisture stress was clearly evident also in disparate forage yields (Table 2, 1969 yields).

This striking difference between Alaskan and more southern-adapted slender wheatgrass ecotypes may be due to the relatively lower growing-

Strain	Latitude of origin (°N)	Seed yield 1967		Seed yield 1968	
		— — — Pounds/acre — — —			
Slender wheatgrasses:					
Alaska composite	62-67	42	de[1]	267	c
Alaska-44S	61.5	602	a	528	a
Revenue	52-53	471	abc	394	b
Primar	46-48	306	b-e	154	cde
Checks:					
Polar bromegrass	61.6	467	abc	96	de
Manchar bromegrass	43-47	221	cde	75	e
Engmo timothy	69-70	24	e	0	

[1] Within each column, means not followed by a common letter are significantly different (5% level) using Duncan's Multiple Range Test.

Table 6. *Seed yields of slender wheatgrass strains from diverse latitudinal origins during two years of acute moisture stress at the Matanuska Research Farm (61.6° N.). (Exp. VI, planted 14 June 1968).*

season temperatures in Alaska than at mid-temperate latitudes where Primar normally is grown. Revenue and Primar, adapted to growing seasons with higher temperatures, logically would be better able to cope with moisture stress. As an indication of differences in growing-season temperatures at different latitudes within the range occupied by slender wheatgrass, mean July temperature for Palmer is 57.7° F, for Pullman, WA 68.0° F, and for Miles City, MT 72.9° F.

With the relatively late first-cutting harvest dates in these tests (mostly 5 to 16 July), the native Alaska composite slender wheatgrass produced good first-cutting forage yields, but frequently very little in the second-cuttings. This extreme imbalance in the two yields can be altered with earlier dates of first harvest. For example, in Experiment I (Table 1), with first harvest on 27 June, all 12 Alaska lines produced better second-cutting yields than following the 10 July harvest in 1967. Optimum first-cutting harvest dates locally (20 to 30 June) for perennial grasses provide good first-cutting yields of high-quality forage, and permit adequate time for regrowth to provide appreciable second-cutting yields. With the first-cutting harvest dates employed in these four experiments, Polar and Manchar bromegrass almost invariably produced higher second-cutting yields than the indigenous wheatgrass.

Total forage yields of the highest-yielding slender wheatgrasses equalled or surpassed those of Engmo timothy (Tables 1, 2, 3, 4) and sometimes Manchar bromegrass (Table 2). However, in all four forage experiments, total yields of Polar brome invariably were significantly higher than the highest yielding slender wheatgrasses. Mitchell (1982) at the Palmer Research Center also found that indigenous slender wheatgrass strains did not produce as much forage as the highest-yielding bromegrasses.

Winter Hardiness

Primar, the southernmost-adapted slender wheatgrass strain, was clearly the least winter hardy. Stands of Primar were badly injured in Experiment I during the winter 1967-68 (Figure 5) and first-cutting yields in 1968 were negligible (Table 1). In the same test, Alaska-44S survived to produce a modest first-cutting forage yield, while the 12 subarctic-adapted indigenous lines sustained no apparent winter injury and produced high first-cut yields.

The relatively severe winter of 1970-71 killed Primar stands completely in Experiments II, III, and IV (Tables 2, 3, and 4). Revenue, although originating from a more northerly source than

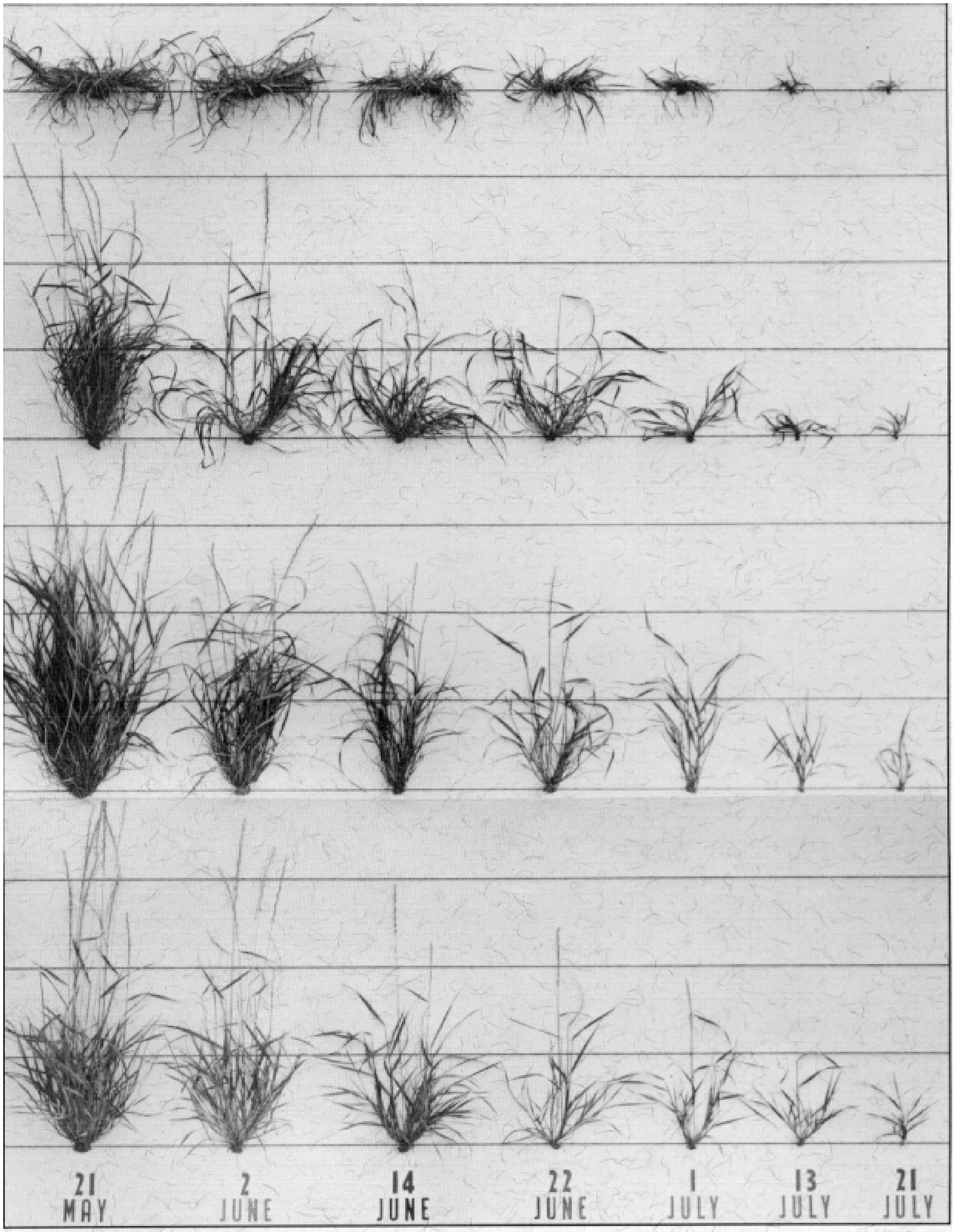

Figure 3. *Representative individual plants of four slender wheatgrass strains of diverse latitudinal adaptation, photographed on 12 October near the end of the growing season, showing growth and heading as influenced by seven planting dates during the same year. Top to bottom: Native Alaskan (62° to 67° N), Alaska-44S (61.5° N), Revenue from Canada (52° to 53° N), Primar from the Pacific Northwest (46° to 48° N). Horizontal lines 8 inches apart.*

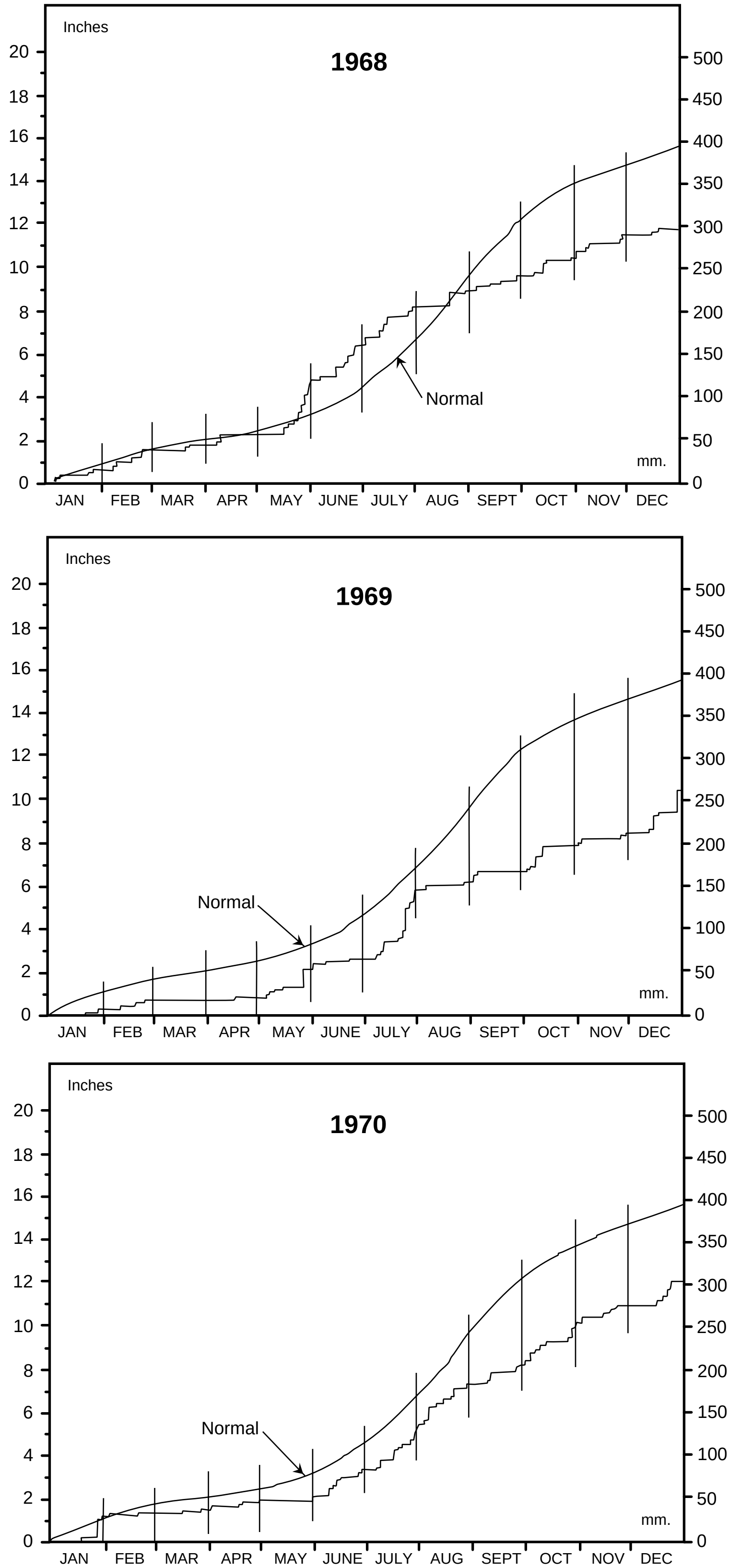

Figure 4. *Normal and actual cumulative precipitation at the Matanuska Research Farm during three years when moisture stress affected grass performance in experiments reported here.*

Primar, was also completely winter killed in Experiment IV during the 1970-71 winter. Although Revenue was severely injured by the 1970-71 winter in Experiments II and III (see 1971 first-cutting yields, Tables 2 and 3), it recovered to persist for the full term of Experiment II (Table 2). Revenue survived for a year longer than Primar in Experiment III before succumbing during the winter of 1971-72 (Table 3).

Strain Alaska-44S was more injured by the winters 1967-68 and 1970-71 than was the native slender wheatgrass, as noted both visually and in significantly lower first-cutting forage yields in 1968 (Experiment I, Table 1) and in 1971 (Experiments II, III, and IV; Tables 2, 3, and 4). However, Alaska-44S was clearly more winter hardy than Primar in Experiments I and II (Tables 1 and 2), and more winter hardy than both Primar and Revenue in Experiments III and IV (Tables 3 and 4), confirming that this strain is intermediate in winter hardiness between the genuinely indigenous Alaska slender wheatgrass and introduced Revenue and Primar.

Some evidence indicates that the indigenous slender wheatgrass is more winter hardy than the very hardy Polar bromegrass (Wilton et al. 1966). Following the relatively severe winter of 1970-71, first-cutting forage yields of the Alaska composite showed less reduction than those of Polar (Table 2). Engmo timothy was less winter hardy than Polar, Manchar, or the native slender wheatgrass, producing very low first-cutting yields in 1971 (Tables 2, 3, and 4).

None of the 12 individual native slender wheatgrass lines (Table 1), nor the native composite strain (Tables 2, 3, and 4), showed any evidence of winter injury in these tests. When stands became visibly unthrifty and less productive in the final year of Experiment III (Table 3) and in the last two years of Experiment IV (Table 4), it is believed the stands had reached senescence common in 4-to-6-year-old stands of this species (Crowle 1968, 1970).

Figure 5. Comparative winter survival of two-year-old, 5-foot-wide plots of two slender wheatgrass strains from widely separated latitudinal origins: Plot to left of center stake: Primar, from the Pacific Northwest (46°— 48° N.); right: native Alaskan collection AK-60-161 from Galena (64.7° N.). Numbered stakes are three feet tall. On the day of photo (27 June 1968), plots on left and right of center stake yielded oven-dry herbage at rate of 0.02 and 2.89 tons per acre, respectively.

Further winter hardiness comparisons among slender wheatgrass strains tested are discussed in the results of Experiments VII and VIII.

Stand Longevity

Polar and Manchar bromegrass, and Engmo timothy, are exceptionally long-lived perennials; stands of these persist indefinitely if not terminated by winter kill or pathogens. Slender wheatgrass, in contrast, is described as a relatively short-lived perennial (Crowle 1968, 1970; Hansen 1972; Schwendiman and Law 1946). The species in general, including cultivars Revenue and Primar (Crowle 1970), normally maintains good stands for three-to-five years. Schwendiman and Law (1946) noted that an annual precipitation of less than 15 inches in the Pacific Northwest region shortened longevity of stands to less than five years, while with 18 inches or more, fertilized plots persisted well beyond five years. Mean annual precipitation at the Matanuska Research Farm is 15.4 inches.

There was no evidence of stand deterioration of native slender wheatgrass or the Alaska-44S strain in the 3-year Experiment I (Table 1), or the 5-year Experiment II (Table 2). However, in both of the 6-year experiments (Tables 3 and 4), there was evidence of diminishing forage productivity with both Alaska strains; this was especially noticeable in the final three years of Experiment IV. Polar and Manchar bromegrass continued to be more productive than the wheatgrasses in the late years of the two six-year tests (Tables 3 and 4).

Seed Production

Experiments V and VI — Indigenous lines of slender wheatgrass grown in rows for seed production survived the winters in Experiment V

(Table 5) with no apparent injury; in contrast, the more southern-adapted Primar sustained severe winter injury (Figure 6). The indigenous lines produced high seed yields during the two years of Experiment V, though most lines produced somewhat less in the second year. Two-year mean seed yield of the 12 indigenous lines was 1082 lb/A, while Alaska-44S averaged 756, and Primar only 93.

These results differ from those reported by Pringle et al. (1975) in Canada where greatly reduced seed yields were obtained at Beaverlodge (55° N) from slender wheatgrass collections originating from 61° to 68° N, compared with ecotypes from three more southern sources. The five northernmost collections in results reported here originated at Fort Yukon (66.6° N), just north of the Arctic Circle; 2-year mean seed yields of those five averaged 1035 lb/A, comparable with yields from more southern collections in Alaska (Table 5). It is possible that in the Canadian work, plants originating from 61° to 68° N and grown at 55° N were too far removed from accustomed photoperiodic environment for seed production at maximum potential.

A second possibility is that northern Canadian ecotypes, accustomed to cooler growing seasons, were under greater evapotranspirational stress at Beaverlodge than would permit normal growth behavior. Mean annual degree days (base 42°F) at the northern Canadian collection sites (Inuvik = 964, Fort Good Hope = 1,269, Norman Wells = 1,598) are considerably lower than at Beaverlodge = 2,085. Growing the northern Canadian ecotypes under warmer conditions could present an unaccustomed, more stressful evapotranspirational environment that may have adversely affected seed production.

The same period of moisture stress that reduced forage yields by the native Alaskan wheatgrass (Table 2) also markedly reduced seed yields (Table 6). In contrast to the high seed yields of the indigenous lines in Experiment V when precipitation and soil moisture were adequate, the cumulative effects of below-normal precipitation in consecutive years 1968, 1969, and 1970 markedly suppressed seed yields of the native Alaska strain in 1969 and 1970 (Experiment VI, Table 6). As in the forage tests, moisture stress affected the various slender wheatgrass strains differentially, and effects were related to latitudinal origins. Revenue and Primar, adapted to more southern and warmer growing seasons with greater evapotranspirational demands, produced 2-year-mean seed yields of 433 and 230 lb/A, respectively, surpassing the greatly drought-stressed indigenous strain which averaged only 155 lb/A. Seed yield of strain Alaska-44S (2-year mean = 565 lb/A) provided further evidence of its being originally an introduction from more southern origins, for that strain's seed yield resembled introduced Revenue and Primar in capacity to endure moisture stress better than the genuinely indigenous slender wheatgrass. Seed yields of Alaska-44S, Revenue, and Primar decreased as latitudinal distance of their origins from this test location increased.

Engmo timothy seed yields were more suppressed by moisture stress than were those of Polar bromegrass (Table 6 vs. Table 5). Seed yields of Manchar were much lower than Polar at all harvests but the differences were not statistically significant.

Seeding-Year Growth

Experiment VII — Growth achieved by mid-October by typical individual plants of four slender wheatgrass strains, as influenced by seven planting dates, is shown in Figure 3. With all strains, the number of elongated culms > 6 inches decreased with progressively later planting dates. Elongated culms-per-plant showed a relationship to latitudinal origin of strains (Figure 7). Primar, of southernmost adaptation, generally produced most culms per seedling plant. With progressively more northern origin, strains generally produced fewer culms/plant in the order: Primar > Revenue > Alaska-44S > Indigenous Alaskan.

Alaska-44S, Revenue, and Primar were relatively similar in producing several elongated culms per plant. A sharp difference in culms/plant was noted, however, between Alaska-44S and the native Alaskan strain, even though they were the closest pair in latitudinal origin. This further supports the premise that Alaska-44S represents an early introduction to the Matanuska Valley and has been modified by natural selection toward adaptation to this subarctic environment.

Pringle et al. (1975) compared four latitudinal ecotypes of slender wheatgrass in Canada and found that seedlings of northernmost (61° to 68°

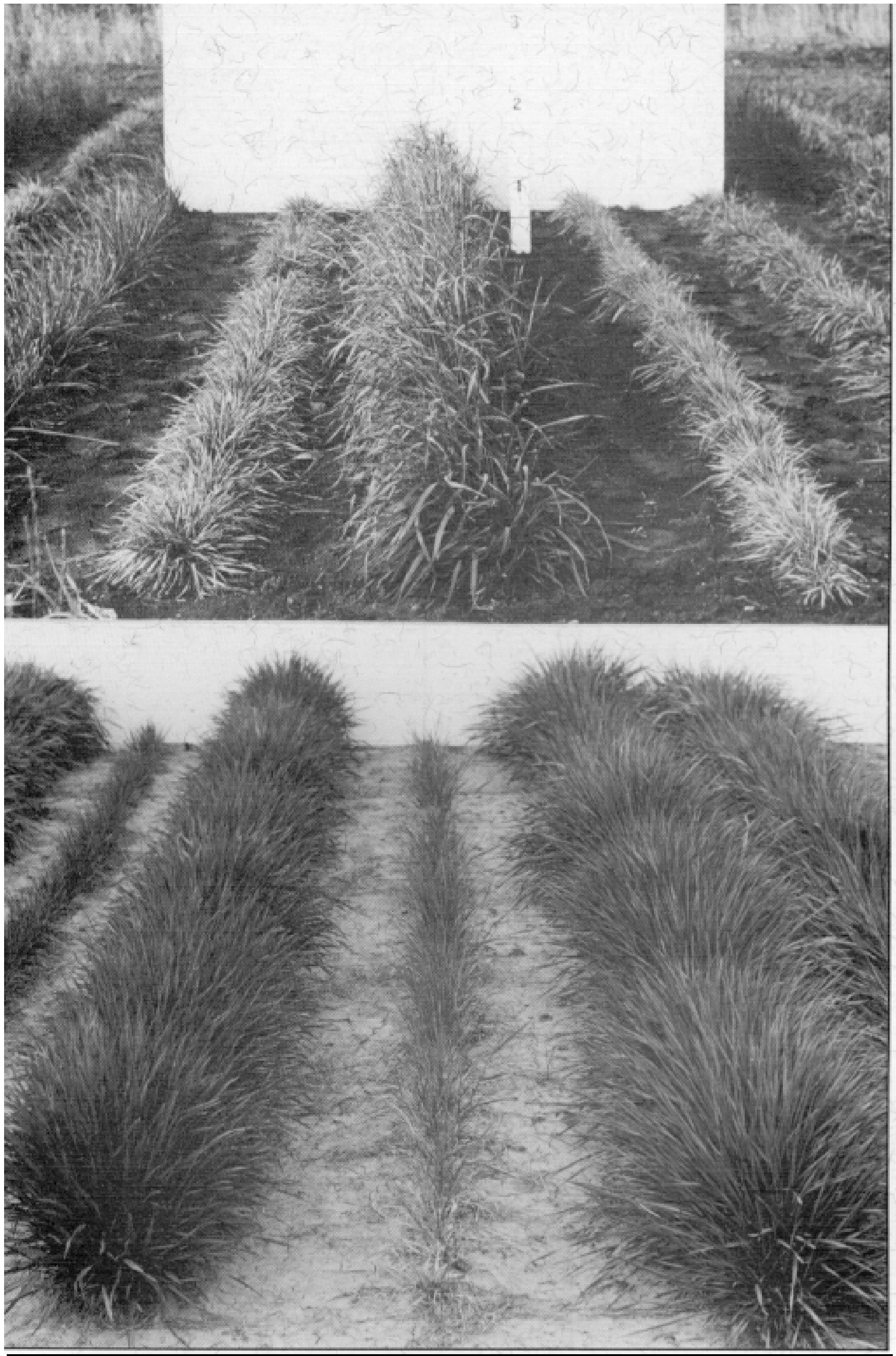

Figure 6. *Upper photo: Slender wheatgrass rows seeded 20 June and photographed 13 October of the same year. Lower photo: The same rows as they appeared on 8 June of the following year. Center row in both photos is the cultivar Primar from Montana; tall, dark-green growth with many elongated culms produced by mid-October of seeding year was followed by severe winter injury apparent in lower photo. Rows to left and right of Primar are indigenous Alaskan collections AK-60-134 and AK-60-156, respectively, both from Fort Yukon. Note low, leafy growth with no elongated culms in seeding year (bleached to yellow-brown on 13 Oct.), followed by vigorous, uninjured growth the following year.*

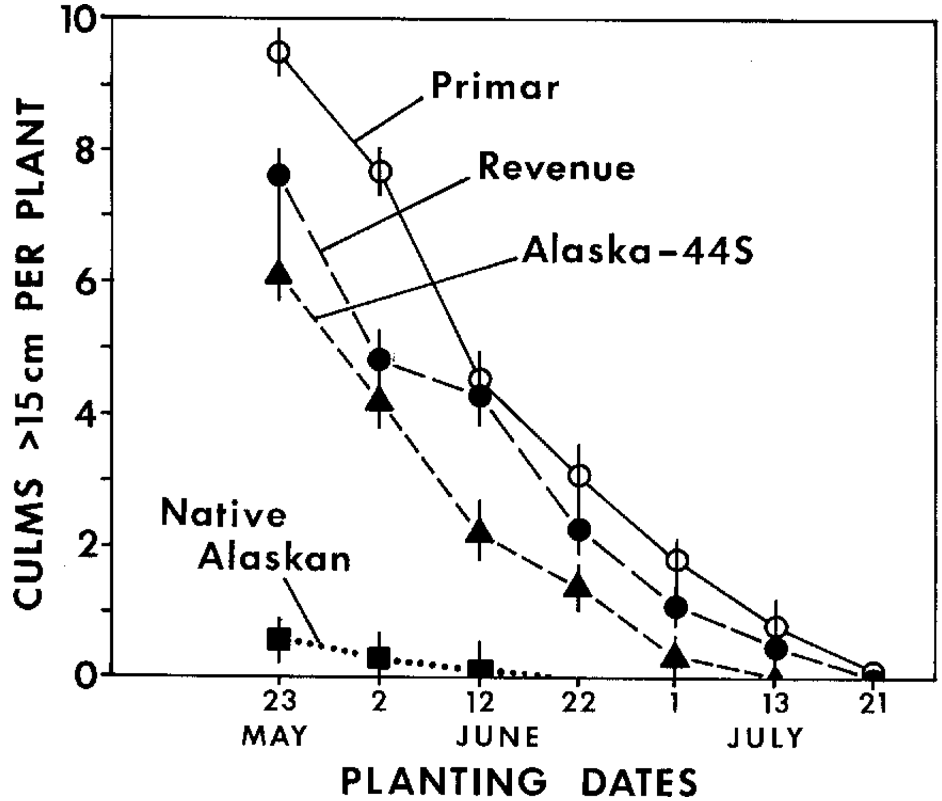

Figure 7. *Two-year means of numbers of elongated culms longer than 15 cm (6 inches) per seedling plant of four slender wheatgrass strains of diverse latitudinal adaptation, as influenced by date of planting. Counts were conducted on 12-13 October, after killing frost in both years. For each date, means not connected by a common vertical line are significantly different (5% level) using Duncan's Multiple Range Test.*

N) collections produced the fewest culms under both 16- and 24-hour diurnal photoperiods. Similarly, Larsen (1947) found strains of little bluestem (*Andropogon scoparius Michx.*) from different latitudinal origins to react very differently under certain photoperiodic treatments. With 14-hour photoperiods, northern strains produced only basal leaves while southern strains produced elongated culms, a pattern paralleling slender wheatgrass relationships in the present study.

A striking contrast was noted in this and earlier experiments among the different wheatgrass strains in foliage appearance during late September and early October in advance of killing frost. Foliage of all indigenous lines became bleached to yellow-brown in coloration. Similar behavior has been noted earlier with other indigenous grass species, including red fescue (*Festuca rubra* L.) (Klebesadel 1985; Klebesadel et al. 1964). In contrast to the indigenous lines, leaves of introduced Revenue and Primar from more southern latitudes, as well as strain Alaska-44S, remained green until killed by frost. This further indicates that Alaska-44S derives from an introduction.

Stored Reserves

Experiment VIII — Comparative levels of food reserves stored by 10 October (the date plants were removed from the field following killing frost in both years) were estimated by harvesting and weighing etiolated growth put forth from trimmed plant storage tissues (Figure 8). Primar, the least winter hardy cultivar and from southernmost origins, exhausted its reserves during the first 2-week growth period in darkness (Figures 8 and 9) and showed a lesser amount of total reserves than the two Alaska strains. The two Alaska strains not only produced more etiolated growth than Primar during the first 2-week period, but they also produced additional etiolated growth during the second 2-week period. The indigenous strain produced more than Alaska-44S (Figures 8 and 9).

Stored food reserves provide the energy needed by perennial plants to develop hardiness in preparation for winter and also to initiate new growth the following spring (Smith 1964). Smith (1964) also states that plants low in food reserves cannot develop a high level of winter hardiness. Whether food reserve storage in Primar is inadequate under Alaska conditions for maximum hardiness development is not known. However, levels of stored reserves in the different wheatgrasses paralleled winter survival of plants in the field (Figure 8); the two Alaska strains that required four weeks for exhaustion of comparatively high levels of stored reserves survived 100%, while Primar, with its lower level of reserves exhausted in only two weeks, averaged only 11% winter survival.

Presumed Ecotypic Evolution

Schwendiman and Law (1946) recognized that the largely self-pollinated slender wheatgrass is quite variable and suggested that perhaps in no other native grass is there better opportunity for selection to obtain the best form for an area where it is adapted. Clausen (1953) states that the genetic mechanisms controlling ecotypes favor the preservation of a sufficiently diverse potential to adjust to new conditions, and that survival under changing conditions depends on the ability to integrate inherent variability with new environmental conditions. This contention appears applicable to what apparently has occurred with the local roadside population of slender wheatgrass from which the Alaska-44S strain was derived.

The roadside population is well established along approximately one-half mile of gravelly roadside near milepost 44 of the Old Glenn Highway, about 2.5 miles southeast of Palmer. The original collection, from which seed was increased for use in these tests, was made in 1964, about 30 years after the road itself was constructed in 1935 through a forested, non-agricultural area connecting two districts of farmlands (Stone 1950).

No records exist of when the roadside population became established or from where it originated. The local farmers' cooperative that started in 1935 provided seed to area farmers and probably obtained its supplies from the Pacific Northwest states. Another possible origin is the Alaska Agricultural Experiment Station's Matanuska Research Farm located about 7 miles west of the roadside wheatgrass population. Slender wheatgrass plantings were made at the Research Farm at least six times between 1922 and 1941 (Irwin 1945). Their sources of seed likely were direct from the Pacific Northwest or via U.S. Department of Agriculture introductions from Beltsville, MD. During the early years of experimental trials in Alaska, it was common Experiment Station practice to disseminate seed of adapted crops to area growers.

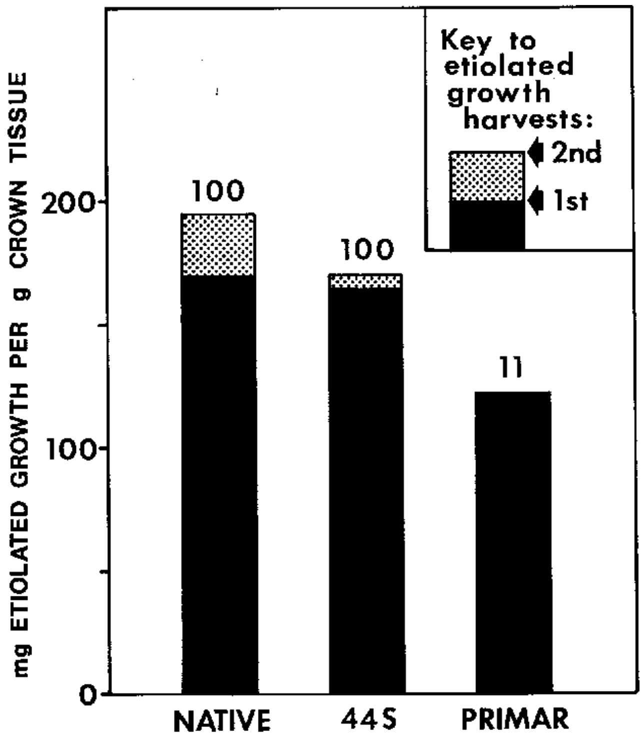

Figure 8. Two-year means of stored food reserves as measured by etiolated growth in darkness harvested at 2-week intervals from crowns of three strains of slender wheatgrass grown near Palmer, Alaska. Plants were removed from field 10 October both years, 111 days after planting, following killing frosts. All weights on oven-dry basis. Numbers above bars indicate 2-year mean winter-survival percentages in the field of undisturbed individual plants in the same rows.

Slender wheatgrass was the most highly recommended grass for hay production in the Matanuska Valley in the early 1930s (Alberts 1933). Two farmers were growing wheatgrass (species not known but probably slender) for horse hay in 1931 in an isolated agricultural area about 2.5 miles south of the Alaska-44S collection site. The road constructed in 1935 was the only avenue to hay customers; earlier travel on that general route was via a wagon trail on nearby riverbed gravel.

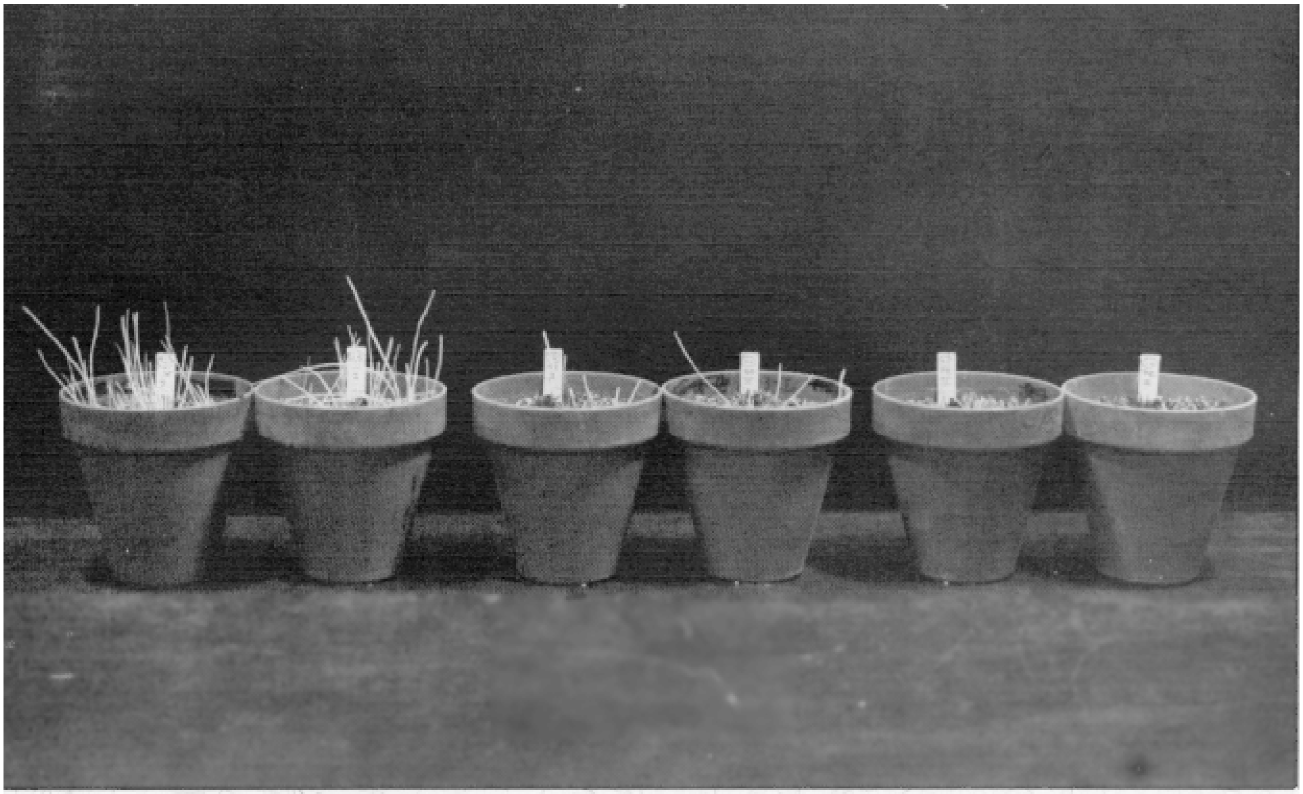

Figure 9. *Etiolated growth produced by three spring-planted slender wheatgrass strains by end of the second, two-week growth period in darkness after having been taken from field on 10 October after termination of the growing season and near onset of winter. Paired pots contain crowns of Native Alaskan (left), Alaska-44S (center), and Primar (right).*

Although only about 30 years passed from road construction to seed collection for natural selection to be operative on an introduced slender wheatgrass at that site (unless other local natural selection preceded its arrival on the roadside), the normally short 3-to-5-year life span of the species would tend to accelerate generational turnover, hastening adaptive change. Enhanced winter survival would be a critical survival mechanism that would ensure reproduction and persistence of the strain in a new environment (Cooper 1965; Wilsie 1962).

A perennial introduced into this area from temperate latitudes and incapable of surviving any winters would shortly be eliminated, never to enter into the natural selection process. At the other extreme, a long-lived perennial, once established and adequately winter hardy, could persist indefinitely without undergoing adaptive genotypic modification. However, a short-lived perennial, such as slender wheatgrass from the Pacific Northwest, with only marginal winter hardiness for initial persistence but with good seed production from a few winter-surviving variants, could be expected to undergo relatively rapid selective modification for improved winter hardiness. The strain Alaska-44S now possesses good winter hardiness here, likely acquired recently through natural selection, while retaining several phenotypic and other characteristics, such as drought tolerance, displayed by the mid-temperate-adapted ecotypes. These latter characteristics, in contrast to winter hardiness, would not be subject to modification for successful acclimatization and persistence here and therefore would tend to be retained.

Production of ripe seed in the seedling year would offset somewhat the rate of natural selection. Although a small amount of seed can reach maturity before killing frost on the earliest-produced heads of seedling Alaska-44S plants, most seed heads produced in the seedling year contain immature seed at the end of the growing season.

Conclusions

Indigenous slender wheatgrass is widespread in Alaska. These evaluations of several individual collections made in Alaska and an Alaskan composite strain revealed that native slender wheatgrass is extremely winter hardy, and produces high yields of seed and forage in this environment. In contrast, the cultivars Revenue and Primar from more southern latitudes generally were not winter hardy, produced lower forage and seed yields, and are poorly adapted for use in Alaska.

In view of the several desirable agronomic characteristics of indigenous Alaskan slender wheatgrass, this grass should be potentially useful for forage production in short rotations where extreme winter hardiness is required. Ideal subarctic adaptation, and good reseeding capabilities that counter its relatively short life-span, should enhance its use for revegetation of disturbed northern sites, as suggested earlier for northern Canadian ecotypes (Pringle et al. 1975).

Although northern-adapted slender wheatgrass strains produce much higher seed yields than Polar bromegrass, the latter surpassed the highest-yielding slender wheatgrasses in forage production. The highly unusual 3-year sequence of significantly below-normal precipitation during these tests afforded the opportunity to note markedly greater moisture-stress susceptibility with lowered forage and seed yields in the indigenous Alaskan slender wheatgrass than in the more southern-adapted, introduced cultivars.

The cumulative weight of evidence in these experiments strongly supports the conclusion that the roadside population, from which Alaska-44S derived, began as an introduction from more southern origins. Alaska-44S exhibits growth characteristics and drought tolerance similar to the more southern-adapted Revenue and Primar, yet it stores higher levels of food reserves in autumn than Primar. This latter characteristic likely contributes to the superior winter hardiness of Alaska-44S over the more southern-adapted strains, a relationship noted here within other forage species (Klebesadel 1971b, 1985; Klebesadel and Helm 1986). Though probably still in the process of adaptive change, the roadside population from which Alaska-44S derived probably represents a distinct ecotype at a well advanced but uncertain stage in the course of adjustment to new environmental conditions.

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Taxonomic Note

Agropyron trachycaulum has been the accepted binomial for this grass and is used in this report; however, a recent taxonomic revision (Dewey 1983) within the wheatgrasses proposes the binomial *Elymus trachycaulus* (Link) Gould ex Shinners.

Explanatory Note

This report summarizes research completed several years ago. During its completion, the investigator/author assumed time-consuming research supervisory responsibilities that delayed more timely publication. It is published now because it represents heretofore unpublished information that augments Alaska's agronomic research data base; moreover, publication can circumvent the need to repeat this already completed research.

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