

# Relationship of Latitude-of-Origin to Winter Survival and to Forage and Seed Yields of Wheatgrasses (*Agropyron* species) in Subarctic Alaska

**Leslie J. Klebesadel**

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

and

**D.J. Helm**

Research Assistant Professor  
Agricultural and Forestry Experiment Station  
Palmer, Alaska

UNIVERSITY OF ALASKA FAIRBANKS

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

## Table of Contents

	Page
Summary .....	ii
Introduction .....	1
Experimental Procedures .....	2
Results .....	2
Wheatgrasses .....	9
Fairway Wheatgrass ( <i>A. cristatum</i> ) .....	9
Thickspike Wheatgrass ( <i>A. dasystachyum</i> ) .....	9
Crested Wheatgrass ( <i>A. desertorum</i> ) .....	10
Tall Wheatgrass ( <i>A. elongatum</i> ) .....	10
Beardless Wheatgrass ( <i>A. inerme</i> ) .....	11
Intermediate Wheatgrass ( <i>A. intermedium</i> ) .....	11
Streambank Wheatgrass ( <i>A. riparium</i> ) .....	12
Siberian Wheatgrass ( <i>A. sibiricum</i> ) .....	12
Western Wheatgrass ( <i>A. smithii</i> ) .....	13
Bluebunch Wheatgrass ( <i>A. spicatum</i> ) .....	13
Slender Wheatgrass ( <i>A. trachycaulum</i> ) .....	14
Pubescent Wheatgrass ( <i>A. trichophorum</i> ) .....	15
Violet Wheatgrass ( <i>A. violaceum</i> ) and Arctic Wheatgrass ( <i>A. sericeum</i> ) .....	15
Wheatgrass-Wildrye Hybrid ( <i>Agroelymus palmerensis</i> ) .....	16
Non-wheatgrass Comparison Species .....	17
Smooth Bromegrasses ( <i>Bromus inermis</i> ) .....	17
Timothy ( <i>Phleum pratense</i> ) .....	17
Siberian Wildrye ( <i>Elymus sibiricus</i> ) .....	18
Discussion .....	18
Environmental Stimuli .....	18
Latitudinal Effects .....	18
Conclusions .....	19
Acknowledgments .....	20
Literature Cited .....	20

## List of Tables and Figures

Table 1 – Names and types of wheatgrasses .....	3
Table 2 – Forage yields from Experiment I .....	4
Table 3 – Forage yields from Experiment II .....	5
Table 4 – Seed yields from Experiment III .....	7
Table 5 – Seed yields and winter survival from Experiments IV and V .....	8
Figure 1 – Precipitation at the Matanuska Research Farm .....	9
Figure 2 – Comparative winter survival of broadcast-seeded plots of wheatgrass cultivars .....	10
Figure 3 – Drilled rows of wheatgrass species with contrasting elongated culms .....	11
Figure 4 – Comparative winter survival of wheatgrass strains as individual plants .....	12
Figure 5 – Comparative winter survival in broadcast-seeded plots of wheatgrass strains .....	13
Figure 6 – Comparative winter survival of subarctic versus mid-temperate-adapted wheatgrasses .....	14
Figure 7 – Comparative winter survival in broadcast-seeded plots of wheatgrass from diverse latitudinal origins .	15
Figure 8 – Comparative winter survival of subarctic versus mid-temperate-adapted wheatgrasses .....	16
Figure 9 – Comparative spring vigor of four grass species .....	17

## SUMMARY

Five field experiments evaluating and comparing numerous grasses were conducted over seven years at the Matanuska Research Farm (61.6°N) near Palmer in southcentral Alaska. Grasses were 34 strains within 14 species of wheatgrass (*Agropyron*) derived from various geographic areas spanning 32 degrees of latitude; also included were the intergeneric hybrid *Agroelymus palmerensis* Lepage, Siberian wildrye (*Elymus sibiricus* L.), two bromegrass (*Bromus*) cultivars, and one timothy (*Phleum pratense* L.) cultivar. They were grown in broadcast-seeded plots for forage (two cuts per year), in drilled rows for seed production, and as individual plants in rows for winter-survival determinations.

- Strains within the following species were the least winter-hardy, and therefore were least productive of forage and seed: thickspike wheatgrass (*A. dasystachyum* [Hook.] Scribn.), tall wheatgrass (*A. elongatum* [Host] Beauv.), beardless wheatgrass (*A. inerme* [Scribn. and Smith]), and pubescent wheatgrass (*A. trichophorum* [Link] Richt.). All 10 strains tested among those species originated from below 47°N.

- A considerable range of winter hardiness was found among strains within the following species: crested wheatgrass (*A. desertorum* [Fisch.] Schult.), bluebunch wheatgrass (*A. spicatum* [Pursh] Scribn. and Smith), pubescent wheatgrass (*A. trichophorum* [Link] Richt.) and, to a lesser extent, slender wheatgrass (*A. trachycaulum* [Link] Malte); this was more apparent with individual plants than in broadcast-seeded plots.

- Canadian cultivars from 51° to 53°N were more winter-hardy and generally more productive of forage than strains from the western states (below 49°N) in fairway wheatgrass (*A. cristatum* [L.] Gaertn.), intermediate wheatgrass (*A. intermedium* [Host] Beauv.), crested, and slender wheatgrass.

- Sodar streambank wheatgrass (*A. riparium* Scribn. and Smith) was unusual in being the only wheatgrass strain tested from below 49°N that was winter-hardy and produced forage yields equivalent to native Alaskan wheatgrasses.

- Sodar streambank wheatgrass, and native Alaskan strains of *A. sericeum* Hitchc., *A. trachycaulum*, *A.*

*violaceum* (Hornem.) Lange, and Siberian wildrye were extremely winter-hardy and produced forage yields approximately equivalent to the two bromegrass cultivars, Polar and Manchar, and surpassed Engmo, one of the most winter-hardy timothy cultivars for this area.

- The hybrid *Agroelymus palmerensis* was slightly less winter-hardy than the native Alaskan wheatgrasses but produced high forage yields.

- Highest seed producers, when moisture was adequate, were four native Alaskan species: slender, arctic, and violet wheatgrasses and Siberian wildrye.

- High seed producers less sensitive to moisture stress than native Alaska grasses were S-7171 crested wheatgrass, selected near 52°N, and the slender wheatgrass strains Alaska-44S, naturalized at 61.6°N, and Revenue, selected at 52°N in Saskatchewan.

- These results demonstrate that latitude-of-origin, and therefore adaptation to climatic influences related to global latitude, governs considerably the performance of wheatgrasses in this northern area. Species that occupy a natural range that does not reach northern latitudes generally perform poorly here. With species that occupy a natural range with an extensive north-to-south dimension, strains from the northernmost areas of the total range possess best adaptation to Alaskan conditions and therefore exhibit superior performance here.

- For several species brought to Alaska from elsewhere and included in these experiments, the strains evaluated may not represent the best-adapted germplasm available within each species for use in Alaska. Building on knowledge gained in this study, future evaluations should seek the northernmost-adapted strains or ecotypes available within each species.

- For superior performance in Alaska, grasses should be brought directly to this area from other high-latitude origins, thereby circumventing the loss of north-latitude adaptational characteristics that would be lost or discarded in selection programs at more southern latitudes.

## INTRODUCTION

The genus *Agropyron* encompasses from 100 to 150 species worldwide; species within this genus are commonly called wheatgrasses. About 100 species are native to Eurasia and from 22 to 30 native to North America (Asay and Knowles 1985). About 12 species and subspecies are native in Alaska, though taxonomists differ on the number and the treatment of Alaskan species and subspecific taxa (Hulten 1968; Porsild and Cody 1980; Welsh 1974).

### Taxonomic Considerations

Taxonomic classification of the wheatgrasses of the world has been unsettled and somewhat confusing during recent years. Various classification treatments of this group of grasses have been formulated by several different authorities, with conflicting viewpoints at genus, species, and subspecific levels (Asay and Knowles 1985; Dewey 1983; Hitchcock 1950; Hulten 1968; Polunin 1959; Porsild and Cody 1980; Tzvelev 1976; Welsh 1974). The traditional taxonomic treatment in the United States places the wheatgrasses in the genus *Agropyron* (Hitchcock 1950; Hulten 1968; Welsh 1974; Table 1).

Recently Dewey (1983) has proposed a taxonomic realignment of the wheatgrasses based on cytotoxic data, other biological relationships, and the work of Tzvelev (1976) in the Soviet Union. The latter's views are based on perceptions derived from extensive collections in the Eurasian land mass, believed to be the world origin of the wheatgrasses and where the greatest species diversity prevails. According to the proposed, revised taxonomic treatment of the wheatgrasses (Table 1), three of the 14 species classified as *Agropyron* in this report are retained in that genus, and the other 11 are shifted through reclassification to the genera *Elymus*, *Elytrigia*, and *Pascopyrum*. It is likely that this new classification system will be adopted over time in the United States as done by Asay and Knowles (1985). However, to relate data and species in this report to previously published literature on the wheatgrasses, all of which have used the traditional U.S. classification scheme, this report follows the latter system as well. Naming relationships for both systems appear in Table 1.

### Economic Importance

Several species of *Agropyron* are of economic importance (Asay and Knowles 1985; Hanson 1972; Hitchcock 1951). Their principal agricultural use in North America is as range forage in the western states and provinces. Most valuable of the native North American wheatgrasses are western (*A. smithii*), slender (*A. trachycaulum*), bluebunch (*A. spicatum*), and

beardless (*A. inerme*). Two native, sod-forming species, thickspike (*A. dasystachyum*) and streambank (*A. riparium*) are valued for soil stabilization as well as for forage (Asay and Knowles 1985).

The most widely used wheatgrasses introduced into North America from Old World sources are crested (*A. desertorum*), fairway (*A. cristatum*), Siberian (*A. sibiricum*), intermediate (*A. intermedium*), pubescent (*A. trichophorum*), and tall (*A. elongatum*).

Quackgrass (*A. repens*) is widely prevalent in the northcentral and eastern states where it contributes to forage production as an invasive species in mixed forage stands. However, it is difficult to eradicate because of vigorous vegetative spreading ability via rhizomes (underground stems); thus it is often considered a problem weed. Introductions of this species are well adapted to Alaskan conditions and quackgrass has effectively spread to most agricultural areas of the state.

### Native Alaskan Wheatgrasses

Numerous wheatgrass species have been grown for experimental evaluations at several locations in Alaska since 1905 (Irwin 1945); however, geographic sources of strains in those early tests were not reported. Some native Alaskan wheatgrasses were planted in early tests also, but species were not identified.

Aamodt and Savage (1949) summarized the cursory knowledge of the performance and usefulness of wheatgrasses in Alaska as of mid-century. They recognized that more extensive trials were necessary to determine the adaptation and relative value of both native and introduced wheatgrasses in Alaska.

Since 1956, Alaskan agronomists have collected throughout the state both seed and vegetative transplants of a wide array of native grasses, including wheatgrasses. Collections were initially grown in individual-plant evaluation nurseries. Those judged potentially useful for forage, soil stabilization, or other purposes were then propagated for further tests. The native Alaskan species included in this study derived from those collections and earlier evaluations.

### This Investigation

The objectives of experiments reported here were to evaluate winter hardiness, forage production, and seed yields of numerous cultivars and strains within several wheatgrass species native elsewhere on this continent or introduced into North America from Eurasia, compared with (a) native Alaskan wheatgrasses, (b) one naturally-occurring Alaskan *Agropyron-Elymus* hybrid (*Agroelymus palmerensis*), (c) native Alaskan Siberian wildrye (*Elymus sibiricus* L.), and (d) standard forage cultivars in common use in Alaska.

Results reported are from five field experiments conducted over a period of seven years at the University of Alaska's Matanuska Research Farm (61.6°N) near Palmer in subarctic, southcentral Alaska.

## EXPERIMENTAL PROCEDURES

All experiments were conducted in field areas with good surface drainage. In each experiment, commercial fertilizer disked into plowed Knik silt loam (Typic Cryorthent) seedbeds before planting supplied elemental nitrogen (N), phosphorus (P), and potassium (K) at 32, 56, and 54 lb/acre, respectively. All experiments were planted without companion crops. In all experiments, four non-*Agropyron* grasses were included as checks: Polar bromegrass (predominantly *Bromus inermis* Leyss. x *B. pumpellianus* Scribn.), Manchard smooth bromegrass (*B. inermis*), Englemont timothy (*Phleum pratense* L.), and indigenous Alaskan Siberian wildrye. Native Alaskan pumpelly bromegrass (*B. pumpellianus*) was included in Exp. II.

With all broadcast-seeded plots, planting rates were adjusted on the basis of germination trials to plant grasses at the following rates in pounds of pure live seed per acre: wheatgrasses and Siberian wildrye 18, bromegrass 22, and timothy 6. Individual broadcast-seeded plots measured 5 x 20 feet. All row and broadcast-plot field plantings utilized randomized complete block experimental designs with four replications. With all forage harvests from broadcast-seeded plots, yields were derived from a swath 2.5 feet wide mowed from the centerline of each plot after a 1.25-foot strip was mowed and discarded from both ends of all plots to remove border effects. Mowing was done with a sickle-equipped plot mower leaving approximately a 2-inch stubble. Small, bagged samples from each plot were dried to constant weight at 140°F to calculate percent of dry matter in harvested herbage. All forage yields are reported on the oven-dry basis.

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

After killing frost each autumn in Experiments III, IV, and V, all aerial growth on rows and individual plants was clipped and removed, leaving a 3-inch stubble, to prevent uneven snow retention on experi-

ments during winter.

**Experiments I and II**—Two separate broadcast-seeded plot tests were planted to compare wheatgrass strains of different latitudinal origins for winter hardiness and forage yields. Exp. I was planted on 20 June 1966 and Exp. II on 13 June 1968. Grasses compared, harvest dates and yields for Exps. I and II appear in Tables 2 and 3, respectively.

**Experiment III**—To evaluate seed production, several wheatgrass strains were seeded in rows 18 feet long and 24 inches apart on 20 June 1966; strains compared appear in Table 4. In August of 1967 and 1968, a 12-foot segment was harvested from the mid-portion of each row; seed was threshed, cleaned, and yields determined.

**Experiment IV**—Another test comparing wheatgrass strains for seed production was planted on 14 June 1968 in rows 18 feet long and 18 inches apart; strains planted appear in Table 5. Seed was harvested the two subsequent years as in the previous experiment.

**Experiment V**—The same strains used in Exp. IV were seeded in rows 38 feet long and 18 inches apart on 17 June 1968. Seedlings were thinned early by hand-pulling to leave individual plants about 6 to 8 inches apart. Living and dead plants were counted in spring of 1969 and 1970, and winter survival percentages were calculated (Table 5).

No forage quality determinations are reported for this study. Forage harvests in these experiments (mean dates = 9 July + 22 September) were somewhat later than optimum for this area (20 to 30 June + 1 to 20 September) for the best combination of high yield plus good quality forage. Later harvests used in this study permitted more time for recovery from winter injury and observations of grass phenology.

## RESULTS

An extended period of sub-normal precipitation at the Matanuska Research Farm began in early August 1968 and continued through the two following years (Figure 1). Those three years were considerably below normal in annual precipitation (normal = 15.4 inches) by the following amounts: 1968 = 4.0 inches, 1969 = 4.1 inches, and 1970 = 3.6 inches.

Supplemental overhead sprinkler irrigation on four dates supplied Exp. II (Table 3) with the following amounts of water: 16 April 1969 (0.9"), 8 May 1970 (1.8"), 6 June 1970 (1.2"), and 16 June 1971 (0.4"). Exp. IV (Table 5) received the same amounts in 1969 and 1970 but none in 1971. The three inches of supplemental irrigation water in spring of 1970, together with a relatively late harvest date, resulted in generally high first-cutting forage yields in July 1970 with all winter-

**Table 1.** Common names, traditional and proposed scientific names, bunch vs. sod growth, and native (to North America) vs. introduced (from Asia) origin of wheatgrasses concerned in this report.

Wheatgrass common name	Traditional scientific name	Proposed scientific name <sup>1</sup>	Bunch-type or Sod-forming	Native or Introduced
Alaska Wheatgrass	<i>Agropyron alaskanum</i> Scribn. & Merr.	<i>Elymus alaskanus</i> (Scribn. & Merr.) A. Löve	Bunch	Native
Arctic Wheatgrass	<i>Agropyron sericeum</i> Hitchc.	<i>Elymus macrourus</i> (Turcz.) Tzvel.	Bunch	Native
Bearded Wheatgrass	<i>Agropyron subsecundatum</i> (Link) Hitchc.	<i>Elymus subsecundatus</i> (Link) A. & D. Löve	Bunch	Native
Beardless Wheatgrass	<i>Agropyron inerme</i> (Scribn. & Smith) Rydb.	<i>Elytrigia spicicata</i> (Pursh) D.R. Dewey	Bunch	Native
Bluebunch Wheatgrass	<i>Agropyron spicatum</i> (Pursh) Scribn. & Smith	<i>Elytrigia spicicata</i> (Pursh) D.R. Dewey	Bunch	Native
Crested Wheatgrass	<i>Agropyron desertorum</i> (Fisch. Link) Schult	<i>Agropyron desertorum</i> (Fisch. ex Link) Schult	Bunch	Intro.
Fairway Wheatgrass	<i>Agropyron cristatum</i> (L.) Gaertn.	<i>Agropyron cristatum</i> (L.) Beauv. ssp. <i>pectinatum</i> (Bieb.) Tzvel.	Bunch	Intro.
Intermediate Wheatgrass	<i>Agropyron intermedium</i> (Host) Beauv.	<i>Elytrigia intermedia</i> (Host) Nevski	Sod	Intro.
Pubescent Wheatgrass	<i>Agropyron trichophorum</i> (Link) Richt.	<i>Elytrigia intermedia</i> subsp. <i>trichophora</i> A. & D. Löve	Sod	Intro.
Quackgrass	<i>Agropyron repens</i> (L.) Beauv.	<i>Elytrigia repens</i> (L.) Nevski	Sod	Intro.
Siberian Wheatgrass	<i>Agropyron sibiricum</i> (Willd.) Beauv.	<i>Agropyron fragile</i> (Roth) Candargy var. <i>sibiricum</i> (Willd.) Tzvel.	Bunch	Intro.
Slender Wheatgrass	<i>Agropyron trachycaulum</i> (Link) Malte	<i>Elymus trachycaulus</i> (Link) Gould ex Shinnars	Bunch	Native
Streambank Wheatgrass	<i>Agropyron riparium</i> Scribn. & Smith ex Piper	<i>Elymus lanceolatus</i> (Scribn. & Smith) Gould	Sod	Native
Tall Wheatgrass	<i>Agropyron elongatum</i> (Host) Beauv.	<i>Elytrigia pontica</i> (Podp.) Holub	Bunch	Intro.
Thickspike Wheatgrass	<i>Agropyron dasystachyum</i> (Hook) Scribn.	<i>Elymus lanceolatus</i> (Scribn. & Smith)	Sod	Native
Violet Wheatgrass	<i>Agropyron violaceum</i> (Hornem.) Lange	(?)	Bunch	Native
Western Wheatgrass	<i>Agropyron smithii</i> Rydb.	<i>Pascopyrum smithii</i> (Rydb.) Löve	Sod	Native
Yukon Wheatgrass	<i>Agropyron yukonense</i> Scribn. & Merr.	<i>Elymus lanceolatus</i> subsp. <i>yukonensis</i> (Scribn. & Merr.) Löve	Sod	Native

<sup>1</sup> As formulated by Dewey (1983).

**Table 2.** Seeding-year and subsequent oven-dry forage yields of *Agropyron* species and strains from diverse latitudinal sources and four non-*Agropyron* comparison grasses grown in broadcast-seeded plots at the Matanuska Research Farm (Experiment 1).

Species and strain	1966	1967		1968		Total
	29 Sep	10 July	25 Sep	27 June	11 Sep	
----- Tons/acre -----						
WHEATGRASSES ( <i>Agropyron</i> spp.):						
Crested ( <i>A. desertorum</i> ):						
Summit	0.91 ab <sup>1</sup>	2.51 cd	1.64 b	0.70 e	1.03 cd	6.79 d
Nordan	1.00 ab	Tr <sup>2</sup>	Tr	(WK) <sup>3</sup>	—	1.00 fg
Tall ( <i>A. elongatum</i> ):						
Alkar	0.06 f	0.63 ef	1.22 d	(WK)	—	1.91 ef
Beardless ( <i>A. inerme</i> ):						
Whitmar	0.40 cd (WK)	—	—	—	—	0.40 g
Intermediate ( <i>A. intermedium</i> ):						
Commercial	0.25 de	0.72 ef	1.85 a	(WK)	—	2.82 e
Arctic ( <i>A. sericeum</i> ):						
Native Alaskan <sup>4</sup>	0.36 cd	3.61 a	0.65 e	2.85 b	1.54 abc	9.01 ab
Siberian ( <i>A. sibiricum</i> ):						
Commercial	0.58 c	0.98 e	1.19 d	(WK)	—	2.75 e
Slender ( <i>A. trachycaulum</i> ):						
Native Alaskan <sup>5</sup>	0.03 f	2.93 bc	0.39 f	2.68 bc	0.89 d	6.92 cd
Alaska-44S	0.81 b	2.70 cd	1.32 cd	1.28 d	1.88 ab	7.99 bcd
Primar	1.08 a	0.64 ef	1.26 cd	Tr	Tr	2.98 e
Pubescent ( <i>A. trichophorum</i> ):						
Commercial	0.14 ef (WK)	—	—	—	—	0.14 g
Violet ( <i>A. violaceum</i> ):						
Native Alaskan	Tr	3.93 a	0.27 f	3.41 a	1.02 cd	8.63 ab
NON- <i>Agropyron</i> CHECKS:						
Smooth brome grass ( <i>Bromus inermis</i> ):						
Polar <sup>6</sup>	0.94 ab	2.76 cd	1.44 c	3.11 ab	1.74 ab	9.99 a
Manchar	1.12 a	2.03 d	1.69 ab	2.90 ab	2.03 a	9.77 a
Timothy ( <i>Phleum pratense</i> ):						
Engmo	0.47 cd	1.99 d	0.76 e	1.47 d	1.96 a	6.65 d
Siberian wildrye ( <i>Elymus sibiricus</i> ):						
Native Alaskan	0.50 cd	3.00 b	0.75 e	2.30 bc	1.35 bcd	7.90 bcd
<sup>1</sup> Within each column, means not followed by a common letter are significantly different (5% level) using Duncan's Multiple Range Test. <sup>2</sup> Trace amount of herbage insufficient for harvestable yield. <sup>3</sup> Stand winterkilled completely. <sup>4</sup> Mean yields for 14 individual collections. <sup>5</sup> Mean yields for 12 individual collections. <sup>6</sup> Predominantly hybrid ( <i>B. inermis</i> × <i>B. pumpellianus</i> ).						

**Table 3.** Seeding-year and subsequent oven-dry forage yields of *Agropyron* species and strains of diverse latitudinal adaptation, one *Agroelymus* hybrid, and five non-*Agropyron* grasses at the Matanuska Research Farm (Experiment II).

Species and strain	1968		1969		1970			1971			1972		Total
	2 Oct	10 July	24 Sep	16 July	30 Sep	8 July	16 Sep	11 July	25 Sep				
----- Tons/acre -----													
WHEATGRASSES ( <i>Agropyron</i> spp):													
Fairway ( <i>A. cristatum</i> ):													
Parkway	1.46 ab <sup>1</sup>	0.49 e-m	0.77 ab	3.30 a	1.76 a-d	0.32 ef	1.20 c-f	(WK) <sup>2</sup>	—	—	—	9.30 gh	
Ruff	0.69 c-h	0.32 f-n	0.31 g-l	1.44 hi	0.99 f-j	(WK)	—	—	—	—	—	3.75 m	
Thickspike ( <i>A. dasystachyum</i> ):													
P-1822	1.50 ab	0.18 l-n	0.41 f-i	0.54 j	0.34 k-n	(WK)	—	—	—	—	—	2.97 m	
Crested ( <i>A. desertorum</i> ):													
S-7171	1.37 abc	0.47 e-m	0.62 cd	3.13 abc	2.00 ab	0.76 d	1.37 bcd	Tr <sup>3</sup>	0.59 bc	10.31 fg			
Summit	1.39 abc	0.53 e-l	0.58 cde	2.40 c-g	1.45 c-f	0.75 d	1.37 bcd	Tr	Tr	8.47 hi			
Nordan	1.25 bcd	0.72 b-f	0.59 cde	2.10 e-i	2.12 a	0.09 fg	0.50 h	(WK)	—	7.37 j			
Nebraska 10a	1.38 a-d	0.40 e-n	0.56 c-f	1.77 f-i	1.93 abc	Tr	0.03 i	(WK)	—	6.07 kl			
Tall ( <i>A. elongatum</i> ):													
Largo	1.31 a-d	(WK)	—	—	—	—	—	—	—	—	—	1.31 no	
Alkar	0.26 gh	0.32 g-n	0.34 g-k	(WK)	—	—	—	—	—	—	—	0.92 o	
Jose	0.20 h	0.26 i-n	0.24 jkl	(WK)	—	—	—	—	—	—	—	0.70 o	
Beardless ( <i>A. inerme</i> ):													
Whitmar	0.66 d-h	0.01 n	Tr	(WK)	—	—	—	—	—	—	—	0.67 o	
Intermediate ( <i>A. intermedium</i> ):													
Chief	1.16 b-e	1.04 ab	0.38 f-j	1.77 ghi	1.47 c-f	(WK)	—	—	—	—	—	5.82 kl	
Commercial	0.78 c-h	0.59 d-j	0.40 f-i	0.46 j	0.85 g-j	(WK)	—	—	—	—	—	3.08 m	
Amur	1.21 bcd	0.53 e-l	0.59 cd	0.11 j	0.16 lmn	(WK)	—	—	—	—	—	2.60 mn	
Greenar	1.06 b-f	0.49 e-m	0.49 d-g	0.21 j	0.32 k-n	Tr	Tr	(WK)	—	—	—	2.57 mn	
Streambank ( <i>A. riparium</i> ):													
Sodar	1.09 b-e	0.60 c-j	0.62 cd	3.16 ab	1.68 a-e	1.15 c	1.82 a	1.07 fg	0.85 ab	12.04 bcd			
Arctic ( <i>A. sericeum</i> ):													
Native Alaskan	0.37 c-h	0.24 j-n	0.34 g-k	3.02 a-d	0.48 j-n	1.97 a	1.29 cde	3.64 b	0.43 cd	12.14 bc			
Siberian ( <i>A. sibiricum</i> ):													
Commercial	0.70 c-h	0.65 c-h	0.29 h-l	2.27 e-h	1.28 d-g	Tr	Tr	(WK)	—	—	—	5.19 kl	
P-27	0.56 e-h	0.20 k-n	0.14 lm	0.36 j	0.08 mn	0.01 fg	0.03 i	(WK)	—	—	—	1.38 no	

Table 3. (Continued).

Species and strain	1968		1969		1970		1971		1972		Total
	2 Oct	10 July	24 Sep	16 July	30 Sep	8 July	16 Sep	11 July	25 Sep		
----- Tons/acre -----											
Western ( <i>A. smithii</i> ):											
Rodan	1.10 b-e	0.35 f-n	0.62 cd	2.13 e-i	1.22 e-h	0.02 fg	0.66 gh	0.05 h	0.32 cde	6.47 jk	
Rosana	1.20 bcd	0.30 g-n	0.52 def	2.25 e-h	1.30 d-g	0.01 fg	0.74 gh	0.02 h	0.02 de	6.36 jkl	
Bluebunch ( <i>A. spicatum</i> ):											
PM-C-29	0.77 c-h	0.44 e-m	0.36 g-j	1.40 i	0.31 k-n	(WK)	—	—	—	3.28 m	
PM-M-161	0.45 gh	0.46 e-m	0.04 m	1.41 i	0.56 j-m	(WK)	—	—	—	2.92 m	
P-739	0.80 c-h	0.21 k-n	0.29 h-l	—	—	—	—	—	—	1.30 no	
Slender ( <i>A. trachycaulum</i> ):											
Native Alaskan	0.27 gh	0.29 h-n	0.20 kl	3.37 a	0.33 k-n	1.92 a	0.74 gh	3.53 bc	0.02 de	10.67 d-g	
Alaska-445	0.48 fgh	0.94 abc	0.30 h-l	2.84 a-e	0.63 i-l	0.79 d	1.21 c-f	3.04 c	0.26 cde	10.49 efg	
Revenue	1.66 ab	0.46 e-m	0.55 c-f	2.42 b-g	1.10 f-i	0.03 fg	1.04 ef	1.40 ef	0.28 cde	8.94 h	
Primar	0.82 c-g	0.80 a-e	0.40 f-i	1.91 f-i	1.07 f-i	(WK)	—	—	—	5.00 l	
Pubescent ( <i>A. trichophorum</i> ):											
Topar	1.24 bcd	0.55 e-k	0.49 d-g	1.95 f-i	1.59 b-f	(WK)	—	—	—	5.82 kl	
Mandan 759	0.69 d-h	1.09 a	0.43 e-h	1.82 f-i	1.58 b-f	(WK)	—	—	—	5.61 kl	
Luna	0.76 c-h	0.29 h-n	0.41 f-i	—	—	(WK)	—	—	—	1.46 no	
Trigo	0.76 c-h	0.13 mn	0.25 i-l	—	—	(WK)	—	—	—	1.14 o	
Commercial	0.28 gh	0.07 n	0.12 lm	—	—	(WK)	—	—	—	0.47 o	
Violet ( <i>A. violaceum</i> ):											
Native Alaskan	0.30 gh	0.19 k-n	0.18 kl	2.52 b-g	0.32 k-n	1.97 a	0.94 fg	4.10 a	0.02 de	10.54 efg	
Hybrid ( <i>Agroelymus palmerensis</i> ):											
Native Alaskan	0.82 c-g	0.93 a-d	0.27 i-l	3.07 a-d	0.42 j-n	1.76 a	1.28 cde	3.16 bc	0.15 de	11.86 b-e	
Non- <i>Agropyron</i> checks:											
Polar bromegrass	1.15 b-e	0.66 c-g	0.68 abc	2.81 a-e	1.46 c-f	1.07 c	1.64 ab	3.08 c	0.97 a	13.52 a	
Manchar bromegrass	1.13 b-e	0.47 e-m	0.79 a	2.65 a-f	1.54 b-f	0.56 de	1.28 cde	1.66 e	1.01 a	11.09 c-f	
<i>B. pumpellianus</i>	0.42 gh	0.62 c-i	0.29 h-l	2.51 b-g	0.75 h-k	1.40 b	1.12 def	3.45 bc	0.41 cd	10.79 c-f	
Engmo timothy	1.83 a	0.13 mn	0.19 kl	1.95 f-i	1.58 b-f	0.01 fg	0.50 h	0.82 g	0.57 bc	7.58 ij	
Alaskan Siberian wildrye	0.78 c-h	0.90 a-d	0.34 g-k	3.10 a-d	0.93 g-j	1.25 bc	1.28 cde	3.18 bc	0.12 de	11.88 b-e	

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

<sup>2</sup> Stand winterkilled completely.

<sup>3</sup> Trace amount of herbage insufficient for harvestable yield.

**Table 4.** Seed yields from drilled rows of indigenous Alaskan and introduced *Agropyron* strains and four non-*Agropyron* grasses during two years at the Matanuska Research Farm (61.6°N) (Experiment III).

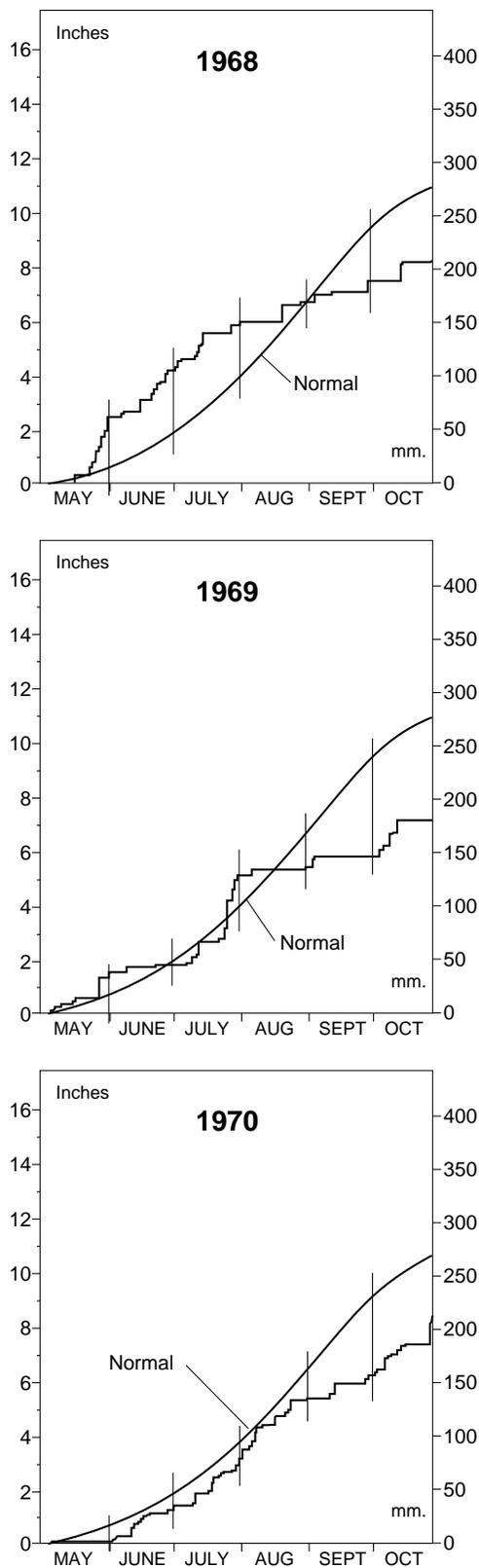
Species and strain	Latitude of origin (°N) <sup>1</sup>	Seed yield	
		1967	1968
WHEATGRASSES ( <i>Agropyron</i> species):		Pounds/acre	
Crested ( <i>A. desertorum</i> ):			
Summit	52-55	189 d <sup>2</sup>	106 d
Nordan	46-47	(WK) <sup>3</sup>	0
Tall ( <i>A. elongatum</i> ):			
Alkar	46-47	(WK)	0
Beardless ( <i>A. inerme</i> ):			
Whitmar	46-47	(WK)	0
Intermediate ( <i>A. intermedium</i> ):			
Commercial	42-46	(WK)	0
Arctic ( <i>A. sericeum</i> ):			
Native Alaskan <sup>4</sup>	61-63	874 b	821 b
Siberian ( <i>A. sibiricum</i> ):			
Commercial	42-46	68 def	10 d
Slender ( <i>A. trachycaulum</i> ):			
Native Alaskan <sup>5</sup>	62-67	1317 a	846 b
Alaska-44S	61.5	991 b	520 c
Primar	46-47	81 def	105 d
Pubescent ( <i>A. trichophorum</i> ):			
Commercial	42-46	(WK)	0
Violet ( <i>A. violaceum</i> ):			
Native Alaskan	67	555 c	562 c
NON- <i>Agropyron</i> CHECKS:			
Smooth bromegrass ( <i>Bromus inermis</i> ):			
Polar <sup>6</sup>	61.6	169 de	129 d
Manchar	43-47	30 ef	28 d
Timothy ( <i>Phleum pratense</i> ):			
Engmo	69-70	141 def	93 d
Siberian wildrye ( <i>Elymus sibiricus</i> ):			
Native Alaskan	61-62	1332 a	1201 a
<p><sup>1</sup> Latitude of location where strain was selected (may differ from latitude of original germplasm source); where both are known, latitude range given embraces both.</p> <p><sup>2</sup> Within each column, means not followed by a common letter are significantly different (5% level) using Duncan's Multiple Range Test.</p> <p><sup>3</sup> All plants winterkilled during first winter.</p> <p><sup>4</sup> Mean yields for 14 individual collections.</p> <p><sup>5</sup> Mean yields for 12 individual collections.</p> <p><sup>6</sup> Predominantly hybrid (<i>B. inermis</i> × <i>B. pumpehianus</i>).</p>			

**Table 5.** Latitudinal origins, two-year seed yields from drilled rows (Exp. IV), and percent winter survival of individual plants in rows in an adjacent experiment (Exp. V), of 34 strains within 14 *Agropyron* species, compared with one *Agroelymus* hybrid and four non-*Agropyron* grasses at the Matanuska Research Farm (61.6°N).

Species and strain	Latitude of origin (°N) <sup>1</sup>	Seed yield		Winter survival of 1968 spaced plants		
		1969	1970	Percent alive in :		
		Pounds/acre		1969	1970	
<b>WHEATGRASSES (<i>Agropyron</i> species):</b>						
Fairway ( <i>A. cristatum</i> ):	Parkway	52	285 c-i <sup>2</sup>	280 c-f	20 k	18 g
	Ruff	41	413 a-e	74 hij	63 d-h	18 g
Thickspike ( <i>A. dasystachyum</i> ):	P-1822	46-47	1 j	5 j	7 kl	0
Crested ( <i>A. desertorum</i> ):	S-7171	52	389 a-e	536 a	51 g-j	46 e
	Summit	52-55	350 b-g	199 d-h	79 bcd	77 c
	Nordan	46-47	162 e-j	189 e-h	16 kl	12 gh
	Nebraska 10a	41	66 hij	110 g-j	3 kl	2 h
Tall ( <i>A. elongatum</i> ):	Alkar	46-47	15 ij	0	65 d-h	1 h
	Jose	35	64 hij	0	69 def	0
	Largo	35-40	0	0	1 l	0
Beardless ( <i>A. inerme</i> ):	Whitmar	46-47	0	0	15 kl	0
Intermediate ( <i>A. intermedium</i> ):	Chief	52	359 b-f	35 ij	68 d-g	44 e
	Amur	35-48	358 b-f	24 ij	60 e-h	22 g
	Greenar	44-47	194 e-j	6 j	51 g-j	12 gh
	Commercial	42-46	229 d-j	8 j	35 j	14 gh
Streambank ( <i>A. riparium</i> ):	Sodar	43-47	75 g-j	19 j	99 a	98 a
Arctic ( <i>A. sericeum</i> ):	Native Alaskan	61-63	626 a	474 ab	99 a	99 a
Siberian ( <i>A. sibiricum</i> ):	P-27	43-47	355 b-f	254 def	51 g-j	44 e
Western ( <i>A. smithii</i> ):	Rodan	46-47	14 ij	5 j	100 a	99 a
	Rosana	45-46	47 hij	7 j	99 a	99 a
Bluebunch ( <i>A. spicatum</i> ):	PM-M-161	45-46 (?)	143 e-j	27 j	88 abc	76 c
	PM-C-29	35 (?)	25 ij	2 j	48 hij	38 ef
	P-739	46-47	14 ij	0	9 kl	0
Slender ( <i>A. trachycaulum</i> ):	Native Alaskan	62-67	42 hij	267 def	100 a	100 a
	Alaska-44S	61.6	602 ab	528 a	98 a	98 a
	Revenue	52	471 a-d	394 bc	99 a	95 ab
	Primar	46-47	306 c-h	154 f-i	71 de	61 d
Pubescent ( <i>A. trichophorum</i> ):	Mandan 759	46-47	269 c-j	31 ij	76 cde	59 d
	Topar	46-47	56 hij	0	3 kl	0
	Commercial	42-46	27 ij	0	6 kl	0
	Luna	35	88 f-j	0	14 kl	0
	Trigo	35	45 hij	0	9 kl	0
Violet ( <i>A. violaceum</i> ):	Native Alaskan	67	522 abc	96 g-j	100 a	100 a
Hybrid ( <i>Agroelymus palmerensis</i> ):	Native Alaskan	61-62	224 d-j	287 cde	93 ab	83 bc
<b>NON-<i>Agropyron</i> CHECKS:</b>						
	Polar bromegrass	61.6	467 a-d	96 g-j	100 a	100 a
	Manchar bromegrass	43-47	221 d-j	75 hij	99 a	99 a
	Engmo timothy	69-70	24 ij	0	92 abc	26 fg
	Alaskan Siberian wildrye	61-62	109 f-j	459 b	99 a	98 a

<sup>1</sup> Latitude of location where strain was selected (may differ from latitude of original germplasm source); where both are known, latitude range given embraces both.

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



**Figure 1.** Normal and actual cumulative precipitation at the Matanuska Research Farm during three years when moisture stress affected grass performance in experiments reported here.

hardy grasses (Table 3).

All row and broadcast-plot seedings resulted in good stands, except for Nordan crested wheatgrass (Figure 2) and slender wheatgrass strains Alaska-44S and Primar in Exp. I; these were rated as approximately 50% of full stands.

During the year of planting, all three native Alaskan wheatgrasses produced mostly leafy rosettes with few, incipiently elongating culms (Figure 3). In contrast, most introduced wheatgrasses from more southern latitudes produced an abundance of elongated culms during the seeding year. Moreover, during late September and early October, foliage on the native Alaskan wheatgrasses turned yellowish-brown while that on the introduced strains remained green until killed by frost. This phenomenon in wheatgrasses parallels earlier observations here in latitudinal ecotypes of red fescue (Klebesadel et al. 1964) and reed canarygrass (Klebesadel and Dofing 1991). Larsen (1947), comparing latitudinal ecotypes of little bluestem *Andropogon scoparius* Michx.), found differential onset of dormancy in autumn to be related to photoperiodic adaptation. Further results of the five experiments are discussed by species.

## Wheatgrasses

**Fairway Wheatgrass (*A. cristatum*):** Two strains of this species compared for forage and seed production (Tables 3 and 5) were Parkway (tested as S-5565), selected at 52°N, and Ruff (tested as Nebraska 3576) from 41°N. The more northern-adapted Parkway produced considerably more forage and lived one year longer than Ruff (Table 3).

A poorly understood deviation from the above pattern occurred in Exp. V (Table 5) where first-year survival of spaced plants was better for Ruff (63%) than for Parkway (20%). Moreover, in drilled rows in the adjacent Exp. IV (Table 5), Ruff tended to produce more seed in the first year, although the difference was not significant. However, in the second year, the more southern-adapted Ruff yielded markedly less seed, while yield of Parkway was similar in both years. After the second winter, spaced plants of both strains had been reduced to 18% of the original populations of each.

**Thickspike Wheatgrass (*A. dasystachyum*):** One strain, P-1822, was evaluated in three experiments (Tables 3 and 5). That strain, selected near 46°N to 47°N, produced low forage yields in broadcast-seeded plots before sustaining total winter kill during the third winter (Table 3). Seed yields during two years were negligible. Only 7% of the individual plants survived the first winter and all were killed during the second winter (Table 5). Thickspike wheatgrass occurs



**Figure 2.** Comparative winter survival of broadcast-seeded plots of two crested wheatgrass (*A. desertorum*) cultivars from different latitudinal origins; (left) Summit, a release from Saskatoon, Sask. (52°N) developed from germplasm obtained from 55°N in the U.S.S.R.; (right) Nordan, selected at Mandan, ND (46.8°N); (Nordan plots were rated at 50% of full stand in seeding year). Plots seeded 20 June; photo taken 8 June of the following year (Exp. I). Numbered stake is three feet tall.

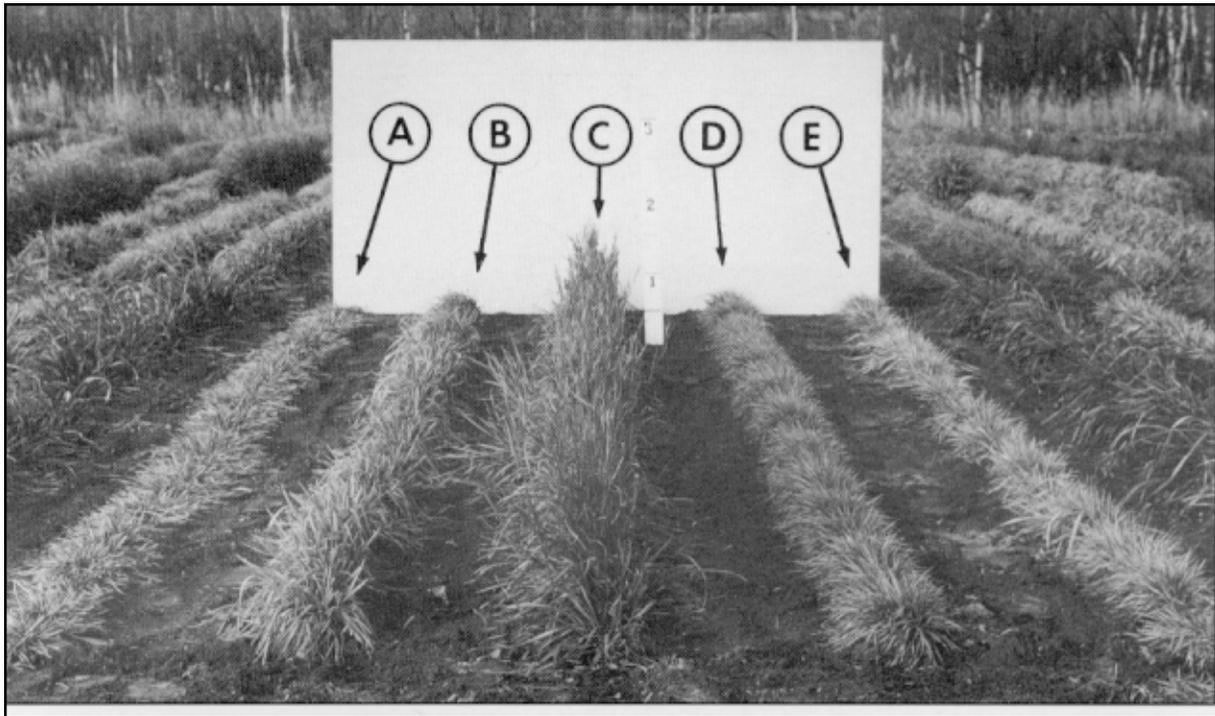
naturally only as far north as British Columbia (Hitchcock 1950) and so appears to have little potential for use at this latitude.

**Crested Wheatgrass (*A. desertorum*):** Nordan was selected at 46.8°N from an introduction originating at 55°N in the U.S.S.R. It was clearly less winter-hardy in Exps. I and V (Tables 2 and 5; Figs. 2 and 4) than Summit, which was selected at 52°N from material that also originated at 55°N in the U.S.S.R. (Hanson 1972). The initially thin, broadcast-seeded stands of Nordan were virtually eliminated during the first winter in that test (Figure 2), while Summit stands persisted for the succeeding two years to produce appreciable forage yields (Table 2). Seed production of the more northern-selected Summit averaged 148 lb/acre over two years in Exp. III while Nordan winter-killed and produced none (Table 4).

Crested strain S-7171, selected near 52°N, surpassed Summit in total forage yields for the five-year duration of Exp. II (Table 3), and produced more seed than Summit during the second year of Exp. IV (Table 5). Nebraska 10a, from 41°N, produced less total for-

age (Table 3) than the somewhat more northern-adapted Nordan; however, both were inferior in winter hardiness, and tended to be lower in forage and seed yields, than the more northern-adapted Summit and S-7171 (Tables 3 and 5). None of the four strains of crested wheatgrass remained productive for the full five years of Exp. II (Table 3), in contrast to the two brome grass cultivars. Knowles (1956) noted that stands of Summit thinned after three years in northern agricultural areas of Canada.

**Tall Wheatgrass (*A. elongatum*):** All three cultivars evaluated (Alkar, Jose, and Largo) succumbed during either the first or second winter in each test (Figure 5). Forage yields were low (Tables 2 and 3), and none produced seed beyond the low yields obtained the first year after planting (Tables 4 and 5; Figure 6). Crowle (1966) found tall wheatgrass to be a poorer seed producer in Saskatchewan than fairway, crested, slender, and intermediate wheatgrasses. As individual plants, Jose (selected at 34.8°N in the United States from germplasm originating at ca. 49°N in Kazakhstan, U.S.S.R.) and Alkar survived the first winter markedly



**Figure 3.** Drilled rows for seed production of four wheatgrass species, planted 20 June and photographed 13 October of the same year. Elongated culms of the introduction (C) from more southern latitudes contrasts with typical basal rosettes with no culm elongation in native Alaskan ecotypes. A = native Alaskan violet wheatgrass from 67°N, B = native Alaskan arctic wheatgrass from 63.1°N, C = introduced Summit crested wheatgrass from 52°N, D and E = native Alaskan slender wheatgrass from 65.2° and 66.6°N, respectively. Numbered stake is three feet tall.

better than Largo (Table 5), which derived from a collection made at 40.3°N in coastal Turkey (Hanson 1972), an area unlikely to require high levels of winter hardiness, or to supply plants well adapted to subarctic latitudes. However, the remaining spaced plants of all three were eliminated during the second winter, so even the hardiest of those tall wheatgrasses were inadequately winter-hardy for use in Alaska.

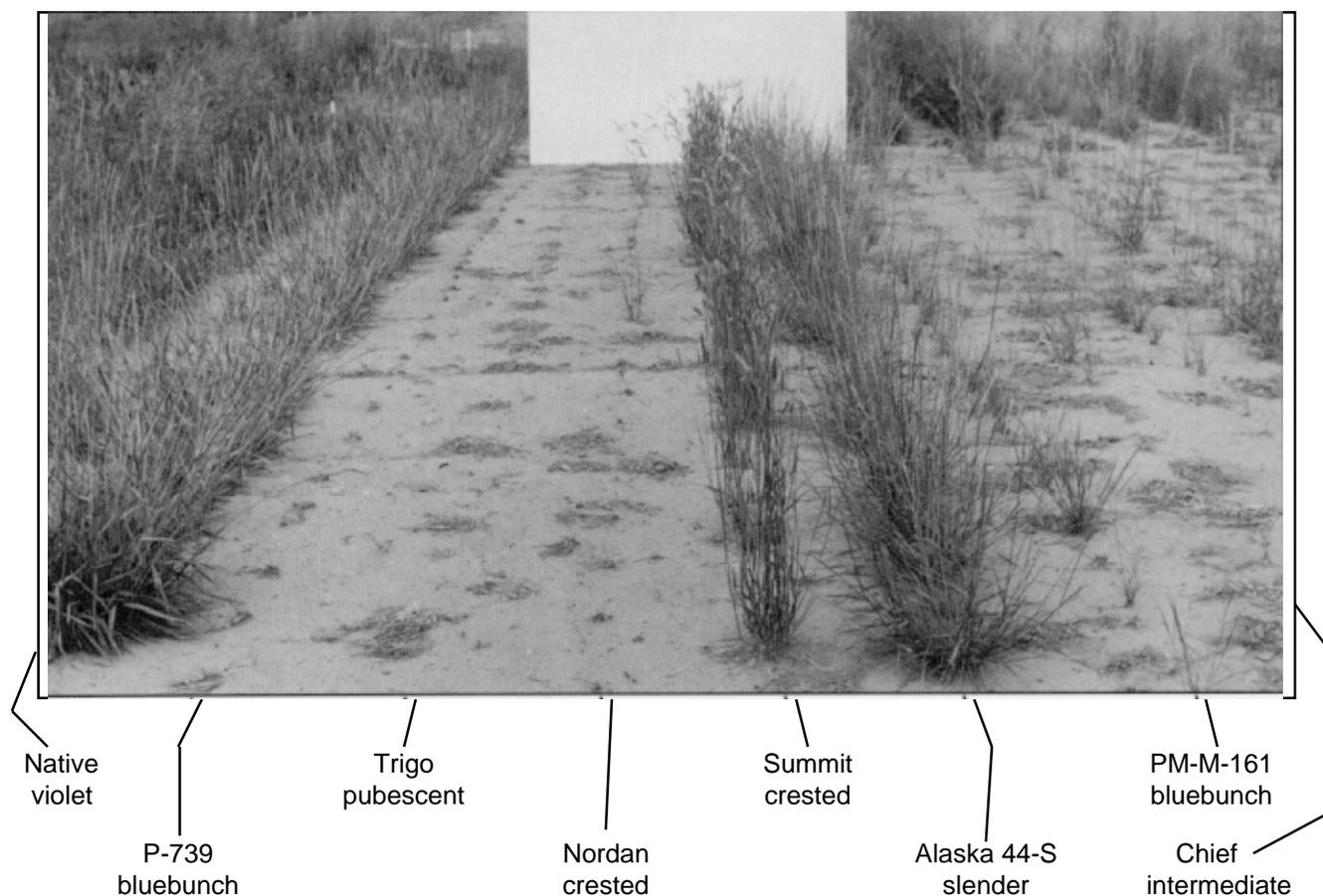
**Beardless Wheatgrass (*A. inermis*):** This species is closely related to bluebunch wheatgrass. Whitmar was the only cultivar of beardless wheatgrass evaluated; it derived from collections in the Palouse prairie region (46° to 47°N) of Washington (Hafenrichter et al. 1968; Hanson 1972). Whitmar stands were either winter-killed completely during the first winter (Figs. 6 and 7) or seriously injured, never surviving beyond the second winter (Tables 2, 3, 4, and 5). Forage yields were low (Tables 2 and 3) and no seed was produced (Tables 4 and 5). The northern limits of the native range of beardless wheatgrass reach only into British Columbia (Hitchcock 1950), so the likelihood of finding adequately winter-hardy beardless wheatgrass for use in Alaska is remote.

**Intermediate Wheatgrass (*A. intermedium*):** A single commercial lot of intermediate wheatgrass,

adapted to 42° to 46°N, survived the first winter in broadcast-seeded plots in Exp. I but with some injury. It produced a low first-cutting forage yield, recovered to produce a good second-cutting yield, but was killed out completely during the second winter (Table 2). It produced no seed (Table 4, Figure 8).

The cultivars Chief from Saskatchewan, Greenar from Washington, and Amur from New Mexico were evaluated with the above-mentioned commercial lot in Exps. II, IV, and V. Chief, from the northernmost origin, produced more forage than the other three strains (Table 3). The higher first-cutting yield of Chief in 1970 was related to less winter injury than occurred with the other strains. Visual estimates of percent of winter kill in broadcast-seeded plots in spring 1970, (means of four replicates) were: Chief 25%, commercial 63%, Amur 78%, and Greenar 80%.

First-year seed yields of Amur (original germplasm from ca. 48°N in Manchuria) and Chief tended to be higher than those of Greenar (original germplasm from 44.6°N in the U.S.S.R.) and commercial, although the differences were not significant (Table 5). Seed yields of all four strains were much lower in the second year than in the first. Dubbs (1970) and Hanson (1972) report that intermediate wheatgrass is slightly inferior to crested wheatgrass in winter hardiness and persistence. This observation is consistent with our results.



**Figure 4.** Comparative winter survival of several wheatgrass strains as individual plants in rows (Exp. V). Photo taken 29 June of rows seeded the previous year on 17 June.

With the generally poorer persistence of all intermediate wheatgrasses (Table 3), the highest yielding intermediate wheatgrass (Chief) produced approximately as much total forage as the lowest-yielding crested strain (Nebraska 10a). Dubbs (1970) found Amur and Greenar to be among the highest forage producers of 17 strains within six wheatgrass species in Montana, an area of relatively severe winters but far south of the latitude of evaluations reported here.

**Streambank Wheatgrass (*A. riparium*):** The cultivar Sodar, originating from a collection in Oregon (Hanson 1972), was included in Exps. II, IV, and V. Douglas and Ensign (1954) and Hafenrichter et al. (1968) report that streambank wheatgrass is not a heavy forage producer; however, because Sodar produces a dense sod, it is used principally for ground cover and erosion control. Seed yields of Sodar were low (Table 5). However, despite Sodar's low seed yields and far-distant latitudinal adaptation, its winter hardiness (Tables 3 and 5) and relatively high forage production in Alaska (Table 3) were somewhat sur-

prising, considering the generally poorer performance of other wheatgrasses in these tests from the same general latitude. Douglas and Ensign (1954) reported that Sodar plants are long-lived. In Exp. II, Sodar was one of few introduced wheatgrasses that persisted and produced appreciable forage for the full five years of the test (Table 3).

**Siberian Wheatgrass (*A. sibiricum*):** A commercial lot of this species was included in all experiments (Tables 2, 3, 4, 5) and strain P-27 was included in Exps. II, IV, and V (Tables 3 and 5). Latitudinal origins of these strains is not precisely known. The original source of P-27 germplasm was somewhere in Kazakstan (Hanson 1972), a large republic in the U.S.S.R.; the original source of the commercial lot (Figure 9), grown in Oregon, could not be ascertained.

The commercial lot winter-killed during the second winter in Exp. I after producing modest forage yields (Table 2). Winter hardiness of the two strains was relatively similar (Table 5), but broadcast stands of the commercial lot produced almost four times as



**Figure 5.** Comparative winter survival in broadcast-seeded plots of (left) native Alaskan slender wheatgrass from 66.6°N, (center) Alkar tall wheatgrass adapted at 46° to 47°N, and (right) native Alaskan arctic wheatgrass from 62.9°N. Numbered stakes are three feet tall. Photograph taken 4 June 1968 of plots seeded 20 June 1966.

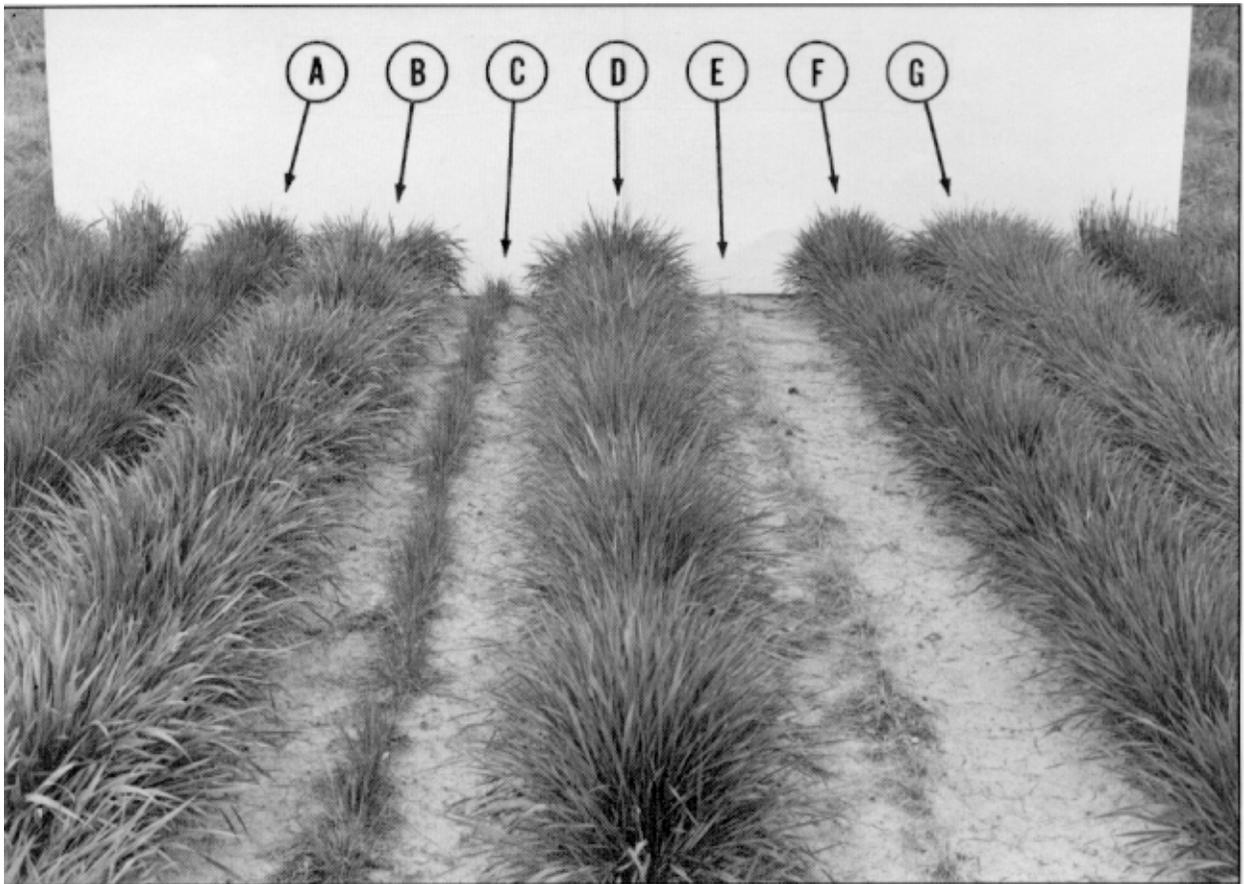
much forage as P-27 before stands of both were virtually eliminated during the third winter of Exp. II (Table 3). Seed yields of Siberian wheatgrass were considerably better in Exp. IV (Table 5) than in Exp. III (Table 4); some of the difference probably was due to irrigation supplied to Exp. IV in the spring of 1970. Overall, the general performance and yields of the two Siberian wheatgrass strains evaluated, both of which were adapted to below 50°N, was mediocre to poor in this unaccustomed northern environment.

**Western Wheatgrass (*A. smithii*):** The cultivars Rodan (evaluated as Mandan 456) and Rosana (evaluated as P-15582) originated from collections in native stands at 46° to 47°N in North Dakota and Montana, respectively, areas far south of Alaska but characterized by severe winters. They were included in Exps. II, IV, and V (Tables 3 and 5).

Both were relatively winter-hardy here, compared with other introduced wheatgrasses. As individual plants in Exp. V, both survived the two winters at 99% (Table 5). In broadcast-seeded plots in Exp. II, both were among the very few wheatgrass strains intro-

duced from lower latitudes that survived for the entire five years of the test (Table 3). Very light first-cutting forage yields in 1969, 1971, and 1972 inferred substantial winter injury during the three prior winters. However, visual estimates of percent of winter kill each spring, of the previous year's stands (means of four replicates) for Rodan and Rosana, respectively, were: 1969 = 3% and 5%; 1971 = 77% and 90%; 1972 = 58% and 73%. Therefore, the reduced yields are believed due to winter injury only in 1971 and 1972; in 1969 the low first-cutting yields are believed due primarily to moisture stress, since very winter-hardy grasses produced low yields then also. Total 5-year forage yields for the two western wheatgrasses were approximately equal; however, those yields were only about half those of the highest yielders in the test (Table 3). There was little difference between the two in seed production and both produced low yields (Table 5). Asay and Knowles (1985) observed that western wheatgrass is a relatively poor seed producer elsewhere as well.

**Bluebunch Wheatgrass (*A. spicatum*):** Three strains of bluebunch wheatgrass, all introduced from



**Figure 6.** Comparative winter survival and spring vigor of subarctic versus mid-temperate-adapted wheatgrasses, in drilled rows for seed production, photographed on 8 June of the second year of growth at the Matanuska Research Farm (61.6°N): A, D, F = native Alaskan slender wheatgrass from 66.6°N; B and G = native Alaskan arctic wheatgrass from 62.9°N and 61.9°N, respectively; C and E = introduced Alkar tall wheatgrass and Whitmar beardless wheatgrass, respectively, both from 46-47°N.

western states, were evaluated for forage (Table 3) and for seed production and winter hardiness (Table 5). As individual plants, the three were markedly different in winter survival in the order: PM-M-161 > PM-C-29 > P-739 (Table 5, Figure 4). In broadcast plots, there were no discernible differences between PM-M-161 and PM-C-29 in winter survival, persistence, or forage yield (Table 3), but both survived the winter of 1969-70 when P-739 succumbed. Although described as a long-lived species (Hanson 1972), none of the three strains survived beyond the first three winters here. Seed yields of all three strains were relatively low; although PM-M-161 tended to produce more than the other two, differences were not significant (Table 5).

The native range of bluebunch wheatgrass in North America is unusually disjunct with its northern limit in central Alaska (Hulten 1968). Collections of this indigenous material should be evaluated for forage and seed production, winter hardiness, and other agronomic characteristics under Alaskan field conditions.

**Slender Wheatgrass (*A. trachycaulum*):** Twelve individual collections of native Alaskan slender wheatgrass, originating between 62° and 67°N, were averaged together for forage production in Exp. I (Table 2) and for seed production in Exp. III (Table 4). In both experiments, they were compared with the cultivar Primar, originating from 46°N to 47°N in Montana. Alaska-44S, a strain originating from a Matanuska Valley roadside population at 61.6°N (Klebesadel 1991) was included in all experiments (Figs. 4 and 7). In Exps. II (Table 3), IV, and V (Table 5), four slender wheatgrass strains were included: (a) several Alaska collections bulked into a single lot, (b) Alaska-44S, (c) Revenue, selected at 52°N in Saskatchewan, and (d) Primar.

The southernmost-adapted Primar was least winter-hardy (Tables 2, 3, and 5) and, in general, produced lowest yields of forage and seed (Tables 2, 3, and 4). The two Alaska strains generally excelled in winter hardiness, and also in forage and seed production. However, the genuinely native Alaska bulk lot was much lower in seed production in 1969 (Table 5) than



**Figure 7.** Comparative winter survival in broadcast-seeded plots of wheatgrasses from diverse latitudinal origins; (left) native Alaskan slender wheatgrass from 66.6°N, (center) Whitmar beardless wheatgrass adapted at 46° to 47°N, and (right) Alaska-44S slender wheatgrass from 61.6°N. Numbered stake is three feet tall. Photo taken 7 July of plots seeded 20 June of the previous year (Exp. I).

the other slender strains when unusually low precipitation caused acute moisture stress. Newell and Keim (1943) evaluated latitudinal ecotypes of bromegrass in Kansas and found strains from southern sources more tolerant of drought stress than those from northern sources, results paralleling these with wheatgrasses in Alaska.

Although low precipitation and moisture stress continued through 1970, sprinkler irrigation was supplied to the forage and seed tests in progress in May and June, 1970 (Exps. II and IV). Forage yields of the native Alaska slender wheatgrass were good in 1970 (Table 3), but seed yields did not return to full potential (Table 5 vs. Table 4). Revenue, intermediate in latitudinal adaptation between the Alaska strains and Primar, was generally intermediate in forage and seed yields when moisture conditions were normal (Tables 3 and 5). A more detailed discussion of performance of strains of slender wheatgrass at this location appears elsewhere (Klebesadel 1991).

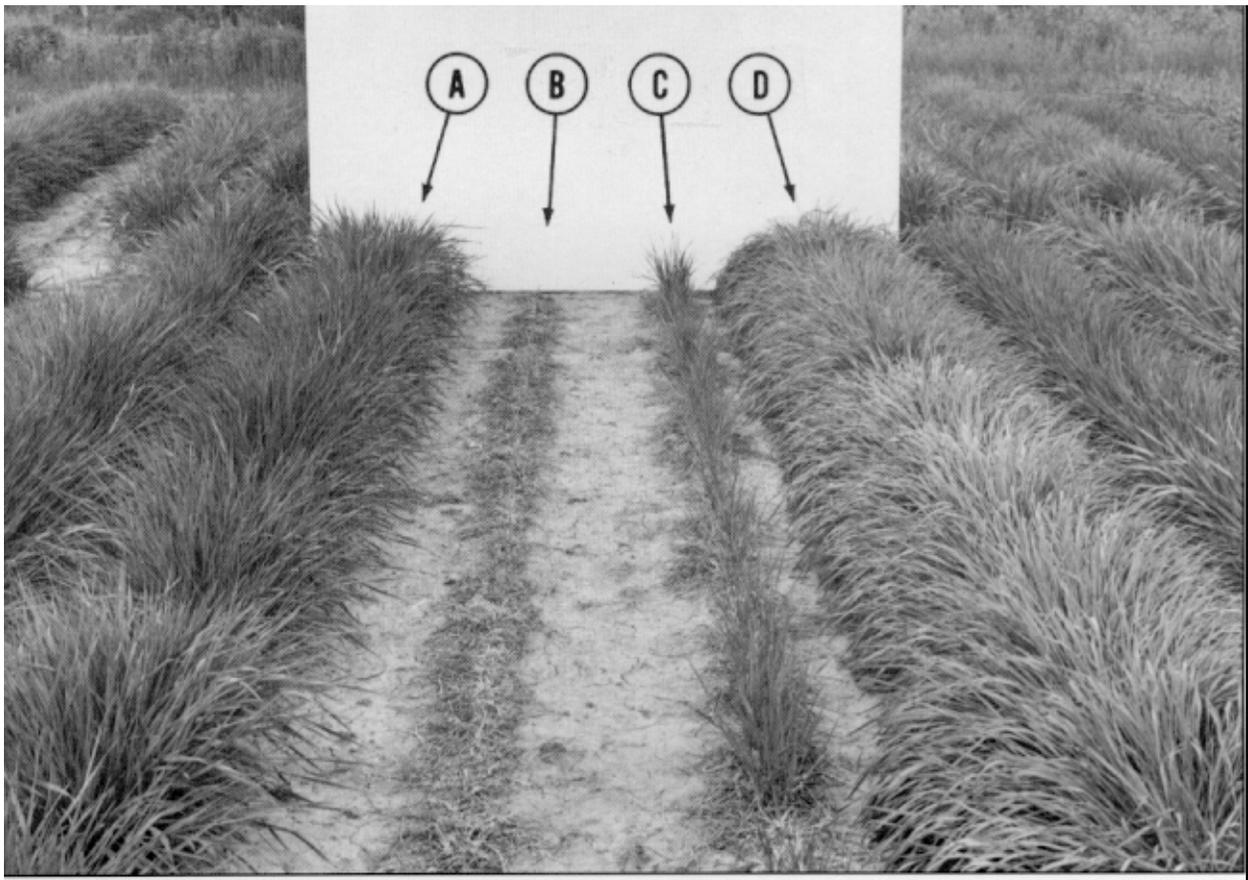
**Pubescent Wheatgrass (*A. trichophorum*):** A single commercial lot of pubescent wheatgrass was included in Exps. I and III; that commercial lot and four other strains were included in Exps. II (Table 3), IV, and V (Table 5). All originated from below 47°N. Germplasm origin for cultivars Trigo (evaluated as A-1488) and

Topar was 41.3°N in the U.S.S.R. (Cornelius 1965).

As individual plants, there was a considerable range in percentages of winter survival among the pubescent strains, with Mandan 759 clearly superior (Table 5). The commercial lot did not survive the first winter in Exps. I and III (Tables 2 and 4; Figure 8). None of the strains survived beyond the third winter in broadcast-seeded plots (Table 3). Mandan 759 and Topar survived one year longer, and produced more forage, than Luna, Trigo, and commercial. Topar and Mandan 759 were equal in forage yields in Exp. II (Table 3), yet Topar was surprisingly inferior in seed yield and winter survival in Exps. IV and V (Table 5).

Seed yields of Mandan 759 in 1969 were not significantly greater than the other four strains in the overall analysis (Table 5), but were significantly higher when the species was analyzed separately. Seed yield of Mandan 759 declined markedly in the second year to only 31 lb/acre while the other four strains produced none. Generally, all five strains of pubescent wheatgrass were inadequately winter-hardy for dependable use in Alaska.

**Violet Wheatgrass (*A. violaceum*) and Arctic Wheatgrass (*A. sericeum*):** These two indigenous Alaskan wheatgrasses were included in all five experiments. The native range of both is relatively wide-



**Figure 8.** Comparative winter survival and spring vigor of subarctic and mid-temperate-adapted wheatgrasses in drilled rows photographed in early June of the year following planting: A = native Alaskan slender wheatgrass from 64.7°N., B, C = introduced commercial pubescent and commercial intermediate wheatgrasses, respectively, adapted at 42-46°N, D = native Alaskan arctic wheatgrass from 61.6°N.

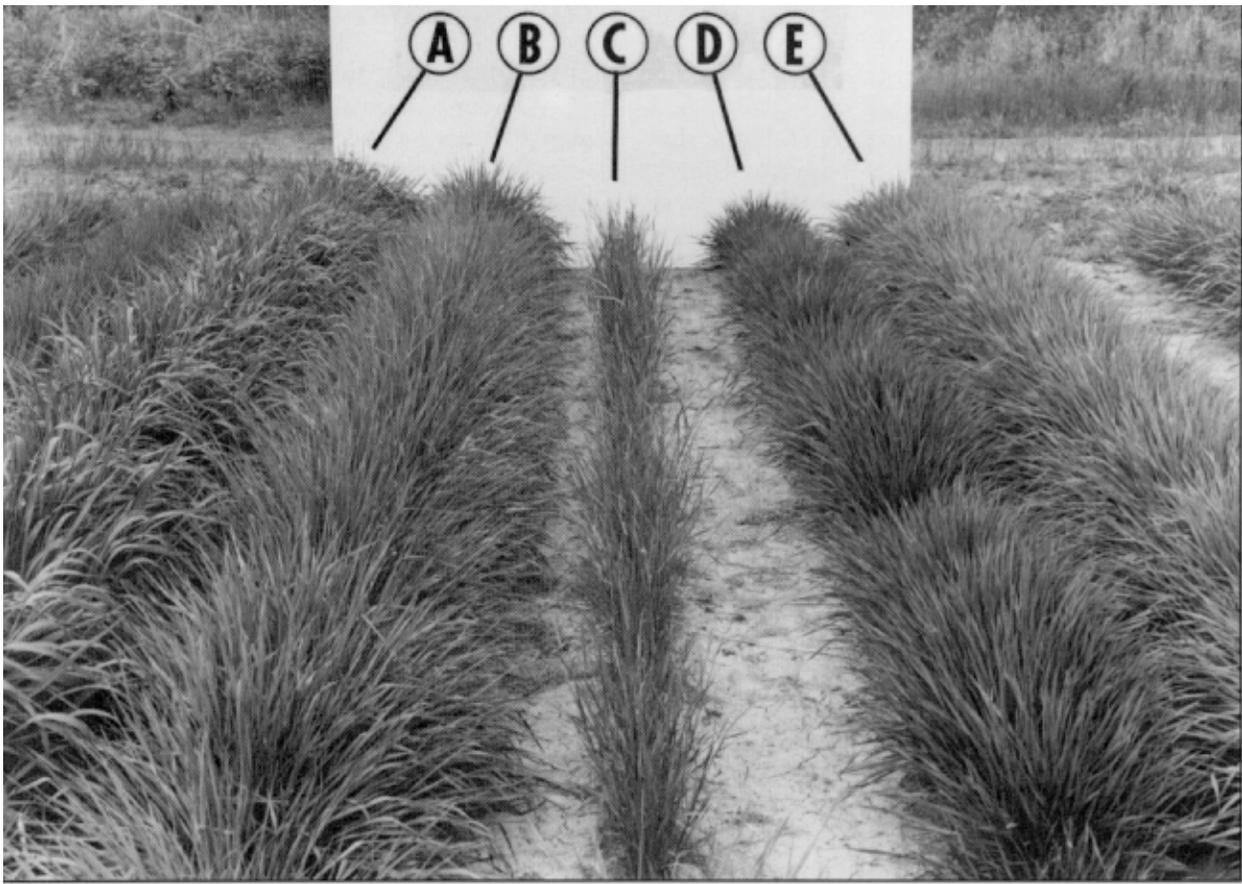
spread in Alaska and Canada, and the total ranges of both are confined to relatively northern latitudes (Hulten 1968; Porsild and Cody 1980). The range of *A. violaceum* is restricted to North America (Hulten 1968). Some consider *A. sericeum* to be synonymous with *A. macrourum* (Turcz.) Drobov (Hulten 1968; Polunin 1959; Welsh 1974; Mitchell 1982), in which case it is amphiberingian in distribution. However, *A. macrourum* is described as rhizomatous while the material used in this study is tufted and non-rhizomatous; therefore, it is tentatively treated as *A. sericeum* here.

*A. sericeum* was included in Exps. I and III as 14 individual collections, and mean yields of the 14 are reported in Tables 2 and 4. A single bulk lot of several collections was included in Exps. II (Table 3), IV, and V (Table 5). The violet wheatgrass included in all five experiments was a single collection from 67°N in north-eastern Alaska.

Neither of these subarctic-adapted species produced elongated culms in the seeding year (Figure 3). Both were extremely winter-hardy in all tests (Tables

2, 3, 4, 5; Figure 4), and forage yields of both were among the highest of the wheatgrasses compared (Tables 2 and 3). Second-cutting yields of both tended to be lighter than those of the two bromegrasses. Like the native Alaska slender wheatgrass, both of these native Alaska species produced very little forage during 1969 (Table 3) under conditions of severe moisture stress. Both produced relatively good seed yields (Tables 4 and 5), but *A. sericeum* surpassed *A. violaceum* in all harvests.

**Wheatgrass-Wildrye Hybrid (*Agroelymus palmerensis*):** This intergeneric hybrid (intrageneric but interspecific according to Dewey 1983) between *Agropyron sericeum* and *Elymus sibiricus* occurs naturally in southcentral Alaska (Hodgson 1964a; Klebesadel 1969; Mitchell and Hodgson 1965). The tetraploid hybrid is sterile, but seed used in Exps. II, IV, and V was produced on fertile, colchicine-induced octoploid plants (Hodgson 1964a; Mitchell and Hodgson 1965).



**Figure 9.** Comparative spring vigor of four grass species in drilled rows for seed production photographed on 8 June of the year after rows were seeded on 20 June (Exp. III). A = native Alaskan Siberian wildrye, B and E = native Alaskan arctic wheatgrass, C = commercial Siberian wheatgrass obtained from Oregon, and D = native Alaskan slender wheatgrass.

The hybrid was relatively winter-hardy (Table 5) and persisted in broadcast plots for the full five years of Exp. II, producing total forage yields equivalent to the highest-yielding wheatgrasses (Table 3). It is of interest that the hybrid produced forage yields under drought stress (Table 3, 1969 yields) virtually identical to the *Elymus sibiricus* parental species, and considerably more than the much-reduced yields of the more drought-susceptible *A. sericeum* parent. Seed yields of the hybrid averaged 256 lb/acre for two years, considerably less than *A. sericeum* (550 lb/acre) and somewhat lower than *E. sibiricus* (284 lb/acre; Table 5). Fertility in the octoploid hybrid is relatively low (Hodgson 1964a; Mitchell and Hodgson 1965).

### Non-wheatgrass Comparison Species

**Smooth Bromegrasses (*Bromus inermis*):** Polar bromegrass, developed locally at 61.6°N (Wilton et al. 1966), showed good winter hardiness in all experiments. Manchur bromegrass, selected at 43° to 47°N in the Pacific Northwest (original germplasm from 43.5°N in Manchuria), was generally winter-hardy but exhib-

ited occasional winter injury. Polar produced the highest total forage yields of all grasses compared (Tables 2 and 3). Manchur produced as much forage as Polar in Exp. I (Table 2) but less than Polar in Exp. II (Table 3), primarily because of some winter injury during the 1970-71 and 1971-72 winters, followed by lowered first-cut yields (Table 3). Manchur produced approximately as much total forage as the highest-yielding wheatgrasses.

Polar produced considerably less seed than the highest-yielding wheatgrasses (Tables 4 and 5), but averaged five times more seed than the more southern-adapted Manchur in one test (Table 4) and twice as much as Manchur in another (Table 5), paralleling earlier results here (Klebesadel 1970; Wilton et al. 1966).

**Timothy (*Phleum pratense*):** Engmo timothy is from a far-northern origin (69° to 70°N) in Norway and ranks among the most winter-hardy timothy cultivars in the world (Klebesadel and Helm 1986). Nonetheless, it is somewhat less winter-hardy in this area than

Polar and Manchur bromegrass (Table 5). Total forage yields of Engmo averaged from 67% (Table 2) to 56% (Table 3) those of Polar; moreover, Engmo forage yields were considerably less than the highest-yielding wheatgrasses as well. In Exp. II (Table 3), low forage yields of Engmo in 1969 were due to drought stress, which timothy typically tolerates less well than bromegrass, Siberian wildrye, and many wheatgrasses. Two-year seed yields of Engmo averaged 117 lb/acre in Exp. III (Table 4), but only 12 lb/acre when under severe drought stress (Table 5).

**Siberian Wildrye (*Elymus sibiricus*):** This species, considered here to be native to Alaska but possibly an early introduction, was totally winter-hardy in all tests (Figure 9), and produced forage yields equal to the highest-yielding wheatgrasses (Tables 2 and 3). Seed yields were high when moisture was adequate (Table 4), but were considerably lower during two years of moisture stress (Table 5). An earlier report (Klebesadel 1969) details more agronomic characteristics of this grass and its performance in this area. Lawrence (1978), at 50.3°N in Canada, found two strains of Siberian wildrye to be non-hardy, while six of the wheatgrass strains that were inadequately winter-hardy in the present study survived without injury there.

## DISCUSSION

Plant winter hardiness implies avoidance of, or tolerance to, the cumulative effects of winter, including freezing, heaving, smothering, and desiccation (Steponkus 1978; Smith 1964). The ability of plants to withstand low temperatures is a phenomenon of annual periodicity, achieved through the interaction of appropriate environmental cues and the genetic potential of the plant for development of cold hardiness (freeze tolerance). Plants must possess the genetic capacity to develop cold hardiness, and this is a selective trait possessed by plants adapted where cold winters prevail.

Of the complex of stresses imposed by winter, the effects of cold are believed the dominant injurious influence in failure of most introduced wheatgrasses to successfully survive Alaskan winters. However, winters in this locality, while perhaps of longer duration, normally impose cold stresses on over-wintering plants no greater than winters in the plains and mountain states of the United States and western provinces of Canada (Klebesadel 1974, 1985b), whence most of the introduced wheatgrasses were obtained.

This implies that introduced strains from areas of more southern latitudes where relatively severe winters prevail do not make adequate physiologic preparation before onset of Alaskan winters; evidence indicates that this is true (Hodgson 1964b; Klebesadel 1971,

1985a, 1985b; Klebesadel and Helm 1986).

## Environmental Stimuli

Although several climatological characteristics may differ among widely separated geographic locations, two dominant plant-governing environmental influences that change with latitude are seasonal temperature pattern (which determines length of growing season), and the seasonal track of changing diurnal photoperiod/nyctoperiod pattern (Klebesadel 1985b).

The trend of progressively lowering temperatures during late summer and autumn is conducive to annual development of cold acclimation (Steponkus 1978). However, also vitally necessary are simultaneously shortening daily photoperiods (lengthening nyctoperiods) of appropriate duration to stimulate the physiologic changes that result in high levels of cold hardiness in perennial forages (Hodgson 1964b; Steponkus 1978; Tysdal 1933), leading to successful winter survival (Klebesadel 1971; 1985b).

## Latitudinal Effects

The interrelationship of these two influences, in particular the duration of diurnal photoperiods/nyctoperiods for those few weeks prior to the occurrence of killing frost, differs appreciably at widely separated latitudes (at similar altitudes). This interrelationship determines how long plants will have been exposed to critical-length photoperiods (that may differ among different ecotypes) that activate food-reserve storage and cold-hardiness development before killing frost destroys the leaves which are receptors of the photoperiodic stimulus (Klebesadel 1985b).

Several investigators have compared plant strains from different latitudinal sources for various performance characteristics when grown at a given location (Cornelius 1947; Klebesadel 1985a; Klebesadel et al. 1964; Klebesadel and Helm 1986; Klebesadel and Dofing 1991; Larsen 1947; Newell and Keim 1943; Olmsted 1944; Rogler 1943). Plant ecotypes resident in one environmental niche for millennia acquire genetically controlled phenological and physiological harmony with prevailing seasonal climatological influences characteristic of that location (Wilsie 1962).

To grow plants at a significant latitudinal distance north from their evolutionary environment, as with many wheatgrasses in this study, divorces the cultivar, strain, or ecotype from its accustomed environmental stimulus patterns. This engenders disharmony in the plant/environment interrelationship, leading to sub-optimal progression of the physiological processes that prepare perennial plants for winter stresses. This in turn prevents plants from achieving winter hardening to the full extent of their genetic potential (Hodgson 1964b), resulting in greater susceptibility to freeze

stress and lowered winter survival (Klebesadel 1971, 1985b).

Olmsted (1944) and Larsen (1947) reviewed early literature on photoperiodic responses of ecotypes from diverse latitudinal sources within two grass species. Cornelius (1947) and Rogler (1943), working with ecotypes from a wide range of latitudinal sources, found considerable differences among ecotypes for winter survival and response to artificially imposed cold stress, with northern-adapted ecotypes surviving best.

Kilcher and Looman (1983) demonstrated that deficient performance, including poor winter survival, resulted when Kansas-adapted grasses were grown in southern Saskatchewan, 10 to 13 degrees of latitude north of accustomed seasonal environmental influences. Work in Alaska with ecotypes of red fescue, bromegrass, slender wheatgrass, and timothy from a broad range of north-to-south origins revealed that the northernmost-adapted that were superior in winter survival also stored higher levels of food reserves in autumn and developed higher levels of tolerance to freeze stress than less hardy, more southern-adapted cultivars (Klebesadel 1985a, 1991, 1992; Klebesadel and Helm 1986).

The generally good winter hardiness and forage production of Sodar streambank wheatgrass was somewhat anomalous among the other generally inadequately winter-hardy wheatgrasses originating from latitudes below 50°N. A partial explanation for Sodar's good performance may lie in that cultivar's germplasm source; Hanson (1972) reports the collection was made at 3,000 feet (915 m) above sea level.

Some similarities exist between growing seasons near sea level at high latitudes and those at high elevations at lower latitudes. At high elevations the growing season typically terminates earlier than at nearby lower elevations. Therefore, perennial plants resident at high elevations are adapted to physiological preparation for earlier onset of winter, and are accustomed to developing cold hardiness under longer photoperiods, a set of conditions somewhat analogous to those occurring at lower elevations at higher latitudes (as in agricultural areas of Alaska). The Matanuska Research Farm is at 200 to 300 feet elevation. By this reasoning, Sodar experiences less environmental change when grown in southcentral Alaska, and therefore makes more timely and adequate preparation for Alaskan winters than wheatgrasses originating from, or selected at, lower elevations in the western United States. However, origin at high elevation at lower latitudes does not invariably confer good winter hardiness at high latitudes. P-739 bluebunch wheatgrass originated from collections between roughly 3,200 and 4,800 feet elevation (Hanson 1972), and that strain was among the least winter-hardy of the wheat-

grasses compared (Tables 3 and 5).

The rhizomatous habit, with regenerative overwintering tissues underground, logically confers upon Sodar, and other grasses of similar habit, greater protection from winter stresses than occurs with bunch-type grasses (Klebesadel and Helm 1986; Smith 1964). Bunch-type grasses are more exposed and have the bulk of their storage and regenerative tissues at or above the soil surface. However, thickspike wheatgrass also is rhizomatous and that introduction survived winters poorly here (Tables 3 and 5). It is possible, too, that a full awareness of the total evolutionary history and ancient origins of streambank wheatgrass might provide a better understanding of why Sodar surpassed other introductions from the Pacific Northwest in total performance here.

## CONCLUSIONS

Many wheatgrass strains and cultivars currently useful in the western states and Canada are inadequately winter-hardy for dependable use in Alaska. Most wheatgrasses introduced into the United States and Canada from Eurasia derived from mid-temperate latitudes and are utilized at similar latitudes in North America (Asay and Knowles 1985; Hanson 1972). Artificial and natural selection for optimum physiological and agronomic performance at mid-temperate latitudes in the conterminous 48 states or Canada obviously selects in other directions than toward genotypes best suited for far-northern environmental conditions, as in Alaska.

This contention is supported by Cornelius (1965) who noted that similar *Agropyron* germplasm introduced from the U.S.S.R. into two U.S. areas widely separated in latitude underwent divergent adaptational change. With perpetuation over several generations in different environments, natural-selection pressures resulted in altered adaptational status that resulted in dissimilar performance when the two were later grown together in a similar new environment.

For optimum winter hardiness in subarctic Alaska, wheatgrasses and other plant species should be obtained from similar northern latitudes around the world. Certain *Agropyron* strains in these tests, marginally promising but inadequately winter-hardy for dependable use here, occurred within the species *desertorum*, *intermedium*, and *sibiricum*. Strains evaluated within the species *crisatum*, *elongatum*, and *trichophorum* generally performed poorly. However, if the northern extent of the native ranges of these introduced species reaches above 60°N in Europe or Asia, collections from such northern areas should be better adapted to the subarctic seasonal climatological patterns of southcentral Alaska and therefore should per-

form better in this environment than the more southern-adapted strains evaluated.

Wheatgrass species native to North America, but whose native ranges do not extend north sufficiently to offer potential for subarctic adaptation and adequate winter hardiness for use in Alaska, include *inermis* and *dasystachyum*. *A. smithii* is marginal, and collections near the northern extent of its range might provide selections that would fare better at these northern latitudes than cultivars Rodan and Rosana.

The generally good performance of native Alaskan *A. trachycaulum*, *A. sericeum*, and *A. violaceum* in these tests and in other local trials (Mitchell 1982; Klebesadel 1991) reveals that they possess ideal northern adaptation, as well as several valuable agronomic traits that contribute to their potential for economic use. Since the native ranges of *A. spicatum* and *A. subsecundum* also reach to central Alaska (Hulten 1968), collections of those species from several Alaska sites also should be evaluated for agronomic merit. Further tests and evaluations of all subarctic-adapted wheatgrasses can delineate their potentials and limitations for agricultural uses and ecological repair in northern latitudes.

## ACKNOWLEDGMENTS

Plant collection trips, early nursery evaluations, and seed increases of native Alaskan wheatgrasses and Siberian wildrye used in this study were supported in part by funding from the Rockefeller Foundation (grants RF58108 and RF61036), and were coordinated by principal investigator R.L. Taylor. Seed of the hybrid *Agroelymus palmerensis* was supplied by H.J. Hodgson and R.L. Taylor. We thank W.W. Mitchell for helpful taxonomic identifications, Darel Smith and Arthur Berglund for technical assistance, Bobbi Kunkel for calculations, and Mrs. Kunkel and Peg Banks for manuscript typing. This study was conducted cooperatively with the Agricultural Research Service, U.S. Department of Agriculture.

## EXPLANATORY NOTE

This report summarizes research completed several years ago. During its completion, the senior 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.

## LITERATURE CITED

- Aamodt, O.S., and D.A. Savage. 1949. Cereal, forage, and range problems and possibilities in Alaska. p. 87-124 In: *Report on exploratory investigations of agricultural problems in Alaska*. USDA Misc. Pub. 700. U.S. Government Printing Office, Washington D.C.
- Asay, K.H., and R.P. Knowles. 1985. The wheatgrasses. p. 166-176. In : M.E. Heath, R.F. Barnes, and D.S. Metcalfe (ed.) *Forages—the science of grassland agriculture*. Iowa State University Press, Ames, IA.
- Cornelius, D.R. 1947. The effect of source of little bluestem grass seed on growth, adaptation, and use in revegetation seedings. *Jour. of Ag. Research* 74:133-143.
- Cornelius, D.R. 1965. *Latitude as a factor in wheatgrass variety response on California rangeland*. Proceedings Ninth International Grassland Congress, Sao Paulo, Brazil. 2:471-473.
- Crowle, W.L. 1966. The influence of nitrogen fertilizer, row spacing, and irrigation on seed yield of nine grasses in central Saskatchewan. *Canadian Jour. of Plant Science* 46:425-431.
- Dewey, D.R. 1983. Historical and current taxonomic perspectives of *Agropyron*, *Elymus*, and related genera. *Crop Science* 23:637-642.
- Douglas, D.S., and R.D. Ensign. 1954. *Sodar wheatgrass*. Idaho Ag. Exp. Sta. Bull. 234.
- Dubbs, A.L. 1970. *Comparison of intermediate, pubescent, tall, Siberian, streambank, and beardless wheatgrass varieties in Montana*. Montana Ag. Exp. Sta. Bull. 637.
- Hafenrichter, A.L., J.L. Schwendiman, H.L. Harris, R.S. MacLauchlan, and H.W. Miller. 1968. *Grasses and legumes for soil conservation in the Pacific Northwest and Great Basin states*. USDA Handbook 339. U.S. Government Printing Office, Washington, D.C.
- Hanson, A.A. 1972. *Grass varieties in the United States*. USDA Handbook No. 170. U.S. Government Printing Office, Washington, D.C.
- Hitchcock, A.S. 1950. (2nd ed., rev. by A. Chase.) *Manual of the grasses of the United States*. USDA Misc. Pub. 200. U.S. Government Printing Office, Washington, D.C.

- Hodgson, H.J. 1964a. Cytology, morphology, and amino acid characterization of the putative intergeneric hybrid, *Agroelymus palmerensis* and its presumed parents. *Crop Science* 4:199-203.
- Hodgson, H.J. 1964b. Effect of photoperiod on development of cold resistance in alfalfa. *Crop Science* 4:302-305.
- Hulten, E. 1968. *Flora of Alaska and neighboring territories*. Stanford University Press, Stanford, CA.
- Irwin, D.L. 1945. *Forty-seven years of experimental work with grasses and legumes in Alaska*. Alaska Ag. Exp. Sta. Bull. 12.
- Kilcher, M.R., and J. Looman. 1983. Comparative performance of some native and introduced grasses in southern Saskatchewan, Canada. *Jour. of Range Management* 36:654-657.
- Klebesadel, L.J. 1969. Siberian wildrye (*Elymus sibiricus* L.): Agronomic characteristics of a potentially valuable forage and conservation grass for the North. *Agronomy Jour.* 61:855-859.
- Klebesadel, L.J. 1970. Influence of planting date and latitudinal provenance on winter survival, heading, and seed production of brome grass and timothy in the Subarctic. *Crop Science* 10:594-598.
- Klebesadel, L.J. 1971. Nyctoperiod modification during late summer and autumn affects winter survival and heading of grasses. *Crop Science* 11:507-511.
- Klebesadel, L.J. 1974. Winter stresses affecting overwintering crops in the Matanuska Valley. *Agroborealis* 6:17-20.
- Klebesadel, L.J. 1985a. Hardening behavior, winter survival, and forage productivity of *Festuca* species and cultivars in subarctic Alaska. *Crop Science* 25:441-447.
- Klebesadel, L.J. 1985b. The critical importance of north-latitude adaptation for dependable winter survival of perennial plants in Alaska. *Agroborealis* 17(1):21-30.
- Klebesadel, L.J. 1991. *Performance of indigenous and introduced slender wheatgrass in Alaska, and presumed evidence of ecotypic evolution*. Alaska Ag. and Forestry Exp. Sta. Bull. 85.
- Klebesadel, L.J. 1992. *Brome grass in Alaska. II. Autumn food-reserve storage, freeze tolerance, and dry-matter concentration in over-wintering tissues as related to winter survival of latitudinal ecotypes*. Alaska Ag. and Forestry Exp. Sta. Bull. 93.
- Klebesadel, L.J., A.C. Wilton, R.L. Taylor, and J.J. Koranda. 1964. Fall growth behavior and winter survival of *Festuca rubra* and *Poa pratensis* in Alaska as influenced by latitude-of-adaptation. *Crop Science* 4:340-341.
- Klebesadel, L.J., and D. Helm. 1986. Food reserve storage, low-temperature injury, winter survival, and forage yields of timothy in subarctic Alaska as related to latitude-of-origin. *Crop Science* 26:325-334.
- Klebesadel, L.J., and S.M. Dofing. 1991. *Reed canarygrass in Alaska: Influence of latitude-of-adaptation on winter survival and forage productivity, and observations on seed production*. Alaska Ag. and Forestry Exp. Sta. Bull. 84.
- Knowles, R.P. 1956. Crested wheat grass. Canada Dept. of Ag. Pub. 986.
- Larsen, E.C. 1947. Photoperiodic responses of geographical strains of *Andropogon scoparius*. *Botanical Gazette* 109:132-149.
- Lawrence, T. 1978. An evaluation of thirty grass populations as forage crops for southwestern Saskatchewan. *Canadian Jour. of Plant Science* 58:107-115.
- Mitchell, W.W. 1982. Forage yield and quality of indigenous and introduced grasses at Palmer, Alaska. *Agronomy Jour.* 74:899-905.
- Mitchell, W.W., and H.J. Hodgson. 1965. The status of hybridization between *Agropyron sericeum* and *Elymus sibiricus* in Alaska. *Canadian Jour. of Botany* 43:855-859.
- Newell, L.C., and F.D. Keim. 1943. Field performance of brome grass strains from different regional seed sources. *Jour. of the American Society of Agronomy* 35:420-434.
- Olmsted, C.E. 1944. Growth and development in range grasses. IV. Photoperiodic responses in twelve geographic strains of side-oats grama. *Botanical Gazette* 106:46-74.

- Polunin, N. 1959. *Circumpolar arctic flora*. Oxford University Press, Oxford, U.K.
- Porsild, A.E., and W.J. Cody. 1980. *Vascular plants of continental Northwest Territories, Canada*. National Museums of Canada, Ottawa, Ontario.
- Rogler, G.A. 1943. Response of geographical strains of grasses to low temperatures. *Jour. of the American Society of Agronomy* 35:547-559.
- Smith, Dale. 1964. Winter injury and the survival of forage plants. *Herbage Abstracts* 34:203-209.
- Steponkus, P.L. 1978. Cold hardiness and freezing injury of agronomic crops. *Advances in Agronomy* 30:51-98.
- Tysdal, H.M. 1933. Influence of light, temperature and soil moisture on the hardening process in alfalfa. *Jour. of Agricultural Research* 46:483-515.
- Tzvelev, N. 1976. Tribe 3. *Triticeae Durn*. Leningrad: Academia Scientiarum U.R.S.S.
- Welsh, S.L. 1974. *Anderson's flora of Alaska and adjacent parts of Canada*. Brigham Young University Press, Provo, UT.
- Wilsie, C.P. 1962. The ecotype concept. p. 66-86. In: *Crop adaptation and distribution*. W.H. Freeman and Co., San Francisco, CA.
- Wilton, A.C., H.J. Hodgson, L.J. Klebesadel, and R.L. Taylor. 1966. *Polar bromegrass, a new winter-hardy forage for Alaska*. Alaska Ag. Exp. Sta. Circ. 26.