

# Winter Survival of Grasses and Legumes in Subarctic Alaska as Related to Latitudinal Adaptation, Pre-Winter Storage of Food Reserves, and Dry-Matter Concentration in Overwintering Tissues

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## SUMMARY

Objectives of this study, consisting of two separate but similar experiments, were to (a) compare winter hardiness in subarctic Alaska of numerous plant species and ecotypes from various latitudinal sources within most species, and (b) seek a better understanding of certain aspects of pre-winter physiologic changes in plants that are associated with successful or with unsuccessful winter survival in this northern area. Both experiments were conducted at the University of Alaska's Matanuska Research Farm (61.6°N) near Palmer in southcentral Alaska.

Latitudinal ecotypes of brome grass<sup>1</sup>, timothy, Kentucky bluegrass, red fescue, slender wheatgrass, alfalfa, and red clover, planted in rows in late June of two successive years, were thinned as small seedlings to individual plants. Seven other legumes (six native Alaskan) were also planted in the second experiment. Plants were compared for storage of food reserves (three samplings/year) during late summer and autumn of the year planted, for pre-winter dry-matter concentration in overwintering tissues, for indications of dormancy, and for subsequent winter survival.

- No entries exhibited stored reserves when sampled 9-11 August, but reserves were present in all entries sampled 22-23 August and later until the final sampling in mid-October during both seasons.
- Overwintering tissues of northernmost-adapted ecotypes increased in dry-matter concentration during the pre-winter hardening period more rapidly than those of southern-adapted ecotypes.
- Northernmost ecotypes within each species generally possessed highest dry-matter concentration in storage tissues and highest level of stored food reserves at the final sampling each season (9-12 October) just prior to freeze-up; they also survived the winters best. Southernmost ecotypes were lowest in percent dry matter, stored lowest levels of food reserves, and were poorest in winter survival. Ecotypes of intermediate-latitudinal origin usually were intermediate in these characteristics.

- Evidence of onset of dormancy (slow expression of stored reserves as etiolated growth in a warm, dark chamber) was detected in legumes more than in grasses; this characteristic was frequently, but not invariably, associated with superior winter survival.

- Grasses generally were more winter hardy than the legumes, although certain of the most winter-hardy legumes surpassed nonhardy ecotypes within grass species.

- Best winter hardiness was noted in (a) Alaska cultivars of brome grass, Kentucky bluegrass, and red fescue, (b) timothy from northern Norway, (c) naturalized strains of slender wheatgrass and Siberian alfalfa, and (d) native Alaskan ecotypes of pumpelly brome, slender wheatgrass, Harrington milkvetch, and alpine sweetvetch.

- A locally adapted ecotype of foliose oxytrope displayed significantly better winter survival than an ecotype of the same species adapted much farther north in arctic Alaska.

- Native Alaskan large-leaf lupine, that grows commonly in habitats supplied with insulating snow cover, winter-killed 100% in the more exposed field environment.

- The very slow growth of native Alaska legumes evaluated preclude their practical use as forages, but their superior north-latitude adaptation and nitrogen-fixation capabilities favor their use for revegetation purposes in subarctic areas.

- Of the introduced grasses from Canada and northern states, species with primarily subterranean overwintering tissues (brome grass, Kentucky bluegrass, red fescue) generally survived well, but species with primarily above-ground overwintering tissues (timothy, slender wheatgrass) did not. None of the introduced legumes (alfalfa, red clover, sweetclover) from Canada or northern states exhibited good winter survival.

<sup>1</sup> Latin names: Smooth brome grass (*Bromus inermis* Leyss.), pumpelly brome grass (*B. pumpellianus* Scribn.), timothy (*Phleum pratense* L.), Kentucky bluegrass (*Poa pratensis* L.), red fescue (*Festuca rubra* L.), slender wheatgrass (*Agropyron trachycaulum* [Link] Malte)<sup>2</sup>, Siberian alfalfa (*Medicago falcata* L.), variegated alfalfa (*M. sativa* L.), red clover (*Trifolium pratense* L.), biennial white sweetclover (*Melilotus alba* Desr.), cicer milkvetch (*Astragalus cicer* L.), Harrington milkvetch (*A. harringtonii* Cov. & Standl.), Williams milkvetch (*A. williamsii* Rydb.), large-leaf lupine (*Lupinus polyphyllus* Lindl.), Mackenzie sweetvetch (*Hedysarum mackenzii* Rich.), alpine sweetvetch (*H. alpinum* ssp. *americanum* (Michx.) Fedtsch.), and foliose oxytrope (*Oxytropis foliolosa* Hook.).

<sup>2</sup> This report uses the traditional nomenclature for this species, rather than *Elymus trachycaulus* (Link) Gould ex Shinnars proposed by Dewey (1983).

## INTRODUCTION

Grasses and legumes are the two most important plant families worldwide in providing food for both humans and animals. They are also useful for a broad spectrum of other valuable purposes; a few of concern in Alaska include stabilization of soils and soil materials against the erosional effects of wind and water, and amenity plantings such as home lawns, playgrounds, and other areas requiring turf cover.

### Grasses are Vital, Varied, and Versatile

Worldwide there are almost 10,000 species of grasses. Collectively they have a wider range of adaptation than any other family of flowering plants; they grow from the warm tropics to arctic regions, from wetlands to arid sites, and from sea level to alpine areas.

Their palatability and nutritional merits are invaluable because grasses represent a major portion of the feed base for domestic and wild animals worldwide. Grasses comprise about three-quarters of the species cultivated as forage crops and include all of the cereal crops.

Grasses are either annuals or perennials. The annual cereal grasses, when grown to maturity, provide valuable grain for both human and animal consumption. At immature stages of growth they are utilized for pasture and harvested forage. Other annual grasses are used only for forage. Annuals require planting each year and are therefore grown on rotational croplands.

Perennial grasses, a major element in this report, are also utilized for pasture and forage. In Alaska, perennial grasses provide the dominant portion of the livestock feed base. Some indigenous species are utilized in native stands while other species, like annuals, are seeded on rotational croplands. Perennial grasses also serve as erosion-resistant ground covers, while providing grazing on sites planted only once, or renovated occasionally, as is done with semi-permanent or permanent pastures. Such pastures often utilize steep, uneven, partially wooded, or otherwise difficultly tilled areas that are more accessible to livestock than to tillage and harvest equipment.

The fibrous roots and sod-forming, soil-binding characteristics of rhizome-producing perennial grasses are valued for ground cover and soil protection not only on agricultural lands but also in many non-agricultural situations. Some grass species, with a proliferation of basal leaves, withstand close grazing without injury. Others that grow taller are suited to machine harvest for green-feeding or preservation in various ways for later feeding.

Regardless of other characteristics or how grasses are utilized in Alaska, whether for agricultural or non-

agricultural purposes, perennial grasses must be dependably winter hardy. If grasses are marginal in winter hardiness, winter injury may occur repeatedly, sacrificing productivity, and often with weed invasion during slow recovery of stands. If total winter kill occurs, production is nil and costly replanting must then be done. Replanting inevitably incurs potential soil-erosion hazards, weed-control problems, and other concerns that can contribute to establishment failures.

### Legumes Are Valuable Also

The legume family is also large with about 12,000 species worldwide. As with the grasses, only a few species have been selected for artificial culture. Those legumes are valued both agriculturally and in low-maintenance ground cover mixtures because they are one of the few plant groups with the ability to capture or "fix" atmospheric nitrogen (Heichel 1985; Klebesadel 1978). Nitrogen, incorporated into legume plant herbage, contributes to the high protein concentration, palatability, and nutritive value of legumes used for livestock pasture or harvested forage. The fixed nitrogen also becomes available to associated vegetation incapable of nitrogen fixation, such as grasses.

Several species of biennial and perennial legumes have been utilized for hundreds of years at lower latitudes for pasture, harvested forage, and soil improvement and stabilization. Few, however, have shown promise of dependable performance in early trials in various areas of Alaska (Irwin 1945). Legumes are utilized successfully in other high-latitude areas such as the Scandinavian countries where winter conditions are less stressful than in this area of Alaska. Efforts have continued in recent decades to identify or develop dependable legumes for use locally (Hodgson et al. 1953; Klebesadel 1971a, 1971c, 1980, 1985a, 1992b, 1992c).

### Native Alaska Legumes

Approximately 40 species of legumes in six genera are native to Alaska (Hulten 1968). In contrast to introduced species, native species collectively are well adapted across a considerable range of ecologic, climatic, and edaphic conditions represented throughout the vast expanse of Alaska (Hulten 1968; Klebesadel 1963).

All examined to date show evidence of ample, effective nodulation (Allen et al. 1963), and their vital nitrogen-fixation role in native plant communities (Klebesadel 1978) suggests potential for utilization in agricultural, revegetation, and other conservation arenas in Alaska (Klebesadel 1971a, 1973a). Moreover, improved understanding of genetic and physiologic factors that contribute to their north-latitude adaptation and generally superior winter hardiness may aid efforts toward adapting legumes from other world areas for utilization in Alaska.

## The Winter Survival Problem

Winter injury, and often total winter kill, have been the dominant deterrents to successful culture in Alaska of most perennial grasses and legumes introduced from more southern sources. Temperate-zone-adapted biennials and perennials, although well adapted for growth and winter survival in their areas of origin, typically sustain winter injury or succumb totally to winter stresses in subarctic Alaska (Hodgson and Bula 1956; Irwin 1945; Klebesadel 1970, 1971c, 1980, 1984a, 1985a, 1985b, 1985c, 1992b, 1992c; Klebesadel et al. 1964; Klebesadel and Dofing 1990; Klebesadel and Helm 1986; Wilton et al. 1966).

## Global Transfers of Plants

The tendency to grow poorly adapted plant strains in Alaska is related at least in part to the political history and characteristics of settlement in this territory, and later, state. Twentieth-century culture of plants for agriculture and other purposes in this subarctic area has been pursued largely by immigrant settlers from temperate-zone areas of the conterminous United States.

New settlers in Alaska, as elsewhere, often attempt initially to grow plant strains and cultivars with which they are familiar. Moreover, seed merchants in Alaska, owing to commercial ties in the "South 48" and ease of import without international restrictions, traditionally have imported and sold crop seed adapted not to subarctic areas but to more southern latitudes.

Historically, immigrant farmers in the United States originated predominantly from Europe. Those settlers were able to transfer and grow successfully in North America many crop strains that were well adapted in their homelands. That successful transfer of crops over longitudinal distances of thousands of miles was possible because the crops were kept within relatively similar latitudinal boundaries within the temperate zone. That long-distance transfer did not subject perennial plants to greatly different photoclimate.

In contrast, the transfer of biennial and perennial crops over lesser distances northward, from temperate to subarctic climatic conditions, has been less successful. The reason for this lies to a considerable extent in the inability of overwintering plants to develop cold hardiness to their full genetic capacity, due to an inappropriate pattern of pre-winter environmental stimuli (Hodgson 1964; Klebesadel 1971b, 1973b, 1985c, 1993b; Moschkov 1935; Pohjakallio 1961).

## Latitudinal Ecotypes

The concept of "ecotypes" incorporated in this study is based on the premise originally set forth by Turesson in Sweden in the 1920s and as discussed by Clausen (1958), Mason and Stout (1954), and Wilsie (1962). An ecotype is a population complex within a

species that, through natural selection over many years, has adjusted physiologically (and sometimes morphologically) to be in harmony with environmental conditions in the general area where it has evolved.

Some plant species are native across great geographic areas and, within that total area, a considerable range of different localized climatic conditions may prevail. Therefore, various localized ecotypes within the total range occupied by a species, although all are classified as identical taxonomically (i.e., as the same species), can differ markedly in genetically controlled physiologic behavior that suits each to the climatic environment where it evolved and is adapted.

## Climatic Conditions

Climatic factors that can differ greatly across the total range of distribution of a species include such variables as length of growing season, amount and distribution of annual precipitation, heat of summer, cold of winter, intensity and prevalence of winter winds, widely oscillating or relatively constant winter temperatures, snow cover, and so on. One variable to which plant populations become adapted over time, and one that differs in a very regular manner with distance north or south of the equator, is the seasonally changing pattern of daily light and darkness (photoperiod and nyctoperiod).

Along with seasonally changing temperatures, the accustomed annual photoperiod / nyctoperiod pattern influences certain major plant functions, such as annual preparation for winter or "winter hardening" (Hodgson 1964; Klebesadel 1971b, 1993b). It follows then that growing a plant ecotype in a photoperiodic / growing-season environment quite different from the one where it is adapted may adversely affect its preparation for winter, leading to poor winter survival.

In the present study, improved crop cultivars developed at widely separated latitudes were considered to represent ecotypes as well. These plant lines had artificial selection inputs, unlike truly natural ecotypes; nonetheless, they represent ideal adaptation in specific latitudinal zones and so were included for evaluation and comparison on that basis. Within this interpretation, the term "latitudinal ecotype" is used without distinction to discuss crop cultivars or regional strains of cultivated or native grasses or legumes.

## Other Investigations

Several earlier studies have compared at one location the performance of "ecotypes," "geographical strains," "ecological races," or crop cultivars adapted to different discrete latitudes (Cornelius 1947; Larsen 1947; Olmsted 1944; Rogler 1943; Vaartaja 1954). Olmsted (1944) and Larsen (1947) compared photoperiodic responses in latitudinal ecotypes of native U.S. grasses collected from diverse north-to-south locations within the ranges occupied by each species.

Principal concerns were directed toward seed-head production; however, Larsen (1947) noted differential responses to autumn photoperiods in Illinois in ecotypes of little bluestem (*Andropogon scoparius* Michx.); northern strains ceased growth and became dormant while southern strains remained green.

Cornelius (1947) found greater winter injury in Kansas with little bluestem obtained from areas south of Kansas than in ecotypes of the same grass from areas north of that state.

Rogler (1943), in North Dakota, compared both cool and warm-season grasses from different latitudinal origins for winter hardiness in the field and for survival in artificial freezing tests. He attributed differential physiological response of strains to photoperiod and climate at Mandan for the lesser ability of southern strains to "harden off" or to adequately withstand cold temperature stress. Although Rogler reported no winter injury to cool-temperature species in the field, regardless of origin, average field survival of warm-temperature strains decreased with progressively more southerly origins.

Vaartaja (1954) reported the existence of latitudinal or photoperiodic ecotypes in woody species. He considered that evolutionary adaptation has conditioned ecotypes to optimum growth at the photoclimate of their accustomed latitudinal environment. Poorer plant performance occurred under altered photoperiodic patterns, as occur during the growing season at latitudes north or south of the origin of an ecotype.

Studies conducted at this station (Bula et al. 1956; Hodgson 1964; Hodgson and Bula 1956; Klebesadel 1992b, 1993a, 1993b; Klebesadel and Helm 1986) have compared the development of freeze tolerance in cultivars and regional strains of alfalfa (*Medicago* species), sweetclover (*Melilotus* species), bromegrass (*Bromus* species), and timothy (*Phleum pratense* L.) from diverse latitudinal sources. The studies showed that physiological adaptation to unique characteristics of north-latitude seasonal climatic patterns conferred advantages on forage crops to be grown in the Subarctic. Not surprisingly, therefore, the best adapted and therefore most winter-hardy crop strains for Alaska are being developed from ecotypes indigenous to the state or to other northern areas (Hodgson et al. 1971a, 1971b, 1978; Hodgson et al. 1953; Mitchell 1979; Wilton et al. 1966).

Hodgson (1964) and Klebesadel (1971b) in Alaska, and Pohjakallio (1961) in Finland, reported enhanced development of freeze tolerance in alfalfa, better winter survival of grasses, and better winter survival of red clover (*Trifolium pratense* L.), respectively, when temperate-adapted ecotypes were exposed to artificially shortened photoperiods in those subarctic areas during late summer and autumn; the photoperiods imposed were similar to those prevailing during the period of cold-hardiness development at their more southern latitude of origin.

Those findings are in agreement with Moschkov (1935) who reported winter hardiness studies in Russia involving several species from diverse latitudinal origins. He attributed much of the failure of perennials to survive winters north of their latitude of adaptation to inappropriate photoperiods during the pre-winter period of lowering temperatures (and cold-hardiness development) rather than to direct effects of winter stresses alone.

Many studies have determined qualitative and quantitative changes in overwintering tissues of biennial and perennial plants prior to winter and related those changes to actual winter hardiness or survival in the field. Earlier literature on this subject has been reviewed extensively elsewhere (Devlin and Witham 1983; Dexter 1956; Levitt 1956; Steponkus 1978; Smith 1964a, 1964b). In general, plants with the capacity to develop winter hardiness respond to lowering temperatures and shortening photoperiods (lengthening nyctoperiods) of late summer and autumn by storing carbohydrate reserves and undergoing protoplasmic changes that render overwintering tissues cold tolerant (Hodgson 1964; Klebesadel 1992b, 1993a, 1993b; Klebesadel and Helm 1986; Moschkov 1935; Tysdal 1933).

### Dry-Matter Concentration in Overwintering Plant Parts

Several investigators have reported increased dry-matter concentration during pre-winter cold hardening in the overwintering tissues of various plant species (Graber et al. 1927; Grandfield 1943; Greathouse and Stuart 1936; Langlet 1943; Metcalf et al. 1970; Paulsen 1968; Sjoeth 1964; Smith 1964a, 1964b; Steponkus 1978).

This phenomenon is closely related to other alterations that occur in plants during the winter-hardening process; however, the causal stimulus is unclear. Paulsen (1968) reported that the percent dry-matter increase over several weeks in crowns of winter wheat (*Triticum aestivum* L.) was closely associated with decreasing temperature during the same period. In contrast, Klebesadel (1993b) found no differences in percent dry-matter in overwintering tissues of biennial sweetclover ecotypes grown in warm vs. chilling controlled-environment chambers. Yet the ecotypes in the chilling chamber displayed markedly less injury from freeze stress. Conversely, considerable differences were seen in an outdoor experiment (a) among the same ecotypes, and (b) as engendered by various photoperiod/nyctoperiod treatments.

The pre-winter increase in dry-matter concentration in overwintering tissues of perennial plants is coincident with other changes, including the progressive increase in freeze tolerance. Generally, during the winter-hardening process there is an increase in "bound" water in cells and a decrease in free water in plant

tissues, simultaneous with an overall decrease in total water content of overwintering tissues (Smith 1964a).

### Stored Food Reserves

Carbohydrate reserves have been measured chemically by utilizing either enzyme or acid hydrolysis (Smith 1981) leading to a quantitative determination of total non-structural carbohydrates (TNC). Another technique used to measure stored food reserves in plants is growing them to exhaustion in a warm, dark environment and considering quantity of etiolated growth produced in the dark as a measure of stored reserves (Graber et al. 1927). Techniques of the former type, with proper tissue treatment, present a relatively precise determination of absolute TNC levels present in plant tissue at the time of tissue demise. A disadvantage of this technique is the inability to supply any indication of rest condition or dormancy achieved within the plant tissues.

In contrast, etiolated growth in a warm, dark chamber may provide a reasonable assessment of dormancy, as described in this and in an earlier report (Klebesadel 1992c). This technique provides a conservative estimate of stored reserves, however, because it does not provide a measure of that portion of total reserves that are volatilized as respiration products during the time required for the test (Graber et al. 1927). Moreover, loss of reserves through respiration also introduces some distortion of reserve storage determinations because of differential loss of respiration products among plants that remain alive for dissimilar terms in the dark environment.

Another source of imprecision in this technique, as it has been employed by others, is the assumption of equal plant-tissue mass within equiponderant or equal-size soil cores extracted for measurement from the field (Baker and Jung 1968; Burton and Jackson 1962). This last weakness was circumvented in the present study by utilizing only plant tissue, and only the principal storage tissues, of entities compared. This permitted measurement of reserve storage within morphologically identical tissue within each plant family, and related expression of measured reserves directly to mass of storage tissues utilized.

Stout (1984) compared measurement of food reserves in alfalfa using both TNC and etiolated-growth techniques. He concluded that the two methods did not measure identical constituents of plant food reserves, but that both could provide useful information.

### Dormancy

The phenomenon of winter dormancy in plants has been both recognized and studied more in woody species than in herbaceous types (Samish 1954; Taylorson and Hendricks 1976; Wareing 1969). Dormancy generally refers to temporary suspension of visible growth, especially that of buds and seeds. Two kinds of dor-

mancy are recognized; "quiescence" describes dormancy that occurs when conditions external to the plant (e.g., drought, unfavorable temperatures) cause cessation of growth, and "rest" is a dormant state, caused by internal plant factors (e.g., increase in growth inhibitors) that restrict growth, even when the plant is exposed to conditions favorable to growth.

In this report, the impeded expression of stored food reserves as rapid etiolated growth in the warm, dark chamber is of the "rest" type of dormancy; that condition was earlier broken or eliminated in sweetclover by subjecting plants to several freeze/thaw cycles (Klebesadel 1992c). In this report, the phenomenon is referred to simply as dormancy.

### Previous Alaska Studies

Several experimental trials at this location have provided reports of comparative winter survival in a broad survey manner (Irwin 1945), or within many discrete groupings of forage grasses and legumes (Hodgson and Bula 1956; Klebesadel 1970, 1971b, 1980, 1984a, 1984b, 1985a, 1985b, 1985c, 1991, 1992a, 1992c; Klebesadel et al. 1964; Klebesadel and Helm 1986; Klebesadel and Dofing 1990; Wilton et al. 1966). In the aggregate, these tests provide a broad general insight into winter-hardiness patterns within adapted and unadapted forage strains, but within very limited plant groups.

In addition to observations of winter survival, certain investigations have studied winter-hardiness problems in Alaska as they relate to freeze tolerance, nitrogen fractions, and chemically determined carbohydrate levels in latitudinal ecotypes within a single crop (Bula et al. 1956; Hodgson 1964; Hodgson and Bula 1956). However, published data are lacking that document actual winter survival of latitudinal ecotypes within a broad array of grass and legume species under uniform experimental conditions and that relate survival to other facets of the pre-winter hardening process.

### This Study

The present investigation compared latitudinal ecotypes within several species of grasses and legumes for relationships between seedling development, pre-winter storage of organic food reserves, dry-matter concentration in overwintering tissues, and subsequent winter survival. The study was conducted at the University of Alaska's Matanuska Research Farm (61.6°N) in the Matanuska Valley of southcentral Alaska.

## EXPERIMENTAL PROCEDURES

Several grasses and legumes were seeded in rows 12 inches apart and 50 feet long on 22 June 1966 (Experiment I) and 20 June 1967 (Experiment II) in

Knik silt loam (Typic Cryochrept) with good surface drainage. Preplant commercial fertilizer disked into the seedbed supplied nitrogen, phosphorus (as  $P_2O_5$ ), and potassium (as  $K_2O$ ) at 32, 128, and 64 lb / A, respectively. Randomized complete block experimental designs were used with four replications. When seedlings were two to three inches tall, rows were thinned by hand-pulling to leave individual seedlings four to eight inches apart.

In both Experiment I and Experiment II, entries planted included latitudinal ecotypes within brome-grass (*Bromus* species), timothy, Kentucky bluegrass (*Poa pratensis* L.), red fescue (*Festuca rubra* L.), slender wheatgrass (*Agropyron trachycaulum* [Link] Malte), alfalfa, and red clover, as listed in Table 1. In Experiment II, seven additional legumes included were single entries of introduced cicer milkvetch (*Astragalus cicer* L.) and six species native to Alaska—Harrington milkvetch (*A. harringtonii* Cov. & Standl.), Williams milkvetch (*A. williamsii* Rydb.), large-leaf lupine (*Lupinus polyphyllus* Lindl.), Mackenzie sweetvetch (*Hedysarum mackenzii* Rich.), alpine sweetvetch (*H. alpinum* ssp. *americanum* [Michx.] Fedtsch.), and foliose oxytrope (*Oxytropis foliolosa* Hook.). The latter species was represented by two ecotypes from diverse latitudinal origins within Alaska. Appropriate bacterial (*Rhizobium*) inoculant was mixed with each legume seed lot before planting.

Seedlings were withdrawn from the field to determine levels of stored food reserves and dry-matter concentration in overwintering tissues during late summer and autumn of the year planted. Near the end of the seeding year in both experiments, 10 to 15 seedlings were dug from each row on each of three sampling dates (9-10 August, 30-31 August, and 10-11 October in Experiment I, 22-23 August, 18-20 September, and 9-11 October in Experiment II). Aerial growth beyond two inches above the soil surface was severed and discarded just before plants were dug to prevent transpirational water loss. Immediately after digging, seedlings were wrapped in saturated paper toweling and kept wrapped except during washing and trimming until weighed for potting.

All roots were severed from grass seedlings and the main stem and tillers were severed one inch above the seminal node. All rhizomes were kept intact, and if they emerged, aerial tissue beyond one inch above the soil surface was severed and discarded. On legumes, all branch roots and taproot growth beyond three inches below the cotyledonary node were severed from taproots and discarded. Legume aerial growth beyond one inch above the cotyledonary node also was severed and discarded.

Final traces of soil and loose plant debris were removed by washing. Surface moisture was blotted from plants with cloth toweling. Grass crowns and legume taproot-crown segments were weighed indi-

vidually and embedded in water-saturated vermiculite in pots. Plants were placed so that tissues that had been below the soil surface were also below the vermiculite surface. Pots measured seven inches in both diameter and height. Five plants of each entry were potted from each replication on each sampling date, except that in Experiment I 10 plants from each legume row were potted at all three samplings.

Five to eight plants from each row, prepared in the same manner as those potted, were weighed fresh, dried to constant weight at 140°F, and reweighed. Percent dry matter in each lot was used to derive extrapolated oven-dry weight of tissues potted.

All pots were placed into a dark chamber maintained at 64°±3°F with the base of each pot immersed in one-quarter to one-half-inch of water. Fungicide (Captan) in water spray was applied as needed, usually about three times weekly, to prevent mold development. All etiolated regrowth was harvested at successive two-week intervals after potting until exhaustion of food reserves and death of plants. With the grasses, red clovers, and oxytropes, etiolated regrowth possessed no nodes and was severed at the point where it emerged from the tiller stubble. With all other legumes, regrowth was harvested back only to the lowermost node on regrowth to ensure presence of regenerative bud sites throughout the test period for continued expression of stored reserves. 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 tissue potted.

After killing frosts in the seeding year of both experiments, aerial growth of plants remaining in the field was clipped and removed (25 October in Experiment I and 20 October in Experiment II) leaving a two-inch stubble to prevent differential snow retention on rows during winter. In mid-May of the second year of both experiments, living and dead plants were counted in all rows planted the previous year and winter survival percentages were calculated.

Data on percent winter survival were transformed to angles prior to statistical analysis to obtain a more normal distribution of values. Duncan's multiple range test comparisons were calculated on angle values. Actual field survival percentages appear in Table 1; all indications of statistical significance are based on 95% confidence limits.

## RESULTS AND DISCUSSION

Certain limited facets of information from this study have been incorporated into previously published, more extensive reports on individual species, reports that assembled findings from many experiments to lend completeness to discussion of adaptation of those species (Klebesadel 1985b, 1991, 1993a;



**Table 1.** Latitudinal adaptation, percent dry matter in storage tissues in mid-October, and subsequent percent winter survival of latitudinal ecotypes of grasses and legumes in two separate tests at the Matanuska Research Farm (61.6°N. Lat.).

| Ecotypes                              | Origin<br>(N. Lat.) | Percent dry matter<br>in storage tissues<br>in mid-October |          |           | Percent winter survival |                     |           |
|---------------------------------------|---------------------|--|----------|-----------|-------------------------|---------------------|-----------|
|                                       |                     | Exp. I   | Exp. II  | 2-yr mean | Exp. I                  | Exp. II             | 2-yr mean |
| <b>Bromegrass:</b>                    |                     |  |          |           |                         |                     |           |
| Native Pumpelly                       | 61.6°               | 19.6 ghi <sup>1</sup>                                      | 20.8 opq | 20.2 ijk  | 100 a                   | 100 a               | 100 a     |
| Polar <sup>2</sup>                    | 61.6°               | 21.1 efg   | 21.1 op  | 21.1 ij   | 100 a                   | 100 a               | 100 a     |
| Manchar <sup>2</sup>                  | 45±2°               | 20.2 fgghi   | 21.6 no  | 20.9 ij   | 98 b                    | 89 de               | 94 bc     |
| Achenbach <sup>2</sup>                | 38±4°               | 18.4 i   | 19.5 qr  | 19.0 lm   | 14 h <sup>3</sup>       | 10 i <sup>3</sup>   | 12 h      |
| <b>Timothy:</b>                       |                     |  |          |           |                         |                     |           |
| Engmo <sup>2</sup>                    | 70°                 | 21.2 efg   | 23.4 lm  | 22.3 gh   | 90 cd                   | 99 ab               | 95b       |
| Climax <sup>2</sup>                   | 45±5°               | 18.5 i   | 20.1 pqr | 19.3 klm  | 4ij <sup>3</sup>        | 0 j                 | 2 i       |
| Clair <sup>2</sup>                    | 38±4°               | 16.5 j   | 20.1 pqr | 18.3 mn   | 2 jk <sup>3</sup>       | 0 j                 | 1 ij      |
| <b>Kentucky bluegrass:</b>            |                     |  |          |           |                         |                     |           |
| Nugget <sup>2</sup>                   | 61°                 | 18.9 i   | 23.3 lm  | 21.1 ij   | 100 a                   | 100 a               | 100 a     |
| Delta <sup>2</sup>                    | 50±5°               | 19.0 hi  | 22.7 mn  | 20.8 ij   | 91 cd <sup>4</sup>      | 83 ef <sup>4</sup>  | 87 de     |
| Merion <sup>2</sup>                   | 44±2° <sup>5</sup>  | 16.2 j   | 19.0 r   | 17.6 no   | 84 de <sup>4</sup>      | 97bcd <sup>4</sup>  | 91 cd     |
| <b>Red fescue:</b>                    |                     |  |          |           |                         |                     |           |
| Arctared <sup>2</sup>                 | 61.6°               | 21.8 ef  | 24.2 kl  | 23.0 fg   | 100 a                   | 100 a               | 100 a     |
| Duraturf <sup>2</sup>                 | 60±5°               | 15.7 j   | 21.7 no  | 18.7 mn   | 93 c <sup>4</sup>       | 98 abc <sup>4</sup> | 96 b      |
| Illahce <sup>2</sup>                  | 45±2°               | 14.6 j   | 20.0 qr  | 17.1 o    | 62 f <sup>3</sup>       | 76 fg <sup>3</sup>  | 69 f      |
| <b>Slender wheatgrass:</b>            |                     |  |          |           |                         |                     |           |
| Native Alaskan                        | 64±2°               | — <sup>6</sup>   | 27.9 gh  | —         | 100 a                   | 100 a               | 100 a     |
| Alaska-44S                            | 61.5°               | 24.0 d   | 26.7 hi  | 25.4 d    | 100 a                   | 100 a               | 100 a     |
| Primar                                | 47±2°               | 22.4 de  | 26.1 ij  | 24.3 e    | 8 hi <sup>3</sup>       | 13 hi <sup>3</sup>  | 11 h      |
| <b>Alfalfa:</b>                       |                     |  |          |           |                         |                     |           |
| Siberian ( <i>M. falcata</i> )        | 61.6°               | 36.0 a   | 34.7 a   | 35.3 a    | 73 ef                   | 92 cde              | 83 e      |
| A-syn.B <sup>2</sup>                  | 64.5°               | 32.2b  | 32.8 bc  | 32.5 b    | 37 g                    | 15 hi               | 26 g      |
| Rambler                               | 50±5°               | — <sup>7</sup>   | 33.2 b   | —         | — <sup>7</sup>          | 2 j                 | —         |
| Rhizoma <sup>2</sup>                  | 50±5°               | 34.3 a   | 32.1 bcd | 33.2 b    | 0 k                     | 1 j                 | 1 ij      |
| California common <sup>2</sup>        | 36±4°               | 28.9 c   | 30.4 f   | 29.6 c    | 0 k                     | 0 j                 | 0 j       |
| <b>Red clover:</b>                    |                     |  |          |           |                         |                     |           |
| Alaskland <sup>2</sup>                | 64.5°               | 24.1 d   | 23.2 lm  | 23.6 ef   | 0 k                     | 0 j                 | 0 j       |
| Altaswede <sup>2</sup>                | 50±5°               | 21.0 efgh  | 21.5 no  | 21.2 hi   | 0 k                     | 0 j                 | 0 j       |
| Lakeland                              | 42±2°               | 20.4 efghi   | 21.2 op  | 20.8 ij   | 0 k                     | 0 j                 | 0 j       |
| Nolin's Red <sup>2</sup>              | 30±2°               | 18.7 i   | 21.2 op  | 20.0 jkl  | 0 k                     | 0 j                 | 0 j       |
| <b>Sweetclover:</b>                   |                     |  |          |           |                         |                     |           |
| Arctic                                | 50±5°               | — <sup>7</sup>   | 28.8 g   | —         | — <sup>7</sup>          | 18 hi               | —         |
| Spanish                               | 40±8°               | — <sup>7</sup>   | 25.2 jk  | —         | — <sup>7</sup>          | 0 j                 | —         |
| <b>Milkvetch (<i>Astragalus</i>):</b> |                     |  |          |           |                         |                     |           |
| <i>A. williamsii</i>                  | 64°                 | — <sup>7</sup>   | 31.4 def | —         | — <sup>7</sup>          | 70 g                | —         |
| <i>A. harringtonii</i>                | 61.6°               | — <sup>7</sup>   | 33.1 bc  | —         | — <sup>7</sup>          | 97 bc               | —         |
| <i>A. cicer</i> (P-498)               | 47±2°               | — <sup>7</sup>   | 33.4 b   | —         | — <sup>7</sup>          | 0 j                 | —         |
| <b>Oxytropis (<i>Oxytropis</i>):</b>  |                     |  |          |           |                         |                     |           |
| <i>O. foliolosa</i> (Umiat)           | 69.5°               | — <sup>7</sup>   | 30.8 ef  | —         | — <sup>7</sup>          | 21 h                | —         |
| <i>O. foliolosa</i> (L. Nelch.)       | 62°                 | — <sup>7</sup>   | 31.8 cde | —         | — <sup>7</sup>          | 83 ef               | —         |
| <b>Sweetvetch (<i>Hedysarum</i>):</b> |                     |  |          |           |                         |                     |           |
| <i>H. alpinum americanum</i>          | 61°-62°             | — <sup>7</sup>   | 33.2 b   | —         | — <sup>7</sup>          | 100 a               | —         |
| <i>H. mackenzii</i>                   | 61°-62°             | — <sup>7</sup>   | 27.3 hi  | —         | — <sup>7</sup>          | 64 g                | —         |
| <b>Lupine (<i>Lupinus</i>):</b>       |                     |  |          |           |                         |                     |           |
| <i>L. polyphyllus</i>                 | 61°-62°             | — <sup>7</sup>   | 27.5 h   | —         | — <sup>7</sup>          | 0 j                 | —         |

<sup>1</sup> Within each column, values not followed by the same letter differ significantly (5% level); values followed by the same letter are not significantly different using Duncan Multiple Range Test.

<sup>2</sup> Ecotypes utilized for data presented in Figure 1.

<sup>3</sup> Surviving plants severely wintered-injured; little spring recovery.

<sup>4</sup> Most surviving plants visibly weakened but survived with fair to good vigor.

<sup>5</sup> Cultivar selected at ca. 38°N.

<sup>6</sup> Data lost.

<sup>7</sup> Not included in test.

Klebesadel and Helm 1986). However, to discuss equally all elements involved in the present study, and to lend completeness, balance, and unity to commentary herein, results with all species involved in this study are discussed in this report, despite some minor instances of repetition between this and the single-species reports.

### Dry-Matter Concentration in Overwintering Tissues

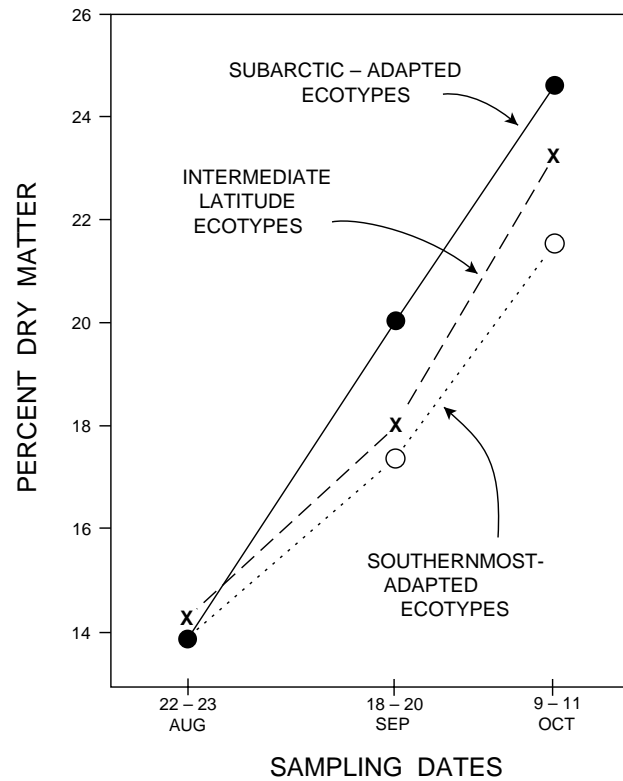
In late August, all latitudinal ecotypes within each species were similar in percent dry matter in overwintering tissues. Thereafter, storage tissue dry matter increased markedly during September and early October in both years (Figure 1). However, ecotypes of northernmost adaptation increased more rapidly in dry-matter concentration than ecotypes of more southern adaptation. Ecotypes adapted to intermediate latitudes were intermediate in this respect. Therefore, at the final sampling in mid-October the pattern of dry matter concentration of ecotypes within each species was quite similar (Table 1). Northernmost-adapted ecotypes were highest in percent dry matter in overwintering tissues, southernmost ecotypes were lowest, and ecotypes of intermediate latitudinal adaptation were intermediate. Specific comparisons and exceptions are noted within discussions of individual species.

Percent dry matter in overwintering tissues at the final sampling in October were quite similar between the two years in alfalfa, red clover, and bromegrass, but were somewhat higher in Experiment II than in Experiment I in timothy, red fescue, Kentucky bluegrass, and slender wheatgrass (Table 1).

In October, the legume taproot-crown segments were higher in percent dry matter than crowns of the grasses, except for red clover which was similar to most of the grasses (Table 1). The lower percent dry matter of red clover was due at least in part to the presence of a considerable amount of succulent petiolar tissue not present in the other legumes. Within the grasses, bromegrass, timothy, Kentucky bluegrass, and red fescue were generally similar in percent dry matter, while slender wheatgrass was somewhat higher and intermediate between the other grasses and most of the legumes.

### Stored Food Reserves

No expression of stored reserves as etiolated growth occurred with any species or ecotypes with the 9-10 August sampling in Experiment I. A slight indication of growth was noted from potted crowns of the northernmost-adapted entry, Engmo timothy, but this growth soon ceased and was not weighed. Amounts of reserves expressed after the 30-31 August sampling in Experiment I were generally intermediate between amounts expressed after the 22-23 August and 18-20



**Figure 1.** Percent dry matter in storage tissues of latitudinal ecotypes within six grass and legume species (species and ecotypes included are indicated by footnote in Table 1). Data are for three sampling dates in Experiment II during the pre-winter period of cold-hardiness development.

September samplings in Experiment II. Inasmuch as several entries included in the second trial did not appear in the first, and patterns of reserve development were similar in the two years, reserve measurements are presented for the three sampling dates of the second experiment only (Figure 2).

All entries generally increased in measured reserves over the three sampling dates. However, rate of expression of reserves as etiolated growth within the two-week growth periods often changed with progressively later sampling dates. When no etiolated growth was produced beyond the first two-week growth period in darkness, an entry was considered to possess no dormancy. All ecotypes reflect this condition with the 22-23 August sampling except the native Alaskan legumes *Hedysarum alpinum* and *Lupinus polyphyllus* (Figure 2). The lupine required a second two-week growth period before reserves were exhausted while the *Hedysarum* continued slow expression of measurable etiolated growth over seven, two-week growth periods.

Slow expression of reserves as etiolated growth, as exemplified by *H. alpinum* in the first sampling in Experiment II, is interpreted as evidence of dormancy assumed by the plant (Klebesadel 1992c). This condition became increasingly evident, particularly with

most legumes, in later samplings. An extreme example is seen in *L. polyphyllus* which expressed slightly more than 100 mg of regrowth/g of storage tissue potted (dry-matter basis) with the 22-23 August sampling (Figure 2). With progressive onset of dormancy during subsequent weeks, only 40 mg/g were expressed during seven, two-week growth periods following the final sampling on 9-11 October.

It is difficult to judge where dormancy actually becomes apparent in the reserve measurements, and where a second two-week growth period was necessary for total exhaustion of reserves in the absence of dormancy. However, it probably is safe to assume that any entries that required more than the second two-week growth period for reserve exhaustion reflect some degree of dormancy. Moreover, when one entry produced proportionately more etiolated growth during the second two-week growth period than another entry that produced more total etiolated growth (e.g., in the October sampling in Figure 2, *B. pumpellianus* vs. Polar brome, Alaskland vs. Altaswede red clover), the former is interpreted as possessing greater dormancy in each case. Other specific comparisons are made in the discussions of individual species.

## Winter Survival

Field areas used for both tests were exposed to prevailing winter winds that kept rows bare of snow cover during most of both winters. Both winters would be considered near average (for this area) in relative stress on overwintering plants.

Minimum air temperatures during the two winters, as recorded near the experimental sites, reached  $-15^{\circ}\text{F}$ , or below, on three occasions during both winters. During the first winter, these were  $-22^{\circ}$ ,  $-25^{\circ}$ ,  $-24^{\circ}$ , and  $-18^{\circ}\text{F}$  (Dec. 9-12);  $-15^{\circ}$ ,  $-19^{\circ}$ ,  $-21^{\circ}\text{F}$  (Jan. 13-15); and  $-17^{\circ}$ ,  $-19^{\circ}$ ,  $-15^{\circ}$ ,  $-22^{\circ}\text{F}$  (Jan. 24-27). During the second winter, they were  $-17^{\circ}$ ,  $-18^{\circ}$ ,  $-20^{\circ}$ , and  $-22^{\circ}\text{F}$  (Dec. 1-4);  $-20^{\circ}\text{F}$  (Feb. 2); and  $-22^{\circ}\text{F}$  (Feb. 5). Although these records suggest slightly more severe temperature stresses during the first winter (lower temperatures and longer durations), comparative winter survival of ecotypes was not greatly different during the two winters (Table 1).

Marked differences in winter survival occurred both among the species compared and among latitudinal ecotypes within each species. Excellent winter survival occurred with the northernmost-adapted ecotypes (above  $60^{\circ}\text{N}$ ) of brome grass, Kentucky bluegrass, red fescue, and slender wheatgrass in both tests, and with the northernmost-adapted timothy (Engmo) in Experiment II. One noteworthy characteristic not apparent in the percents winter survival reported was the relative vigor of surviving plants. In all of the northern-adapted ecotypes referred to above, plant vigor was excellent. In contrast, surviving plants within the more southern-adapted grasses often were severely winter-injured but were counted as living if

only one or more green tillers were observed. Cultivars among which surviving plants exhibited visible injury are noted in Table 1 and in discussions of the separate species.

## GRASSES

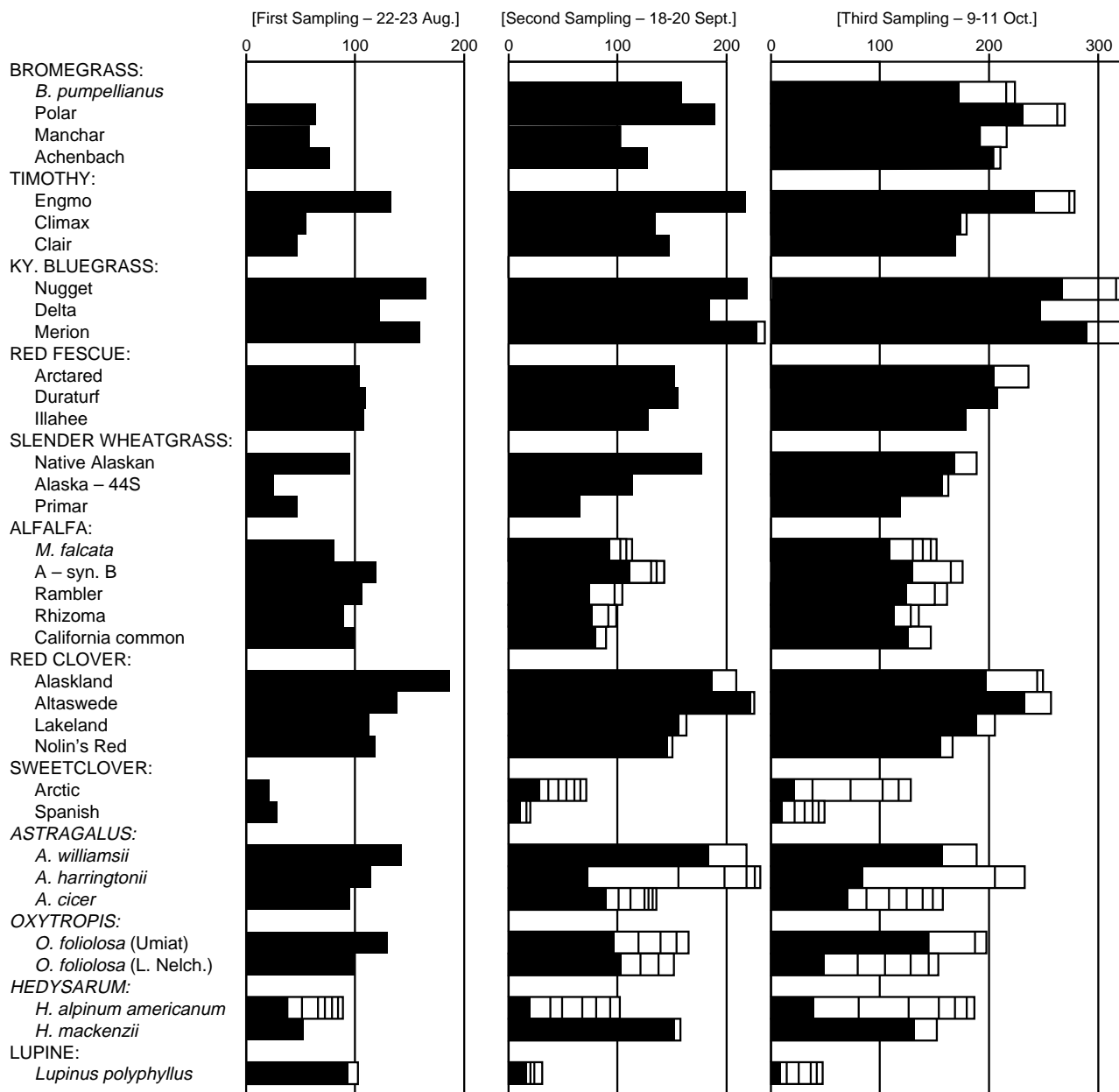
**Brome grass:** Native Alaskan pumpelly brome grass (*Bromus pumpellianus*), closely related to smooth brome grass (Klebesadel 1984b), was included as a separate species for comparative purposes. Seed planted was collected locally from indigenous plants; therefore, the native brome grass possessed ideal adaptation to the test area. Pumpelly brome was similar to the two northernmost-adapted smooth brome grasses in percent dry matter in storage tissues (Table 1). The native brome gave evidence of slightly greater dormancy, particularly more so than Manchar or Achenbach, as indicated by the amounts of reserves expressed as etiolated regrowth during the second and third two-week intervals in darkness (Figure 2). Pumpelly brome sustained no winter kill in either test (Table 1, Figure 3).

Within the brome grass cultivars, Polar and Manchar were similar in percent dry matter in storage tissues but both surpassed the southern-adapted Achenbach significantly in this respect in Experiment II and in the two-year mean (Table 1). Polar was superior to Manchar and Achenbach in total level of stored reserves expressed; moreover, the slower release of reserves as etiolated growth by Polar following the October sampling may indicate that cultivar had assumed a more dormant condition by the final sampling. Total of measured reserves stored during autumn was somewhat higher for Manchar than Achenbach; furthermore, Manchar reserves were expressed as etiolated growth more slowly than those of Achenbach, perhaps indicating a more dormant condition in Manchar.

Polar, a cultivar incorporating northern-adapted pumpelly brome germplasm and selected at  $61.6^{\circ}\text{N}$  (Wilton et al. 1966), sustained no winter kill in either test. Manchar winter survival was slightly but significantly less than Polar or native pumpelly brome, but vigor of surviving plants was good (Figure 4). Manchar has been perpetuated at  $47^{\circ}\pm 2^{\circ}\text{N}$  since its introduction in 1935 from  $44^{\circ}\text{N}$  in eastern Asia (Hanson 1972). The more southern-adapted Achenbach averaged only 12% winter survival for both tests (Table 1) and the few surviving plants were severely winter-injured with one to very few living tillers per plant.

**Timothy:** Plants of Engmo, a cultivar from northern Norway, differed from those of Climax and Clair by the end of the seedling year in being very leafy and prostrate with no elongated culms. Plants of Climax and Clair, cultivars from southern Canada and Ken-

MILLIGRAMS GROWTH IN DARKNESS PER GRAM OF STORAGE TISSUE (OVEN-DRY BASIS)



**Figure 2.** Stored food reserves in latitudinal ecotypes of grasses and legumes sampled at three different times during late summer and autumn (measured as milligrams etiolated growth in darkness per gram of storage tissue, oven-dry basis). Total length of each bar represents cumulative total of etiolated growth, with each vertical division indicating an additional increment of etiolated growth harvested at the end of a two-week growth period. Black portion of bars indicates etiolated growth produced during first two-week period in darkness.

tucky, respectively, were conspicuously more upright than Engmo and possessed few to several elongated culms per plant with up to three floral spikes wholly or partly exerted per plant.

Engmo storage tissues were significantly higher in percent dry matter than those of Climax or Clair in October of both years (Table 1). Moreover, Engmo exhibited markedly more stored reserves at all samplings than Climax or Clair (Figure 2). Climax was

slightly superior to Clair in reserve storage in October of both years and in higher dry-matter concentration in storage tissues in Experiment I only. Winter survival of subarctic-adapted Engmo was vastly superior to the two cultivars from more southern sources. Engmo survived well in both years, averaging 95%, while the more southern-adapted Climax and Clair were virtually eliminated in Experiment I and winter-killed completely in Experiment II (Table 1). These winter survival compari-

sons parallel other results reported for this area (Klebesadel 1970; Klebesadel and Helm 1986).

**Kentucky Bluegrass:** All three Kentucky bluegrass cultivars produced non-heading, leafy tufts during the seedling year. In October, seedlings of Delta were largest, Nugget smallest, and Merion intermediate in size. Nugget leaves were conspicuously darker green than the other cultivars.

Overwintering crown tissues of Merion, the southernmost-adapted bluegrass, were markedly lower in percent dry-matter than Nugget and Delta in October of both years (Table 1), and thus probably more susceptible to freeze injury than the more northern-adapted Nugget (Metcalf et al. 1970). Delta was similar to Nugget in percent dry matter in storage tissues.

At all samplings in both years, Merion was virtually equal to subarctic-adapted Nugget in total level of stored reserves. Both surpassed mid-latitude-adapted Delta in this respect. The high level of reserves expressed by the southernmost ecotype of bluegrass, equaling that of the subarctic ecotype, is a noteworthy exception to an otherwise consistent pattern found in this study. In virtually all other species, there were lower levels of stored food reserves at the final sampling with progressively more southern-adapted ecotypes. Nugget, however, expressed a somewhat greater portion of total reserves during the second two-week growth interval than Merion, especially in Experiment I.

Nugget was outstanding both in winter survival and in vigor of spring growth the following year. Delta and Merion were about equally inferior to Nugget in winter survival and vigor of subsequent spring growth. During more severe winters in southcentral Alaska, Merion and Delta have winter-killed completely when Nugget and other subarctic-adapted Kentucky bluegrass ecotypes sustained minor winter injury (Klebesadel 1984a; Klebesadel et al. 1964). In another study at this location (Klebesadel 1992a), differences in winter survival of these cultivars were much greater in younger seedlings.

**Red Fescue:** None of the three red fescue cultivars exhibited culm elongation or panicle exertion during the seedling year, behavior consistent with other results at this location (Klebesadel 1992a). Although size differences in October were minor, Duraturf seedlings were largest, Arctared intermediate, and Illahee smallest.

Arctared, adapted to subarctic Alaska, surpassed the two more southern-adapted cultivars markedly in dry-matter concentration in crown tissues in October of both years (Table 1). Although Arctared did not exceed the other red fescue cultivars in level of stored reserves after any of the August or September samplings in either year, the subarctic-adapted cultivar was superior to the other two at the October sampling in both years (Figure 2). Moreover, Arctared was superior to Duraturf and Illahee also in winter survival and in subsequent spring vigor of plants (Figures 3, 4).

Mid-latitude-adapted Duraturf surpassed the more southern-adapted Illahee, both in percent dry matter in overwintering tissues and also in level of reserves stored prior to winter.

The degree of winter stress in both tests resulted in greater differences in survival between Duraturf and Illahee than between Arctared and Duraturf. Under more severe winter stress in an earlier study (Klebesadel et al. 1964), however, the inherently greater winter hardiness of Arctared resulted in more conspicuous superiority in winter survival over the less hardy cultivars. In that test, Arctared (evaluated as Accession 339) winter-killed only 16%, while Duraturf and Illahee sustained estimated 88% and 98% winter kill, respectively.

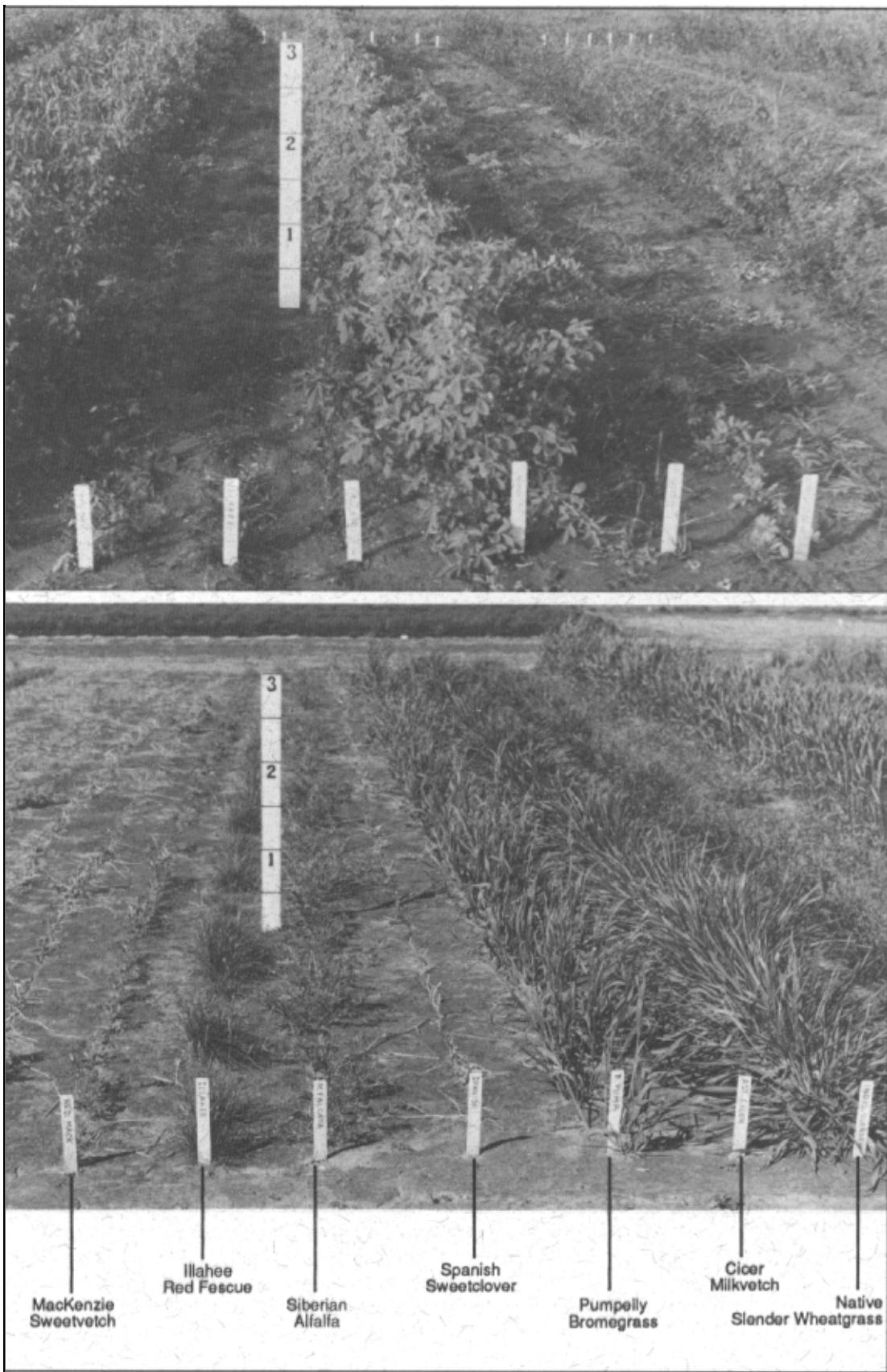
**Slender Wheatgrass:** Three latitudinal ecotypes of slender wheatgrass were compared (Table 1). The strain Alaska-44S was originally believed to be indigenous to Alaska; however, considerable evidence now supports the view that this roadside population was introduced and has been resident in the Matanuska Valley for a sufficient term to undergo considerable adaptational change (Klebesadel 1991).

At the final sampling in October in Exp. II, all plants of Primar were headed with one to six exerted spikes per plant. All plants of Alaska-44S displayed culm elongation with up to three exerted spikes per plant. Plants of Primar were more erect than those of Alaska-44S. Native Alaskan slender wheatgrass, representing material collected in central Alaska ( $64^{\circ}\pm 2^{\circ}\text{N}$ ), produced only prostrate, leafy tufts in October with no culm elongation (Figure 3).

Moreover, in contrast to the green leaves of the other two ecotypes, leaves of the native Alaskan ecotype were yellow-brown by mid-October, indicating early cessation of growth; similar foliar bleaching/browning in autumn has been noted here in northern-adapted ecotypes in other species (Klebesadel 1984b, 1985b, 1993a; Klebesadel et al. 1964; Klebesadel and Dofing 1990).

Alaska-44S did not surpass Primar significantly either year in dry-matter concentration within storage tissues; however, the difference was significant in the two-year means. In the second experiment, the native Alaskan ecotype was significantly higher than Primar in percent dry matter but did not differ from Alaska-44S.

The native ecotype surpassed both Alaska-44S and Primar in total level of stored reserves at all samplings and in slower expression of stored reserves at the final sampling in October. Primar, representing more southern-adapted germplasm originating in Montana (Hanson 1972), exhibited a markedly lower level of reserves in September and October than the more northern-adapted ecotypes. Native Alaskan slender wheatgrass and Alaska-44S sustained no winter kill and produced vigorous growth in the second year



*Figure 3. (Upper): Appearance of seeding-year growth of some grasses and legumes in rows of Experiment II seeded 20 June and photographed 2 October. (Lower): The same rows photographed 12 June of the following spring showing differential winter survival and plant vigor. Numbers on white stake indicate height in feet.*

(Figure 3). Winter survival of Primar was markedly inferior to the two subarctic ecotypes and averaged only 11% over the two tests. Moreover, surviving plants of Primar were visibly inferior in spring vigor (Figure 4) to those of the more northern ecotypes, indicating winter injury of surviving Primar plants.

## LEGUMES

**Alfalfa:** A strain of yellow-flowered “Siberian” alfalfa (*Medicago falcata* L.), perpetuated in Alaska for several decades, was included as a separate species to compare with three strains of variegated alfalfa (*M. sativa* L. = *M. media* Persoon) in the first experiment and with four strains in the second.

“A-syn.B” represents one of the best adapted strains of variegated alfalfa currently available for use in Alaska (Klebesadel 1971c). This strain was derived over approximately two decades of selection from numerous individual plants that displayed superior persistence in many alfalfa trials at the College Experiment Farm near Fairbanks (64.5°N). The cultivars Rhizoma and Rambler from Canada, and California common, completed the sequence of latitudinal ecotypes.

Percent dry matter in taproot-crown segments of the Siberian alfalfa was consistently higher in September and October samplings than in the other alfalfas (Table 1). Siberian alfalfa exhibited a lower level of reserve storage but somewhat more dormancy by early October than the variegated strains.

A-syn.B was similar in percent dry matter in root-crown tissues in October to the two Canadian cultivars, but surpassed the southern-adapted California common in this respect. In both tests, however, A-syn.B possessed a higher level of stored reserves than Rhizoma and also surpassed Rambler when the latter was included. In October of both tests, California common expressed stored reserves virtually equivalent to Rhizoma and Rambler; however, dry matter concentration in taproot-crown tissues of California common was always significantly lower than all other strains in both experiments and in the two-year means.

Siberian alfalfa sustained some winter kill in both tests but averaged 83% survival and clearly surpassed the most winter hardy of the variegated strains. Of the latter, A-syn.B averaged only 26% survival in the two tests but survived significantly better than Rambler, Rhizoma, and California common which were virtually or actually eliminated by winter kill in both tests (Table 1; Figure 4).

Winter stress in these tests was too severe to reveal the well recognized difference in winter hardiness between such relatively winter-hardy cultivars as Rhizoma and Rambler and the nonhardy California common. The present results indicate that the superior winter survival of A-syn.B in this area apparently is

related to relatively higher levels of pre-winter storage of food reserves than occurs in the introduced variegated cultivars compared. In an earlier study (Klebesadel 1971c), A-syn.B was much less injured by artificial freeze stress than Vernal, a Wisconsin cultivar intermediate in winter hardiness in Alaska between Rhizoma and Rambler on the one hand, and nonhardy California common.

Bula et al. (1956), at this location, found that a southern, nonhardy alfalfa (Arizona common) contained higher levels of chemically determined total available carbohydrates (TAC) than relatively winter-hardy Ranger which, in turn, surpassed TAC levels in the more winter-hardy *M. falcata*. Tolerance of strains to artificial freeze stress, however, revealed a reverse relationship by early October with *M. falcata* least injured, mid-latitude-adapted Ranger intermediate, and southern-adapted Arizona common most damaged. Those freeze-tolerance results agree with relative field winter survival of similarly adapted strains in the present study and in other trials at this location (Klebesadel 1971c, 1980, 1985a).

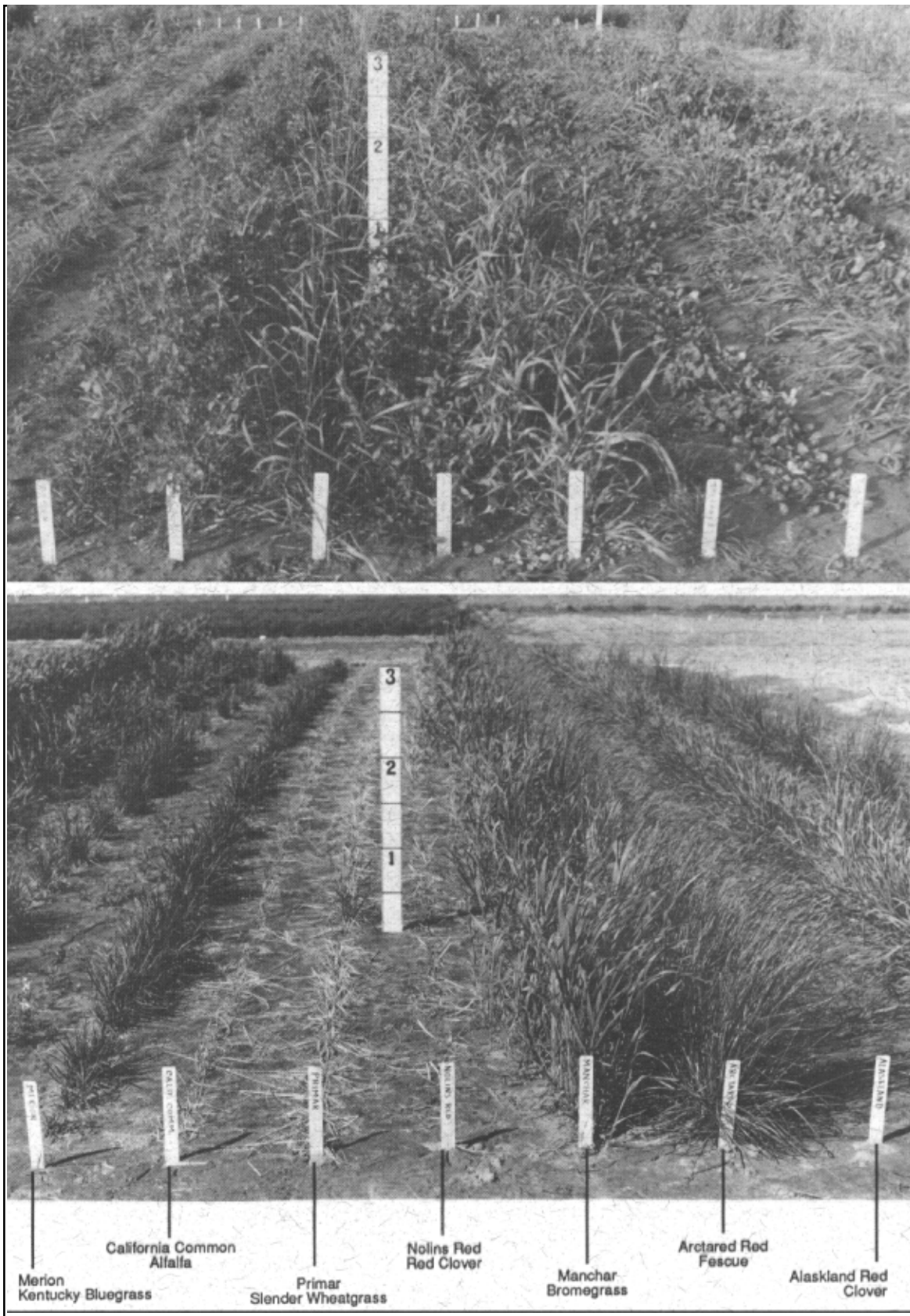
**Red Clover:** Alaskland and Altaswede are mammoth or late types of red clover and Lakeland and Nolin’s Red are medium or early types. At the time of growth cessation at the final sampling in October of both years, seedlings of Alaskland (Figure 4) and Altaswede had produced only basal leaves with no stem elongation or flowering evident. Lakeland plants possessed up to six elongated stems per plant and approximately one-third of the plants had attained flowering stage. Each Nolin’s Red plant possessed two to eight elongated stems and virtually all plants were flowering (Figure 4).

Percent dry matter in Alaskland crown tissues was significantly higher than in any of the other red clovers (Table 1). A trend of decreasing dry-matter concentration in the four red clovers paralleled their decreasing latitudinal origins, though differences were not always statistically significant.

Stored food reserves were highest in Alaskland at the 22-23 August sampling, intermediate in Altaswede, and lowest and similar in Lakeland and Nolin’s Red. At the 18-20 September sampling, Alaskland began to exhibit some dormancy (more reserves expressed in second regrowth period than the other cultivars), and, as in the final (9-11 October) sampling, the two mammoth cultivars surpassed the two medium red clovers in total reserves. Lakeland, more northern-adapted than Nolin’s Red, exhibited a higher level of reserve storage at the final sampling than the Louisiana cultivar.

All of the red clover cultivars winter-killed completely in both tests, regardless of latitudinal adaptation or differences in either dry-matter concentration in root-crown tissues or stored reserves. The variety Alaskland was selected in the Tanana Valley in Interior Alaska (Hodgson et al. 1953). Although mini-





*Figure 4. (Upper): Appearance of seeding-year growth of some grasses and legumes in rows of Experiment II seeded 20 June and photographed 2 October. (Lower): The same rows photographed on 12 June of the following year showing differential winter survival and plant vigor. Numbers on white stake indicate height in feet.*



mum winter temperatures in that area are considerably lower than in southcentral Alaska, snow cover in the Tanana Valley normally accumulates to a considerable depth and persists throughout the winter, insulating overwintering forage plants from low air temperatures.

In the Matanuska Valley, where winter conditions are quite different (Dale 1956; Klebesadel 1974), Alaskland survives winters best when established with a small-grain companion crop harvested to leave a tall stubble (Klebesadel 1992a). Such stubble effectively holds snow cover in place against the evacuation force of strong winter winds, providing vital insulation required by even the most winter-hardy red clovers when grown in this area. In the present study, the rows were swept bare of snow during both winters by occasional strong winds, and plant crowns were exposed to prevailing air temperatures.

In a broadcast-seeded, three-replicate experiment unrelated to the present study and similarly without benefit of companion-crop stubble to retain snow cover, Alaskland survived at 15%, Altaswede at 1%, and LaSalle and Lakeland, both medium-type cultivars, winter-killed completely. Though very poor overall survival, these percentages generally parallel the indicators of winter hardiness (percent dry matter values and levels of stored reserves) found in the present study (Table 1).

**Sweetclover:** Two biennial white cultivars, of Canadian and conterminous U.S. origin, were compared in the second experiment only. The Canadian cultivar Arctic was significantly higher in percent dry matter in root-crown tissues in October than the more southern-adapted Spanish (Table 1). The relative dry-matter concentrations are consistent with artificial-freeze test results with the same cultivars in earlier studies (Hodgson and Bula 1956; Klebesadel 1992c, 1993b) at this location.

The two sweetclovers did not differ in reserves expressed following the August sampling (Figure 2); however, at both later samplings Arctic surpassed Spanish. Both cultivars showed evidence of assumed dormancy in the September and October samplings when plants continued a slow release of reserves over several weeks.

Relative winter survival of Arctic at 18% and Spanish at 0% (Table 1; Fig. 3) was consistent with freeze-tolerance tests and other results at this location (Hodgson and Bula 1956; Klebesadel 1992c, 1993b).

**Milkvetch:** (*Astragalus* species): Three species of milkvetch were included as individual entries in the second experiment with no comparisons of latitudinal ecotypes within any of those *Astragalus* species. The cicer milkvetch strain used in this test, identified as P-498, was brought to the United States around 1935 from the Stockholm Botanical Gardens (ca. 59°N). Since that time it has been perpetuated in the Pacific Northwest. Inasmuch as this introduction very likely

has undergone adaptational change toward harmony with climatic conditions in the Pacific Northwest, the cicer milkvetch was considered adapted to that latter area (Table 1).

All three species of milkvetch grew very slowly as seedlings, but height in mid-October of the imported *A. cicer* (three to six inches) was greater than the two native Alaskan milkvetches (one to three inches). Alaskan *A. harringtonii* and the cicer milkvetch were similar in percent dry matter in root-crown tissues in October and both were significantly higher than *A. williamsii* (Table 1).

Stored food reserves expressed at the first sampling (22-23 August) were progressively higher from entries originating from progressively higher latitudes (Figure 2). Reserves differed little in each of the three milkvetches between the September and October samplings. Rates and amounts of etiolated growth of the three milkvetch species are difficult to compare with assurance. Although the two Alaska species displayed higher total reserve levels, the species that were highest in percent dry matter (*A. harringtonii* and *A. cicer*) gave evidence of greatest dormancy. Moreover, the long term during which etiolated growth was expressed by *A. cicer* infers a considerable release of reserves as unmeasured respiration products.

The strain of *A. harringtonii* used, indigenous to the Matanuska Valley, survived the winter somewhat better (97%) than *A. williamsii* (70%) from interior Alaska. Imported *A. cicer*, adapted at more southern latitudes, winter-killed completely. Although both of the native Alaskan milkvetches surpassed all of the introduced legumes in winter survival, the extremely slow seedling growth of these native milkvetches suggests they possess little potential for practical use as cultivated forage crops.

**Oxytropes** (*Oxytropis* species): The mature plants of *O. foliolosa*, from which seed was collected at two widely separated locations for use in this test, were indistinguishable in size and general appearance. However, seedlings of the arctic ecotype, grown from seed collected at Umiat (69.5°N) in far-northern Alaska, achieved conspicuously less growth in size in the test than those from seed collected at the Little Nelchina, Alaska site (62°N).

The slower growth of the northernmost ecotype probably was a response to shorter photoperiods than prevail during the growing season at Umiat. Photoperiods at that location, 200 miles north of the Arctic Circle and about 550 miles north of the experimental site, are 24 hours in duration from 20 May to 25 July, and exceed 20 hours for most of the growing season. In contrast, photoperiods at Palmer decrease from 19.5 to 11 hours during the period 20 June to 1 October. Exposure to abnormally shortened photoperiods during the growing season is known to cause poorer growth of woody species at more southern latitudes

than their area of adaptation (Vaartaja 1954).

Percent dry matter in root-crown tissues was similar in the two ecotypes (Table 1), and they differed little in total amounts of stored reserves measured at each of the three samplings (Figure 2). Some onset of dormancy was apparent in both ecotypes at the 18-20 September sampling. Rate of food-reserve expression was similar for the two ecotypes at the second sampling but differed considerably at the 9-11 October sampling. In October, the southcentral Alaska ecotype had assumed considerably greater dormancy, as indicated by slower rate of reserve expression, than the arctic ecotype.

Curiously, the more northern-adapted ecotype from Umiat didn't survive the winter as well (21%) as the one that originated from near the test site (83%). Relative severity of winter conditions (winter winds, snow cover, etc.) on overwintering plants at Umiat, in comparison to the Matanuska Research Farm, is unknown.

Certainly the arctic ecotype, when grown in the Matanuska Valley, was divorced from accustomed pre-winter environmental conditions under which it normally undergoes successful preparation for winter. Results somewhat parallel to the poorer winter survival of the arctic oxytrope were noted earlier (Klebesadel 1971b, 1973b) at this location when native pumpelly bromegrass was subjected to artificially shortened photoperiods (lengthened nyctoperiods) for several weeks prior to onset of winter (conditions akin to growing the arctic ecotype in subarctic Alaska). In spring of the following growing season, that treatment (compared to the grass being exposed to normal subarctic pre-winter photoperiod / nyctoperiod) was harmful in (a) greatly diminishing heading, and (b) causing somewhat stunted, less vigorous growth indicative of winter injury (Klebesadel 1971b, 1973b, 1985c).

It is well established that plants grown far north of their latitude of adaptation are disadvantaged by unaccustomed interrelationships of pre-winter photoperiod / nyctoperiod and growing-season termination, to the extent they are not induced to prepare adequately for winter stresses and therefore display poor winter survival. The opposite scenario apparently is operative also. The meager results with the arctic oxytrope, the aforementioned response of pumpelly bromegrass, and strong evidence in woody species (Vaartaja 1954) all indicate that ecotypes may also be disadvantaged if grown in an unaccustomed photoclimate far south of their latitude of adaptation.

Habj rg (1979) in Norway reported poor winter survival of arctic ecotypes of Kentucky bluegrass grown south of their region of adaptation. That change in growth environment in Norway, as with the oxytropes in Alaska, involved not only transfer to more southern latitudes but also from a continental to a maritime winter climate. This change exposes plants to unac-

customed winter stresses (Klebesadel 1985c).

The Umiat oxytrope, like Engmo timothy, represents a far-northern, arctic ecotype brought south over several degrees of latitude to a subarctic area. However, the pattern of winter survival in *Oxytropis* did not parallel that of timothy. In the latter species, excellent survival occurred with Engmo, a cultivar that originated from a latitude in Norway similar to that of Umiat, Alaska.

**Sweetvetch** (*Hedysarum* species): Two species of *Hedysarum*, both native in the Matanuska Valley, were included in the second experiment (Table 1). Both species of sweetvetch displayed very slow seedling growth in comparison to the cultivated legumes (alfalfa, red clover, and sweetclover).

In the 22-23 August sampling, alpine sweetvetch (*H. alpinum*) already possessed considerable dormancy as evidenced by the slow expression of reserves over several two-week growth periods before exhaustion. An outward indication of early onset of dormancy in *H. alpinum* was a conspicuously early senescence and browning of foliage in September, very different from all other legumes compared. Mackenzie sweetvetch (*H. mackenzii*) displayed little dormancy, as indicated by rates of expression of reserves, even at the October sampling, although a marked increase in total reserves in this legume was noted between the 22-23 August and the 18-20 September samplings.

At the 9-11 October sampling, *H. alpinum* surpassed *H. mackenzii* in degree of dormancy, level of reserves stored, and in significantly higher dry-matter concentration in taproot-crown tissues (33.2% vs. 27.3%). This superiority in indicators of hardening behavior in *H. alpinum* during autumn was reflected in 100% winter survival of that species in contrast to only 64% survival in *H. mackenzii*. Despite its fair-to-good winter survival, rate of spring growth of MacKenzie sweetvetch was very slow, compared to the winter-hardy grasses (Fig. 3).

Both species of *Hedysarum* are widespread in Alaska, ranging from the southcentral area to the arctic coastal plain (Hulten 1968). As with several other native legumes, including the aforementioned Harrington milkvetch and foliose oxytrope, both species of *Hedysarum* tend to be pioneer species in vegetational advance into disturbed sites, as along roadway verges, areas exposed by glacial retreat, or changing river channels. There their nitrogen-fixation capabilities permit growth in relatively sterile sandy and gravelly substrates (Allen et al. 1963; Klebesadel 1971a, 1978). The winged, papery seed pods (disarticulating articles in a loment) of both species are effectively distributed by wind and water.

Both have pink flowers; the larger ones of *H. mackenzii* suggest some potential of that species as an ornamental. The very slow seedling growth of both

species augurs poorly for their consideration as cropland legumes; however, both species might be useful for artificially guided revegetation of disturbed areas (Klebesadel 1973a).

**Lupine** (*Lupinus* species): The lupine (*L. polyphyllus*), one of three species common in Alaska (Hulten 1968), was grown from seed collected in the Matanuska Valley. Only this species besides *H. alpinum* displayed any dormancy, as indicated by slow expression of stored reserves, at the first sampling 22-23 August (Figure 2). At the September and October samplings, onset of more pronounced dormancy permitted only a small percentage of stored reserves indicated as present in August to be expressed as etiolated growth.

*L. polyphyllus* winter-killed 100%, despite its high degree of dormancy. The considerable difference in winter survival between *L. polyphyllus* and other native Alaskan legumes undoubtedly is related to differential winter exposure of the habitats typically occupied by those respective species. In its natural habitat, this lupine occupies sites, often in dense woods, where snow cover remains in place during winter. In the present field experiment on open cropland exposed to winter winds (Klebesadel 1974), absence of insulating snow cover probably was responsible for the total winter kill, despite this being a subarctic-adapted legume.

A parallel to this is seen in disparate winter survival of a subarctic-adapted grass, drooping woodreed (*Cinna latifolia* [Trev.] Griseb.) in dissimilar environments. This grass, common locally in dense forests, survives well in that protected habitat but winter-kills when grown in cropland fields where plants are subjected to greater exposure to winter stresses (unpublished information, Alaska Agric. and Forestry Exp. Sta.)

## Native Alaskan Species

Within the indigenous Alaskan flora, there are both grasses and legumes that are extremely winter hardy in this area. Of legume species so far considered, however, other agronomic deficiencies preclude their practical utilization as forage crops (Klebesadel 1971a). Although poorly suited for cropland forage production, wild-growing legumes nonetheless are valuable sources of grazable herbage and edible seeds for wildlife (Graham 1941).

Additionally, the combination of their widespread occurrence throughout Alaska (Hulten 1968) and their widely varied habitat affinities (Klebesadel 1963) encompassing wet to dry sites, shorelines to high altitudes, sands and gravels to heavy soils, open sites to shaded woodlands, etc., ensure that species and ecotypes of native legumes exist for seeding in virtually any situation susceptible to natural revegetation or those requiring artificially guided ecologic repair (Klebesadel 1973a). They serve as attractive ground cover, control wind and water erosion, and contribute

symbiotically fixed nitrogen that over time becomes available to associated non-leguminous species, substantially circumventing the need for ongoing fertilizer applications for vigorous growth. Moreover, acquiring insights into factors that contribute to their generally good winter hardiness may assist in strategies for developing winter-hardy strains of introduced forage legumes for use in Alaska.

Native Alaskan *H. alpinum* in particular, and to a somewhat lesser extent, *H. mackenzii*, *O. foliolosa*, and *A. harringtonii*, represent pioneer legume species that frequently are among the first plants to colonize riverbed gravels, areas exposed by glacial retreat, and other sites lacking other vegetation (Klebesadel 1963, 1971a). These relatively barren habitats, when subjected to strong winter winds, retain little insulating snow cover, in contrast to areas supporting a diversified flora. Such exposure to winter stresses and attendant natural selection for tolerance to low temperatures, probably account for the superior survival of those legumes in the unprotected field areas occupied in these tests. Conversely, total winter kill of the lupine and considerable winter kill of Williams milkvetch is believed due to their inability to tolerate cold and other winter stresses in the open field environment since their normal habitat is in more protected environs with mixed vegetation that retains insulating snow cover.

The lupine compared in the second experiment exhibited a high degree of dormancy, yet winter-killed 100% in the exposed field habitat. This suggests that the identified dormancy is involved with winter hardiness, but separate from freeze tolerance. It is known from other studies (Klebesadel 1993b) that shortening photoperiods/lengthening nyctoperiods are the causal stimulus for development of the dormancy condition, rather than seasonally lowering temperatures.

The dormancy characteristic, common to many of the legumes in this study, was especially pronounced in the lupine, the alpine *Hedysarum*, and the foliose oxytrophe from southcentral Alaska. This condition has also been noted to occur conspicuously, and has been extensively examined, in a naturalized local Matanuska Valley roadside strain of biennial whitesweetclover (Klebesadel 1992c).

All of the legumes that strongly exhibited this pre-winter dormancy have evolved to possess this characteristic in southcentral Alaska. That dormancy may simply be a restrictive influence which prevents basal buds from elongating until the following year. Alternatively, the consistent appearance of this phenomenon in several legume species suggests that it may be a selectively acquired mechanism of some value in winter survival, perhaps operative in protecting plants against harmful de-hardening effects of mid-winter thaw periods common in this area. Winter conditions in this area, transitional between maritime and interior climatic effects (Dale 1956), are characterized by occasional mid-winter thaws and refreezings with wide oscillations of temperature (Klebesadel 1974).

Legumes will maintain a winter-hardened, freeze-tolerant condition for many months if kept at a constant low temperature just below the freezing point (Jung and Smith 1960). Conversely, thawing periods during winter are harmful to maintenance of the winter-hardened condition in plants (Dexter 1941).

Dexter (1941) also reported that plants caused to dehardened (lose freeze tolerance), as a result of warm temperatures during winter, were able to re-harden with return to low temperatures only if high levels of carbohydrate reserves were available. This may be one of the factors contributing to the superior winter hardiness (Table 1) of northern-adapted ecotypes that generally possessed the highest levels of stored food reserves near the onset of winter (Figure 2).

### Adaptive Modification

Aspects of adaptive change within formerly temperate-adapted introductions toward harmony with subarctic climatic conditions are indicated in this study. Selective modification for superior winter survival at this latitude is apparent in A-syn.B alfalfa and in the introduced, subarctic ecotype (Alaska-44S) of slender wheatgrass, when compared with more southerly-adapted strains within the two respective species. Similar adaptive modification has been noted in biennial yellow sweetclover (*M. officinalis* [L.] Lam.) that was subjected to natural-selection pressures over several years near the Arctic Circle (Klebesadel 1985a, 1992b).

The concepts and mechanisms operative in such adaptive modification have been reviewed by Stebbins (1950), Wilsie (1962), and Mason and Stout (1954). In concert with elements of physiological adaptation noted in the present study, Mason and Stout state: "The interbreeding population with its varied individuals serves as the reservoir of genetic variables, and the environment, through natural selection, selects variables favorable to it . . . climatic races (ecotypes) owe their precise capacity for survival in a given climatic complex to genetically controlled characters which, in turn, control physiological processes . . . With respect to climatic races . . . there has been a synchronization with the diurnal and seasonal periodicities of the environment."

Subarctic environmental stresses have imposed selectivity toward better adaptation to northern climatic patterns during many generational cycles. The resultant populations of each are capable of more efficient food-reserve storage and logically more appropriate physiologic responses to the unique interrelationships of photoperiod / growing-season termination peculiar to subarctic latitudes (Klebesadel 1985c, 1992b). This adaptive modification is expressed in superior winter hardiness, indicative of physiologic harmony with environmental conditions and critical to perpetuation of the ecotype population.

## CONCLUSIONS

These results reveal the importance of high-latitude adaptation for successful winter survival in this subarctic area. Of all cultivated species of grasses and legumes evaluated experimentally over many years in subarctic Alaska, the species included in this study were among the most winter hardy. However, the present results reveal that, for this area, a wide diversity in winter hardiness exists within each of the major crop species tested.

Winter survival of ecotypes within each species was strongly influenced by latitude of origin or adaptation. The northernmost-adapted ecotypes, that displayed superior winter survival within each species, possessed either highest level of pre-winter food-reserve storage or highest percent dry matter in overwintering tissues just prior to onset of winter conditions. Usually both criteria were associated and, in addition, best winter survival within each species often was associated with evidence of greatest dormancy as indicated by slowest release of stored food reserves when grown to exhaustion indoors in a warm, dark chamber.

The actual levels of stored food reserves measured were unrelated to relative winter hardiness among species. For example, reserve levels in the two northernmost-adapted red clovers, which consistently winter-killed completely, were higher than those measured in the two northern-adapted slender wheatgrasses which survived without injury. This emphasizes that other factors in addition to food reserves, including levels of freeze tolerance developed, determine winter survival differences among species.

Winter stress on grasses was inadequate in these tests to differentiate among the northernmost-adapted, and therefore most winter-hardy, ecotypes of brome-grass, Kentucky bluegrass, red fescue, and slender wheatgrass. However, among the southernmost-adapted ecotypes of the same grasses, Kentucky bluegrass and red fescue cultivars were clearly more winter hardy than those of brome-grass, timothy, and slender wheatgrass.

The most winter-hardy ecotypes of introduced grasses were superior in survival to the most winter-hardy introduced legumes; these findings are consistent with those of Ouellet (1976) in Canada. These results parallel actual agricultural practice in subarctic Alaska where winter hardiness of perennial forages is a dominant requisite and grasses are relied upon currently to the virtual exclusion of biennial and perennial legumes.

Within the introduced legumes, the northernmost-adapted ecotypes of sweetclover and alfalfa were more winter hardy than red clover and cicer milkvetch. The relative survival of sweetclover, alfalfa, and red clover

in this study agrees with a similar ranking of cold tolerance in locally adapted ecotypes of those legumes in Wisconsin (Bula and Smith 1954) and with actual winter survival at numerous Canadian locations (Ouellet 1976). Bula and Smith (1954) reported that red clover not only developed less freeze tolerance than alfalfa and sweetclover, but also showed greater respiratory loss of TAC from mid-October to late March. This indicated a higher rate of winter metabolic activity by red clover than the other two legumes which, along with more exposed overwintering tissues, also could contribute to poorer winter survival.

Of the introduced grasses from Canada and the conterminous states, species with primarily subterranean overwintering tissues (bromegrass, Kentucky bluegrass, red fescue) generally survived the winters well; in contrast, those with predominantly above-ground overwintering tissues (timothy, slender wheatgrass) did not. That association of better winter survival of plants with more protected overwintering tissues has been noted elsewhere (Smith 1964b).

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