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Bromegrasses

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The bromegrasses belong to the genus *Bromus* of which there are some 100 species (Gould & Shaw, 1983). The genus includes both annual and perennial cool-season species adapted to temperate climates. Hitchcock (1971) described 42 bromegrass species found in the USA and Canada of which 22 were native (Gould & Shaw, 1983). Bromus is the Greek word for oat and refers to the panicle inflorescence characteristic of the genus. The bromegrasses are C3 species (Krenzer et al., 1975; Waller & Lewis, 1979).

Of all the bromegrass species, only two are cultivated for permanent pastures to any extent in North America. Smooth bromegrass is by far the most important and is widely grown throughout the northern half of the USA and into Canada. It also is known as Russian brome, Austrian brome and Hungarian brome (Carlson & Newell, 1985). Meadow bromegrass (*B. riparius* Rehm.) is the only other introduced perennial bromegrass commonly grown as a pasture grass. The binomial *B. biebersteinii* R. & S. has been incorrectly applied to the meadow bromegrasses in North America until recently. Based on Tsvelev's (1984) description of the species, most of the North American cultivars and plant introduction that have been described as *B. biebersteinii* should be classified as *B. riparius*. Meadow bromegrasses are grown primarily for pasture in the northwestern states of the USA and Canada.

Several perennial bromegrasses are important native range grasses in the intermountain region of the western USA. These include mountain bromegrass, California bromegrass, nodding bromegrass, and fringed bromegrass (Carlson & Newell, 1985; Stubbendieck et al., 1992).

[1] Common names for plants have been used throughout the chapter. Refer to the appendix for the scientific name.

Annual bromegrasses are primarily regarded as weedy species, but can be an important source of early spring forage under range conditions. Downy bromegrass, Japanese brome, hairy chess, cheatgrass, ripgutgrass, and soft chess are annual bromegrasses that can be an important source of forage under range conditions. Rescuegrass and field bromegrass are two introduced bromegrasses that are used for forage to a limited extent (Carlson & Newell, 1985).

SYSTEMATICS AND MORPHOLOGY

The bromegrasses (*Bromus* spp.) belong to the subfamily Pooideae of the Poaceae (Watson & Dallwitz, 1992). They are assigned to the Bromeae tribe which is characterized by a chromosome number of $x = 7$ with a mean diploid 2c DNA value of 9.8 pg with a range of 6.5 to 12.5 pg (Watson & Dallwitz, 1992). Bromegrasses have a panicle inflorescence with multiple-flowered spikelets, unequal glumes with one or both shorter than the lowest lemma (Watson & Dallwitz, 1992; Gould & Shaw, 1983; Tsvelev, 1984). The *Bromus* genus consists of species with leaves that generally have broad, flat, and thin blades and closed sheaths. Spikelets are from 13 to 45 mm in length and glumes have one to five nerves, are unequal in length, and are generally without awns. Disarticulation occurs between florets and above the glumes. Lemmas have five or more nerves and typically a single awn. The palea is generally shorter than the lemma and is adnate to the caryopsis (Gould & Shaw, 1983; Hitchcock, 1971).

Proposed evolution schemes in the genus are based on taxonomy, chromosome size, polyploidy, and hybridization among and within subgenera (Armstrong, 1991; Walton, 1980). The evolutionary relationships among bromegrasses still have many unresolved areas and the nomenclature for *Bromus* varies with authority. According to Armstrong (1991) bromegrasses were subdivided into six sections by P. Smith, subgenera by G.L. Stebbins, and genera by N.N. Tsvelev. The grouping of species within each section, subgenera, or genera are similar (Armstrong, 1991). Smooth bromegrass, meadow bromegrass, and pumpelly or arctic bromegrass are in Tsvelev's (1984) genus *Bromopsis*. Reported chromosome numbers for B. inermis (smooth bromegrass) are $2n = 28$, 42, and 56 while *B. riparius* (meadow bromegrass) has $2n$ numbers of 56 and 70 (Tsvelev, 1984; Hill & Myers, 1948; Carnahan & Hill, 1960; Armstrong, 1987). Stomatal size is associated with ploidy level in smooth bromegrass, high ploidy levels have larger stomates (Tan & Dunn, 1973).

The commonly grown form of smooth bromegrass is an autoallooctaploid with a chromosome number of $2n = 56$ while the tetraploid ($2n = 28$) is an allotetraploid (Armstrong, 1973; Elliot & Wilsie, 1948; Hill & Myers, 1948; Carnahan & Hill, 1960). In polyhaploid, 28-chromosome forms, Carnahan and Hill (1960) found predominately bivalent chromosome pairing at meiosis in smooth bromegrass. When the chromosome numbers were doubled, the resulting plants crossed readily with normal 56 chromosome plants. The common octaploid form of smooth bromegrass is irregular at meiosis and forms predominately quadravelents and bivalents at meiosis (Elliott & Love, 1948; Hill & Carnahan, 1957; Armstrong, 1973). In studies using a chlorophyll mutant, Ghosh and Knowles (1964) demonstrated that the trait was inherited on a tetrasomic basis. The inheritance patterns for the mutant indicated an intermediate chromosome-chromatid type of segregation. Schulz-Schaeffer (1960) also reported two pairs of chromosomes bearing large satellites that appeared to be identical. These and other cytogenetic studies (Armstrong, 1979, 1982, 1991) support the hypothesis that the genomic formula for the tetraploid and octaploid cytotypes of smooth bromegrass are AABB and AAAABBBB, respectively. Research by Armstrong (1979) indicates that the A and B genomes are closely related. Cultivars of meadow bromegrass have $2n = 70$ chromosomes (Knowles et al., 1993).

Interspecific hybridization between *B. erectus* Huds. ($2n = 28$) and smooth bromegrass demonstrated that the genome of *B. erectus* was one of the parental genomes of smooth bromegrass and was designated the A genome (Armstrong, 1991; Walton, 1980). A similar genome is found in the diploid form of *B. variegatus* Bieb. and a diploid that resembles smooth bromegrass (Armstrong, 1991). The source of the B genome is unknown (Armstrong, 1991). Intergeneric hybrids between smooth bromegrass and and *B. pumpellianus* spp. *dicksonii* had regular chromosome pairing with a low frequency of abnormalities indicating that the chromosomes of the two species are very similar, likely differing only by inversions or translocations (Armstrong, 1982).

Some of the taxonomic and phylogenetic problems of *Bromus* may be resolved using molecular genetic approaches including restriction mapping of chloroplast DNA (Pillay & Hilu, 1990). The chloroplast restriction patterns for smooth bromegrass, meadow bromegrass and pumpelly bromegrass are identical (Pillay & Hilu, 1990) which supports the previous research using more conventional approaches. Conventional cytogenetic approaches may be hindered in *Bromus* because genes controlling chromosome pairing during meiosis appear to be at low frequency in the diploid populations and may not be fully functional in intraspecific hybrids, limiting the utility of intraspecific hybridization in determining phylogenetic relationships (Armstrong, 1991). Genes controlling pairing are present and functional in allotetraploid and higher ploidy levels in *Bromus* (Armstrong, 1991).

CENTERS OF ORIGIN

Smooth bromegrass and meadow bromegrass are of Eurasian origin (Tsvelev, 1984). Tevelev (1984) indicates that smooth bromegrass is a very polymorphic species and could be divided into several subspecies or ecotypes that are related to their origin. Occurrence of reasonably distinct types within the species smooth bromegrass that differ in morphology and adaption was first described by Zerebina (1931, 1933, 1938) whose research was subsequently summarized by Knowles and White (1949). The following is a condensed version of their summary of Zerebina's research. Zerebina collected bromegrass strains from different districts of the USSR and studied this material and small collections from western Europe, USA, and Canada at the plant breeding station of Detskoe Selo (60°N lat) and Kammenaya Steppe (51°N lat). Zerebina recognized two main ecological-geographical groups: (i) the "meadow" group or northern climatype, and (ii) the "steppe" group or southern climatype. Descriptions of these groups correspond to the northern and southern types of smooth bromegrass later recognized in North America (Newell & Keim, 1943). Zerebina observed that the steppe group had a deeper root system and the canopy height of vegetative tillers was one-half that of the reproductive tillers whereas in the meadow group, the main level of vegetative tillers approached two-thirds that of the reproductive tillers. The steppe group also had coarser leaves that were shorter, narrower, and more erect than in the meadow group. The meadow types were found from Murmansk in the north to the Caucasus in the south although south of the central Chernozem region, they were found only in valleys and moist habitats. The steppe type was found with the meadow type in the central Chernozem region and was the principal ecotype in the dry steppe areas of the mid- and lower Volga districts, Kazakstan, the northern Caucasus, the eastern Ukraine, and the southern Altai regions of USSR. Meadow bromegrass is native to southeastern Europe, the Caucasas, Turkey, and central Asia (Knowles et al., 1993).

DISTRIBUTION AND ADAPTATION

Smooth bromegrass is widely adapted because of the ecotypic variation that exists in the species in its native range. Smooth bromegrass was introduced into the USA and Canada in the 1880s (Newell, 1973; Carlson & Newell, 1985). The first introduction was by the California Experiment Station in 1884 (Newell, 1973). Major introductions were from central Europe including Hungary, northern Germany, and the Penza region of Russia (Newell, 1973). By the late 1890s bromegrass was being grown in the midwestern USA and Canada. The initial spread and distribution of smooth bromegrass in North America was based on the simple increase and distribution of the introduced strains. Smooth bromegrass was one of the few cool-season grasses that persisted during the drought years of the 1930s, which lead to renewed interest in the species and to the establishment of smooth bromegrass breeding programs at several experiment stations and with the research agencies of the U.S. Department of Agriculture and the Canadian Department of Agriculture. The current adapted area of use of bromegrass is the area where bromegrass cultivars are more suitable for specific grassland uses than are cultivars of other cool-season species. Utilization of meadow bromegrass in North America began in 1966 with the release of the cultivar Regar which was selected from a plant introduction from Turkey (Knowles et al., 1993; Hanson, 1972).

In North America, smooth bromegrass is best adapted to regions north of 40°N lat and east of 100°W long that have 500 mm or more annual precipitation or in areas that have similar temperature ranges because of elevation. In Europe and Asia bromegrass is found primarily in areas north of 40°N lat except in arctic areas and at higher elevations in mountainous areas (Tsvelev, 1984). Smooth bromegrass can survive periods of drought and also extremes of temperature. It is not as well adapted south of 40°N lat in North America because of disease problems. It is better adapted north of 40°N lat because of its superior cold tolerance and winter hardiness. Smooth bromegrass is more winter hardy and drought tolerant than orchardgrass and ryegrasses. Wheatgrasses are better adapted west of 100°W long because of better drought tolerance. In its primary area of use, smooth bromegrass is more productive than Kentucky bluegrass or timothy and it does not have the alkaloid problems of reed canarygrass. Timothy is more widely used in the northeastern USA than smooth bromegrass, however. Meadow bromegrass is not as winter hardy or drought tolerant as smooth bromegrass and is adapted to the cooler, more moist regions within the adaptation range of smooth bromegrass (Knowles et al., 1993). It has been used in irrigated pastures in Idaho, Wyoming, and Montana, USA, and in Alberta and Saskatchewan, Canada (Knowles et al., 1993).

Knowles and White (1949) compared southern and northern types of smooth bromegrass at several sites in Canada and found no distinct differences in forage yield between types. At some sites southern types of smooth bromegrass were best while at other sites, northern types were superior. In Canada, northern types produced about twice the seed yield of southern types. Northern types of smooth bromegrass flowered about 4 d earlier. Other characteristics of northern and southern types as indicated by Zerebina were confirmed by Knowles and White (1949). They also indicated that southern strains had less anthocyanin development in panicles than northern strains but both types had similar self and cross fertility. Controlled matings confirmed that the two types of bromegrass are cross-compatible. Southern types were as winter hardy in Canada as northern types. The southern types of smooth bromegrass are more drought and heat tolerant than the northern types (Newell, 1973; Carlson & Newell, 1985).

Smooth bromegrass can be grown on an array of soil types as long as they are well drained, but is best adapted to loam soils of the former prairie or steppe regions of North America (Carlson & Newell, 1985). Stands will not persist on wet sites. Bromegrasses that are highly regarded in other areas of the world often are unadapted to the primary area of adaptation of smooth bromegrass. For example, in yield trials in Iowa and Wisconsin, 'Matua' rescuegrass did not survive winter (I.T. Carlson & M.D. Casler, personal communication).

GENERAL DESCRIPTION

Smooth bromegrass is a leafy, tall-growing, sod-forming perennial cool-season (C3) grass. The flowering culms are 0.5 to 1.0 m in height (Fig. 17–1). The inflorescence is a panicle that is erect and 7 to 20 cm long with whorled branches, and becomes contracted and purplish brown at maturity (Stubbendieck et al., 1992; Hitchcock, 1971). The spikelets are terete, pointed, 5- to 13 flowered and from 1.5- to 3.0 cm long. The lemmas are awnless or with a very short awn (1–2 mm). Glumes are papery, lanceolate, and unequal. The first glume is one-nerved, 4 to 6 mm long while the second glume has three nerves and is 0.6 to 1.0 cm long (Stubbendieck et al., 1992; Hitchcock, 1971). The sheath of smooth bromegrass is closed, glabrous to scabrous and predominately veined. The blade is flat, 15- to 40 cm long and 0.5- to 1.5 cm wide, largely glabrous with scabrous margins and a conspicuous "W" leaf constriction on the upper surface about one-third the distance from the tip. The ligule is membranous, 0.5 to 2.5 mm long,

Fig. 17–1. Smooth bromegrass (*Bromus inermis* Leyss.).

and minutely ciliate-erose. Smooth bromegrass has very vigorous, creeping rhizomes. Smooth bromegrass seedlings are generally pubescent but mature plants have smooth stems and leaves (Knowles, 1980). Inermis means "unarmed" and refers to the awnless nature of the spikelet. Detailed anatomical studies of bromegrass were conducted by Knobloch (1944). In general, the anatomy of smooth bromegrass is similar to other cool-season grasses.

Meadow bromegrass is fairly similar in appearance to smooth bromegrass (Fig. 17–2). The principal distinguishing differences between smooth bromegrass and meadow bromegrass are the awns and leaf pubescence on meadow brome-

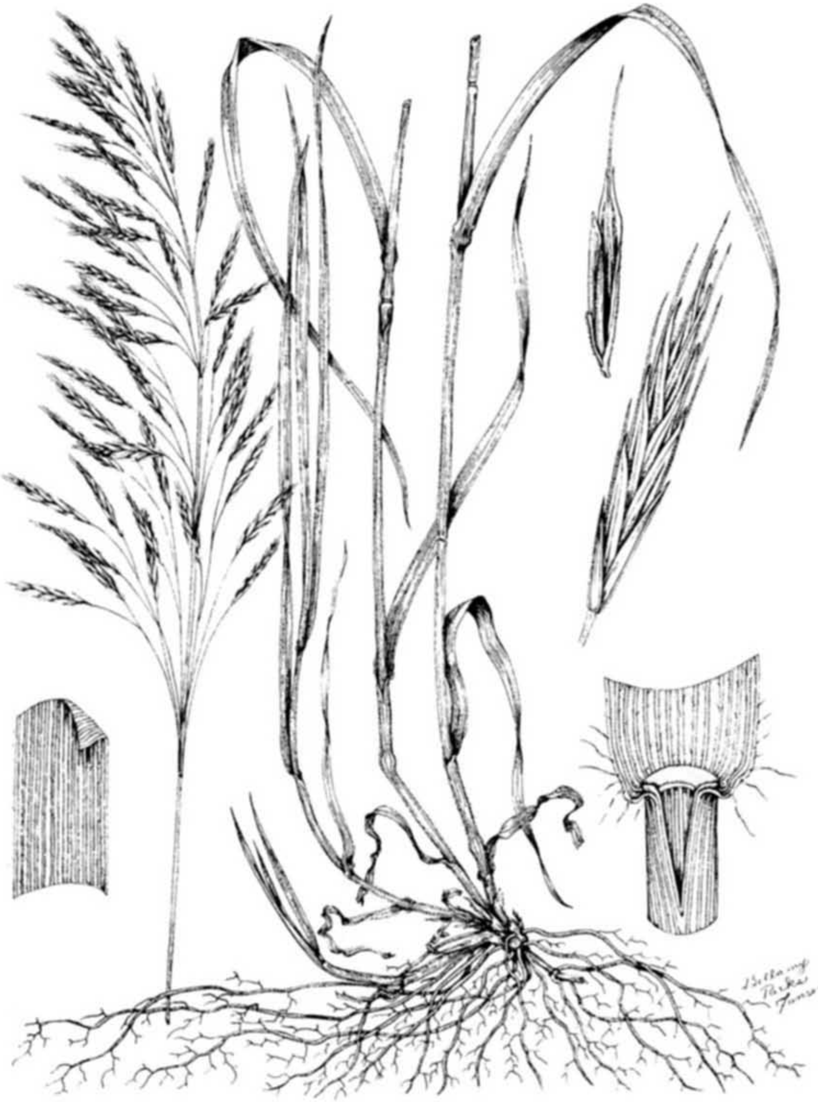

Fig. 17–2. Meadow bromegrass (*Bromus riparius* Rehm.).

grasses (Knowles et al., 1993; Tsvelev, 1984). Meadow bromegrass also has much shorter rhizomes than smooth bromegrass and it is more caespitose. It has narrower leaves than smooth bromegrass, the leaves have pubescence which is particularly noticeable on the margins, stems and seeds also may have some pubescence (Knowles et al., 1993). Leaves also tend to be more lax than those of smooth bromegrass. Meadow bromegrass has a divaricately branched panicle and is more caespitose than bieberstein bromegrass. The panicles of bieberstein bromegrass are more racemelike with short vertical branches that are shorter than the spikelets (Tsvelev, 1984).

IMPORTANCE TO AGRICULTURE

Smooth bromegrass has numerous attributes that contribute to its wide distribution and use in grassland agriculture. It is an excellent seed producer and produces reliable seed yields year after year. Its seed size is large in comparison to that of many forage grasses (300 000 seeds/kg) (Wheeler & Hill, 1957). Smooth bromegrass has excellent seedling vigor and establishes readily if planted in early spring or in the fall. Once established, bromegrass is very persistent in its area of adaptation. Bromegrass has very vigorous rhizomes that can rapidly fill in areas with thin stands.

Smooth bromegrass has three primary uses: pasture, hay, and soil conservation. In its primary area of adaptation, smooth bromegrass will outyield other cool-season grasses with the possible exception of reed canarygrass (Marten & Donker, 1968). It has been preferred to reed canarygrass for use in pastures and hayfields because it does not have alkaloid or other antiquality problems. In pastures it is often used in combination with legumes such as alfalfa or clover (Newell, 1973; Carlson & Newell, 1985). It is rarely used in pure stands as a hay crop, but in many parts of the Midwest it is used in mixtures with alfalfa. It aids in soil stabilization and it fills in spots in fields where alfalfa losses occur.

Smooth bromegrass is probably the most important grass for soil erosion purposes in the north central states. Throughout this region, smooth bromegrass is used on roadsides and other similar areas for erosion control. It also is widely used for grass waterways and for borders of fields. In recent years, some state highway departments have been promoting the use of native prairie grasses for roadside plantings, but smooth bromegrass still is the predominant grass used for roadside and other similar uses in the north central states. On steep roadside slopes, smooth bromegrass sod may slough off, particularly in wet years. Bromegrass has a smaller root diameter and tensile strength than crested wheatgrass (Stevenson & White, 1941) and possibly other grasses which may explain why smooth bromegrass is not as good as other grasses for holding soil in place on steep road cuts.

The principal use of smooth bromegrass is as a cool-season pasture grass in the north central states of the USA and adjacent Canadian provinces. It is the principal component of these pastures although legumes, particularly alfalfa, are usually included in the plantings. In the past, smooth bromegrass also was often included as a minor component of seed mixtures used to establish hay fields in which alfalfa was the dominant component. At the present time, alfalfa for hay production is usually seeded in pure stands. In the region of primary adaptation, smooth bromegrass is used on land that is not suitable for cultivated crop production because of high erosion potential. No agricultural statistics are available on the number of hectares of smooth bromegrass or smooth bromegrass-dominated pastures in the USA but probably several million hectares of smooth bromegrass pastures are being utilized in grassland agriculture in North America.

The number of hectares planted to meadow bromegrass also is unknown, but it is considerably less than that seeded to smooth bromegrass. It is used primarily in irrigated pastures in the USA and as a pasture grass in Saskatchewan and Alberta (Knowles et al., 1993).

GROWTH PATTERNS

Seedling Growth and Establishment

Smooth bromegrass has a festucoid type of seedling morphology and development (Hoshikawa, 1969; Newman & Moser, 1988a). The germination process begins rapidly in smooth bromegrass. If soil moisture and temperature conditions are adequate, the caryopsis swells within 2 d after planting, the radicle grows and pushes the coleorhiza against the pericarp (Knobloch, 1944). The coleorhiza then emerges near the base of the caryopsis and the primary root breaks out of the thin side of the coleorhiza. In a greenhouse after 5 d, the primary root was 18 mm, the first adventitious root had appeared in the scutellar region, the coleoptile was 10 mm long and had developed chlorophyll, and the first foliage leaf had developed chlorophyll (Knobloch, 1944).

According to Knobloch (1944) by the 14th d the primary root was 80 mm long and had several lateral roots, the scutellar adventitious roots were 30 mm long, and the first foliage leaf was 85 mm long. Twenty-eight days after planting, the primary root system still comprised the largest part of the root system and had as many as 13 large lateral roots and the largest adventitious roots were about the same diameter but were only half as long. By the 54th d the coleoptile had been shed and the largest adventitious roots were 150 mm long and some seedlings had up to three leaves (Knobloch, 1944). One hundred and ten days after planting, the coleoptile node had become greatly swollen due to development of adventitious roots and had several rooted tillers. Primary roots were still present 189 d after planting but caryopsis remnants were no longer attached. Rhizomes were noted on plants 220 d after planting (Knobloch, 1944). Because of the festucoid type of seedling root morphology, planting depth determines coleoptile length and seedling crown depth in smooth bromegrass (Newman & Moser, 1988b). Optimal seeding depth is 0.5 to 1 cm but it can be planted 2.5 cm deep and still achieve excellent stands (Plummer,. 1943).

Vegetative Growth

Vegetative development of smooth bromegrass follows the development pattern described by Moore et al. (1991). Most of the growth of smooth bromegrass occurs within 12 wk of spring greenup in the U.S. Central Great Plains with the most rapid rate of growth in the first month (Fig. 17–3). Smooth bromegrass produces both sterile (nonflowering) and fertile (flowering) tillers. The sterile tillers will elongate and have 2 to 12 internodes.

The crop growth rate for irrigated, well-fertilized smooth bromegrass in eastern Nebraska was at its maximum in the spring of the year with a rate of

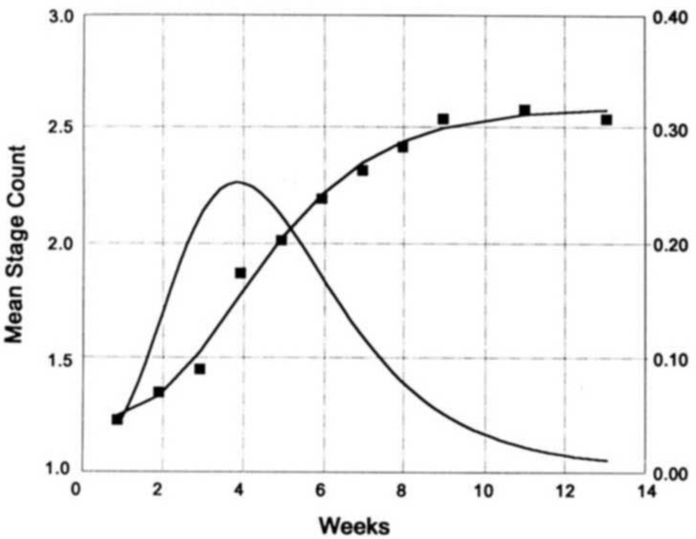

Fig. 17–3. The development of smooth bromegrass from spring greenup to the initiation of flowering in eastern Nebraska expressed as Mean Stage Count (MSC) using the Nebraska staging system (Moore e tal., 1991). In the Nebraska system, 1 = emergence of first leaf, 2 = onset of stem elongation, and 3 = boot stage. The line without means is the first derivative of the other line and represents the rate of morphological development in MSC units/week.

190 kg ha^{-1} d^{-1} (Engel et al., 1987). Growth rates in the summer and fall periods as measured by live herbage were about one-third as large. Although the relative magnitude of the yields may vary in the region where bromegrass is grown, the relative proportions of yield from spring, summer, and fall growing seasons will be similar. Tillering is enhanced when the fertile tillers are removed demonstrating that the presence of fertile tillers retards development of new tillers (Krause & Moser, 1977). When smooth bromegrass is defoliated, regrowth is initiated from crowns and rhizomes but meadow bromegrass reinitiates growth from existing tiller bases (Knowles et al., 1993). Meadow bromegrass has a faster rate of regrowth than smooth bromegrass in the first 20 d of regrowth (Knowles et al., 1993).

Root Growth

Roots of bromegrass are relatively long-lived. Weaver and Zink (1946) banded roots of several species including smooth bromegrass and monitored their survival over 3 yr. Root survival of banded roots of smooth bromegrass was 92, 93, and 36% at the end of the first three growing seasons. Root growth of smooth bromegrass ceased within 1 or 2 d after tillers are clipped at heights of 5 or 7.5 cm and does not resume for 1 to 2 wk afterward (Crider, 1955, p. 1–23). Root growth typically stops when more than 50% of the aboveground portion of the plant is removed. In Canada, 1- to 5-yr old stands of bromegrass had 3000 to

5000 kg ha^{-1} roots in the top 0.3 m of soil (Stevenson & White, 1941). Over 80% of the roots were in the top 0.3 m, but roots did penetrate to a depth of 1.5 m.

Reproductive Growth and Development

Although the initial research on the photoperiod requirements of smooth bromegrass indicated that it was a long-day plant (Allard, 1941), more recent research indicates that it is a short-day, long-day plant in which short days (autumn) followed by long days (spring and early summer) are required to induce flowering (Newell, 1951; Kirshin et al., 1977; Heide, 1984). The length of the short- or long-day periods vary with ecotypes and genotypes. Vernalization is not required to induce flowering, seedling plants will flower if exposed to proper light treatments without cold treatments (Heide, 1984).

In bromegrass as in many other grasses, blooming is basipetal, beginning near the apex of the inflorescence and progressing to the base (Grabe, 1956; Vinall & Hein, 1937, p. 1032–1102). The opposite or acropetal development occurs in the spikelet with lower inflorescences blooming first (Grabe, 1956; Vinall & Hein, 1937, p. 1032–1102). The average pollen dispersal period for a single inflorescence is about 7 to 10 d (Jones & Newell, 1946; Grabe, 1956). The pollination period of a population of plants will vary with the composition of the population, but it may be as long as 2 wk (Jones & Newell, 1946). In the midwestern area of the USA, most pollen is shed between 1600 to 1800 h.

Pollen dispersal distances vary with wind conditions. Almost all pollen is dispersed downwind, very little is dispersed upwind (Jones & Newell, 1946). The number of pollen grains collected by Jones and Newell on peak pollination days were 26.7, 7.1, 2.4, 0.9, and 0.4 × 10^6 m^{-2} at 25, 75, 125, 200, and 300 m downwind from a smooth bromegrass field. Smooth bromegrass invests about one-half of its total reproductive effort in pollen production (McKone, 1987).

Macrosporogenesis in smooth bromegrass is normal and results in the development of an egg apparatus with two synergids and an egg at the micropylar end, two polar nuclei, and three antipodals (Nielsen, 1947). Fertilization of the egg and polar nuclei occurs 15 to 18 h after anthesis (Nielsen,1947). Smooth bromegrass seeds develop rapidly following fertilization. Caryopses achieve their full length within 7 d after flowering (Knobloch, 1949). Some seeds can germinate 5 d after anthesis (Grabe, 1956). Because the anthesis period is 7 to 10 d for a typical smooth bromegrass field and 17 d are required to reach physiological maturity, seed can be harvested from bromegrass seed production fields as early as 27 d following the initiation of anthesis if the seed is artificially dried following harvest.

Smooth bromegrass is a cross-pollinated grass that is moderately to highly self-incompatible although some plants can produce varying amounts of seed when selfed (Adams, 1953; Ghosh & Knowles, 1964; Cheng, 1946; McKone, 1985). The type of incompatibility system in bromegrass is unknown. Meiosis in octaploid smooth bromegrass plants can be very irregular (Elliot & Love, 1948; Jalal & Nielsen, 1965; Nielsen, 1955). In a set of clones from Iowa, the number of bivalents ranged from 2 to 28 and the average number of chromosomes involved in associations of 5 to 8 ranged from 1 to 10 (Elliott & Love, 1948).

Irregular meiosis can result in the selective elimination of gametes that can affect population structure both in nature and in breeding populations, because successful viable gametes probably represent only a portion of the total potential gametes. Nielsen and Drolsom (1972) reported that the progeny of smooth bromegrass were more uniform than expected for a random-mated polyploid.

Legume Compatibility

Legumes are often seeded with smooth bromegrass in pastures and in hay fields. Smooth bromegrass-alfalfa mixtures are the most widely used in the areas where bromegrass is the most widely grown (Walton, 1980) but smooth bromegrass also can be successfully managed in mixtures with Ladino white clover (Sprague & Garber, 1950). The productivity and persistence of smooth bromegrass in intensively managed alfalfa varies with latitude and cutting management (Casler, 1988; Bittman et al., 1991). In the southern half of its primary area of use, smooth bromegrass will not contribute significantly to forage yields in intensively managed alfalfa except in the first cut the first 2 yr of production (Casler, 1988). In pastures, smooth bromegrass is usually the largest component of the stand and legumes are seeded to provide N to the bromegrass stand and also to improve the protein concentration of the forage grazed by livestock. In hay fields, legumes are the most important components of the stand. Bromegrass is added because its spreading ability allows it to fill in gaps in the legume stand and extends the life of a planting. The growth pattern of smooth bromegrass does not exactly match the growth pattern of any specific legume so the management practice that should be used for any particular pasture or hayfield depends on the objectives of the producer. When seeded in pure stands, the recommended seeding rate ranges form 12 to 16 kg ha^{-1}, the rate is reduced with increasing levels of legume in the mixture (Newell, 1973).

Smooth bromegrass may not persist well in a mixture with alfalfa that is harvested for hay (Marten & Hovin, 1980). In the first growth of smooth bromegrass nearly every tiller elongates and elevates the shoot apex at about the same time making them vulnerable to removal by mowing or close grazing (Krause & Moser, 1977). The lack of persistence is associated with the shoot apex elevation as it relates to reserve carbohydrate level and new shoot development. In a three-cut system Casler (1988) found that smooth bromegrass was not as competitive with alfalfa as was orchardgrass.

Smooth bromegrass will persist best when cut at the pre-elongation stage or near anthesis. In many temperate areas the first harvest of the bromegrass-alfalfa mixture is based on the maturity stage of the alfalfa and is taken when the smooth bromegrass is at the stem elongation or early head stage. New basal tillers on smooth bromegrass are not developed sufficiently yet to provide regrowth and the reserve carbohydrate level is low (Smith et al., 1973) which may further delay growth from new tillers. With vigorous alfalfa cultivars the second growth comes rapidly. Smooth bromegrass is at a disadvantage for the rest of the growing season and does not remain a mixture with alfalfa. Paulsen and Smith (1968) found that there was better smooth bromegrass persistence when an alfalfa-smooth bromegrass mixture was harvested five times compared to three times per season. With the five-cut treatment the first cut was taken before elongation so the shoot apices of smooth bromegrass were not removed with the first cut, and the alfalfa was less vigorous under a five-cut system compared to a three-cut system. Knieval et al. (1971) reported that the highest persistence and yields of smooth bromegrass occurred when the first crop of smooth bromegrass was cut at anthesis compared to inflorescence emergence or the tillering (elongation) stages. When smooth bromegrass is cut near anthesis, basal tillers have developed and will provide the mechanism for a second growth.

There was little difference between smooth bromegrass and six other cool-season grasses in their competitive ability with cicer milkvetch. Cicer milkvetch is very competitive with grasses. After several growing seasons cicer milkvetch made up 75 to 90% of the forage in most of the grass-cicer milkvetch mixtures (Townsend et al., 1990).

PRODUCTION LIMITATIONS

Environmental Stresses

Drought

Bromegrass is less drought tolerant than many of the wheatgrasses grown in the western half of the USA but it is more drought tolerant than orchardgrass, timothy, and other cool-season grasses grow in the eastern half of the USA. In Minnesota, reed canarygrass produced more forage than smooth bromegrass under a limited soil moisture regime over a 3-yr period (Sheaffer et al., 1992). Although reed canarygrass had higher yields than bromegrass in this specific trial, Sheaffer et al. (1992) indicated that smooth bromegrass may have the best long-term yields and persistence in the north central states of the USA. During the drought years of 1934 to 1936, it survived in central states of the USA when many of the bluegrass pastures were killed by drought (Wheeler & Hill, 1957). Smooth bromegrass cultivars developed from strains that became naturalized to the central Great Plains are more drought tolerant than strains from more northern regions (Anderson, 1941). Smooth bromegrass forage produced under drought conditions is usually higher in in vitro dry matter digestibility (IVDMD) than forage produced under more optimal moisture conditions (Wurster et al., 1971) probably because of reduced internode elongation. Meadow bromegrass is not as productive as smooth bromegrass in the central Great Plains of the USA where moisture stress can occur during the growing season (Vogel, 1983).

Heat

Although the morphological development of smooth bromegrass is controlled by response to photoperiod, environmental factors can modify the response. The morphological stage of development of smooth bromegrass was closely related to accumulated growing degree days when a 5°C base was used (Buxton & Marten, 1989). The optimal daytime temperature for herbage growth of smooth bromegrass is between 18 and 25°C and temperatures above 35°C reduce growth rates (Baker & Jung, 1968). In a controlled study, Morrow and Power (1979) demonstrated that bromegrass can grow in soil temperates ranging from 3 to 33°C. Optimal plant growth was achieved with a soil temperature of 18.3°C.

Smooth bromegrass becomes semidormant during the hot summer months in the central Great Plains (Anderson, 1941). It resumes growth in the fall when rains and cooler temperatures occur. Genetic variation exists in smooth bromegrass for regrowth yields at elevated temperatures (Atwood & McDonald, 1946). In areas where summer dormancy of smooth bromegrass is a production problem, agronomists have chosen to use adapted warm-season grasses during the hot summer months in a combined cool- and warm-season grass grazing system rather than attempting to improve the heat tolerance of smooth bromegrass.

Smooth bromegrass establishment can be adversely affected by hot temperatures. Sprague (1944b) evaluated the emergence and early seedling growth of several species of forage grasses including smooth bromegrass under temperature regimes of 4 to 13°, 13 to 21°, 21 to 29°, and 29 to 38°C and under daylengths of 9 or 16 h. Under these conditions, smooth bromegrass had emergence greater than 80% for all temperature-daylength regimes except 16-h d at 29 to 38°C where the germination was 49%. Bromegrass had almost twice as much dry matter (DM) accumulation with a 16-h as compared to 9-h daylength except at the highest temperature regimes. Almost no growth occurred after emergence at the highest temperature regime and most of the seedlings died at the end of 6 wk.

Cold

Smooth bromegrass ecotypes persist over a broad geographical area in Eurasia. Winter hardy ecotypes can be found that are adapted to most temperate areas of North America except for alpine regions. Smooth bromegrass plants are tolerant of ice sheet formation during the winter months. They have survived encasement in ice for 60 d at –4°C without damage. Similar conditions did not damage timothy but did damage orchardgrass (Freyman, 1969). Once established, winter killing of smooth bromegrass is not a problem in the USA and adjacent regions of Canada. Meadow bromegrasses are not as winter hardy as smooth bromegrass (Knowles et al., 1993). In studies in Canada, meadow bromegrass had 50% damage to sods at temperatures of –22°C while smooth bromegrass did not have similar levels of damage until temperatures reached –28°C (Limin & Fowler, 1987).

Soil Fertility

The response of smooth bromegrass to N fertilization is similar to other cool-season grasses and is well documented (Carter & Scholl. 1962; Colville et al., 1963; Duell, 1960; Look-Kin & MacKenzie, 1970; Rehm et al., 1971; Vanderlip & Pesek, 1970; Meyer et al., 1977). In general, N fertilization requirements for smooth bromegrass are directly related to available moisture and length of the growing season. Minimal levels of P and K also are required to optimize forage yields (Rehm et al., 1971; Vanderlip & Pesek, 1970).

In most N fertilization studies, the response to N fertilization was measured as hay yields. Rehm et al. (1971) conducted a comprehensive series of studies in northeastern Nebraska in which they also showed the response of beef cattle grazing fertilized smooth bromegrass pastures. In eastern Nebraska, DM yields increased with N rates up to 180 kg ha^{-1}, 90 to 135 kg N ha^{-1} produced yields only slightly lower (Rehm et al., 1971). Forage protein concentration increased markedly at rates up to 90 kg N ha^{-1}, but above that level, protein concentration increases were small. In comparisons of pastures fertilized with 67 kg N ha^{-1} vs. unfertilized pastures, beef yearlings gained 155 vs. 61 kg ha^{-1} and had average daily gains of 0.7 vs. 0.5 kg d^{-1} (Rehm et al., 1971). In the study by Rehm et al. (1971) 1 kg N ha^{-1} produced an increase of 1 kg beef ha^{-1}. Fertilization of bromegrass pastures is economical as long as the cost of the fertilizer and the application cost of 1 kg N is less than the price of 1 kg beef cattle at recommended N rates. In a grazing trial that was conducted in Indiana, Lechtenberg et al. (1974) also demonstrated the effectiveness of N fertilization in increasing beef production per hectare.

Two to three years after smooth bromegrass is established on a new site, bromegrass develops what is known in the older literature as a sod-bound condition (Anderson et al., 1946). It is essentially a N deficiency condition that is characterized by low forage yields and the production of only a limited number of fertile tillers. The condition can be easily remedied by application of N fertilizer (Anderson et al., 1946; Rehm et al., 1971). A 22-yr study in North Dakota demonstrated that bromegrass yields and stands can be maintained for at least 22 yr if properly fertilized and managed (Meyer et al., 1977).

Smooth bromegrass is moderately tolerant of saline soils. Its tolerance range—as measured by electrolytic conductivity (S m^{-1}) of the saturated soil extract—is 0.4 to 1.4 S m^{-1}, which is similar to alfalfa (Forsberg, 1953). Meadow bromegrass is less tolerant of saline conditions than smooth bromegrass (Knowles et al., 1993).

Smooth bromegrass receiving large amounts of N early in the season grows very rapidly and reaches the elongation stage with very little nonstructural carbohydrates in basal portions of the plants. If smooth bromegrass is closely defoliated from the elongation to early heading stages, the stand will often be severely thinned since basal buds have not developed sufficiently at that time to form new tillers. Marten et al. (1979) reported that smooth bromegrass stands were severely damaged in plots receiving waste water effluent providing 224 or 336 kg N ha^{-1}. After the second harvest in the 1st yr the bromegrass stands were very poor because of the lack of development of new tillers.

Herbicide Tolerance

Smooth bromegrass is tolerant of 2,4-D (2,4 dichlorophenoxy acetic acid) and dicamba (3,6-dichloro 2-methoxybenzoic acid) at rates of up to 1.1 kg ha^{-1} although some leaf chlorosis may occur at this rate (McCarty & Scifres, 1968). It can tolerate only 0.14 kg ha^{-1} of picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid) if applied in the fall, or 0.28 kg ha^{-1} if applied in the spring (McCarty & Scifres, 1968). Glyphostate [N-(phosphonomethyl)glycine] can be used to kill existing stands of smooth bromegrass if applied in the fall, but it is not always effective on vigorous stands of smooth bromegrass when applied in the spring (Vogel & Waller, 1990).

Special Pest Problems

Insects

The insect that probably causes the most economic damage to smooth bromegrass seed production is the bromegrass seed midge (*Stenodiplosis bromicola* Marikovskiy and Agafonova) (Nieman & Manglitz, 1972). The bromegrass seed midge overwinters as diapausing larvae in shattered florets (Nieman & Manglitz, 1972). The adult midges emerge about the time bromegrass is heading in late May or early June. The adults lay eggs in the developing florets, the larvae emerge and feed on the developing florets. In Nebraska, there are three generations per year. The first two summer generations have a life cycle of 14 to 18 d and develop without diapause. The last summer generation enters diapause and develops into the overwintering population. The diapausing larvae can survive the harvesting process and at least 1 yr of seed storage (Nieman & Manglitz, 1972). Damage to smooth bromegrass seed production can range from 0 to over 50% in some years. A species of wasp [*Tetrastichus* spp. (Hymenoptera: Eulophidae)] parasitized all stages of bromegrass seed midge. In some instances, parasitism rates greater than 90% were observed. The relative damage of the bromegrass seed midge to the bromegrass seed crop probably depends upon the relative parasite-midge population dynamics as well as environmental factors. In Saskatchewan, Canada, the insecticides carbofuran [2,3-dihydro-2,2-dimethyl-7-benzofuranyl methylcarbamate] (0.14 kg a.i. ha^{-1}) or dimethoate (*O,O*-dimethyl *S*-(*N*-methylcarbamoylmethyl0 phosphorodithioate] (0.56 kg a.i. ha^{-1}) applied just before the appearance of adult midges at the boot or flowering stage significantly reduced the numbers of midges and parasites (Curry et al., 1983).

Other insects that have been reported to affect bromegrass seed production in Eurasia include other midges, flies (*Dicraeus tibialis* Mg. and *D. ingratus* Zu.), gall mite (*Eriophyes* spp.), and thrips (*Limothrips consimilis* Pr. and *L. cerealium* Hald.) (Agafonova, 1974). Agafonova (1974) reported that the number of seed pests, their frequency, and their damage increased from north to south in the former USSR. Seed losses were substantial in all regions (60–98%) and no resistance was found among bromegrasses.

Diseases

Over 24 diseases occur on smooth bromegrass including diseases caused by bacteria, fungi, and viruses (Allison, 1946; Braverman, 1986; Braverman et al., 1986; Drolsom et al., 1966; Sprague, 1950; Zeiders & Sherwood, 1986). The principal bacteria and fungal diseases are listed in Table 17–1. It is likely that nematodes also cause economic losses to smooth bromegrass, but no reports on nematode diseases of smooth bromegrass are available. Diseases or disease-like problems also can be caused by mineral deficiencies or other environmental problems.

Brown leaf spot is one of the most serious fungal diseases of smooth bromegrass and the disease is found throughout the bromegrass growing region of the

Table 17-1. Bacterial and fungal diseases of smooth bromegrass.

Common name	Organism
Bacterial diseases	
Brown stripe	*Pesudomonas setariae* (Okabe)
Bacterial brown stripe	*P. Avenae* Manns
Blackish-brown stripe or bacterial blight	*P. syringae* pv. coronfaciens (Elliot) Stevens,
Translucent leaf stripe or bacterial stripe	*Xanthomonas camestris* pv. *hordei* pv. *translucens*
Fungal diseases	
Crown rust	*Puccinia coronata* Cda.
None	*P. recondita* Rob. ex. Desm.
Stripe smut	*Ustilago striiformis* (West.) Niessl.
Flag smut	*Urocystis agropyri* (Preuss)
Head smut	*Ustilago, Sorosporium,* and *Sphacelotheca* spp.
Powdery mildew	*Erysiphe graminis* DC. ex Merat.
Ergot	*Claviceps purpurea* Tul.
Leaf scald	*Rhynchosporium secalis* (Oud.) Davis
Brown leafspot	*Drechslera bromi* (Died.) Shoem.
Bipolaris foot rot, leaf blight, seedling blight	*Bipolaris sorokiniana* (Sacc. ex. Sorok.) Shoeml. formerly *Helminthosporium sativum*
Leafspot	*Stagonospora bromi* A.LK. Sm. & Ramsb.
Septoria leafspot	*Septoria bromi* Sacc.
Ascochyta leafspot	*Ascochyta sorghi* Sacc.
Selenophoma leafspot	*Selenophoma bromigena* (Sacc.) Sprague & A.G. Johnson
Rhizoctonia blight	*Rhizoctonia solani* Kuehn

USA and Canada. The causal agent *Drechslera bromi* (imperfect stage), or *Pyrenophora bromi* (Died.) Drechs. (perfect stage) is specific to species of bromegrass (Braverman et al., 1986; Chamberlain & Allison, 1945). Brown leaf spot is most prevalent during the cool, wet weather of spring and fall. Resistant cultivars are the best method of control. The inheritance of brown leaf spot resistance was studied by Berg et al. (1983) and their results indicate that lesion size is regulated by multiple genes and susceptibility to the fungus may be dominant or epistatic to resistance. Selenophoma leaf spot is another important disease that occurs widely on smooth bromegrass and can result in considerably leaf loss in heavily infected stands (Allison, 1945; Braverman et al., 1986).

The two principal virus diseases of bromegrasses are bromegrass mosaic caused by the bromegrass mosaic virus (BMV) and barley yellow dwarf virus caused by the barley yellow dwarf virus (BYDV) (Braverman et al., 1986). Brome mosaic virus causes a mild mosaic on a broad array of grasses and although it is commonly found in bromegrass, it does not appear to cause much economic damage (Lane, 1974; Braverman et al., 1986). The senior author (K.P. Vogel) has noted genotypic differences in symptom severity in smooth bromegrass breeding nurseries. Barley yellow dwarf virus occurs on numerous grasses worldwide and causes chlorosis and stunting (Braverman et al., 1986). It is transmitted by several species of aphids and is a systemic virus (Braverman et al., 1986). Breeding for resistance appears to be the most economical control procedure. Ryegrass mosaic virus (RMV) also has been reported to infect bromegrass but does not appear to be an economic problem (Braverman et al., 1986).

Genetic resistance has been reported for bipolaris foot rot, blackish-brown stripe, translucent leaf stripe, crown rust, powdery mildew, leaf scald, brown leaf spot, leaf spot, and Selenophoma leaf spot (Braverman, 1967; Braverman, 1986; Braverman et al., 1986; Drolsom et al., 1966). The mountain bromegrass cultivar Bromar was initially resistant to head smut (Braverman et al., 1986), but the resistance broke down in seed production fields (Meiners, 1952). It is usually not economic to apply fungicides or other chemical treatments for control of smooth bromegrass diseases and the best method of control is by the development of resistant cultivars or by harvest or grazing management that can reduce canopy herbage and alter the canopy microenvironment. Flag smut and powdery mildew can be controlled with systemic fungicides in breeding nurseries or seed production fields (Braverman et al.,1986).

Leaf and other foliar diseases can reduce forage quality. In vitro dry matter digestibility of herbage on field-grown plants of 'Saratoga' smooth bromegrass decreased 1.2 g kg^{-1} with each 1% increase in disease area of leaves infected with brown leaf spot (*Dreshlera bromi*), leaf scald (*Rhynchosporium secalis*), and Selenophoma leaf spot (*Selenophoma bromigena*) (Gross et al., 1975). Inoculation with brome mosaic virus did not affect IVDMD. Root rots can damage smooth bromegrass stands at both the seedling and mature plant stages (Sprague, 1944a). Smooth bromegrass does not persist well in the southeastern part of the USA because of diseases caused by *Rhizoctonia* and *Helminthosporium* (Craigmiles et al., 1965). Ergot can have a very detrimental effect on seed yields and seed quality.

Grazing and Harvest Management

Management of smooth bromegrass as a pasture or hay crop depends upon the management objectives of the producer. A producer that is using bromegrass to produce gains on yearling beef cattle will have a different objective than a producer that is using bromegrass pastures to maintain dairy heifers. The management of smooth bromegrass hayfields likewise depends upon the objectives of the producers. Regardless of the management objectives, successful management of bromegrass is dependent upon knowledge of its response to defoliation.

Bromegrass is a determinate species and forage quality declines as the plants mature (Fig. 17–4). Herbage IVDMD and crude protein concentration are highly correlated with calendar day and accumulated growing degree days (Fig. 17–4). Because bromegrass swards contain both reproductive and vegetative tillers, the quality of forage in a sward is determined by the maturity of tillers in the sward and the frequency of each tiller class in the sward (Buxton & Marten, 1989; Sanderson & Wedin, 1989a). Tillering can be manipulated by grazing. Krause and Moser (1977) showed that tillering was increased when elongated tillers were removed. Removal of the growing point in a tiller by mowing or grazing stops tiller growth in bromegrass, new growth is produced by basal buds producing new tillers.

Bromegrass is most easily damaged by intensive defoliating after the meristem has elongated (Eastin et al., 1964). At this growth stage, total available root

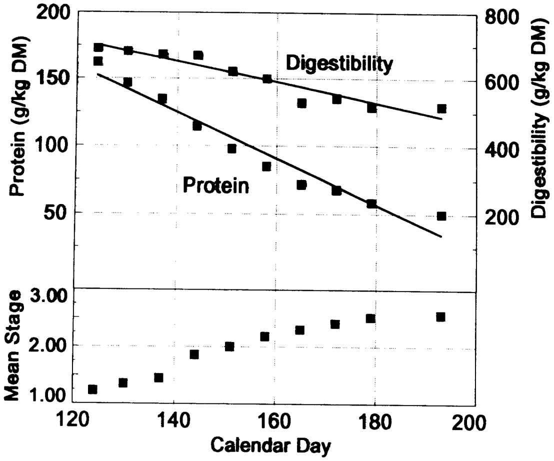

Fig. 17–4. Protein and IVDMD changes in smooth bromegrass in relation to mean stage and calendar day in eastern Nebraska (data from USDA-ARS research at the University of Nebraska (K.J. Moore & K.P. Vogel, personal communication, 1993).

and stem base carbohydrate reserves are at their lowest levels (Paulsen & Smith, 1968). Smooth bromegrass tillers cut before meristem elongation continue to grow from unelongated tillers. Frequent cutting or grazing usually favors the grass component of a grass legume mixtures as compared to infrequent cuttings (Burger et al., 1958, 1962; Sprague et al., 1964). Yields of bromegrass in pure stands are maximized by delaying the first harvest until after panicle emergence and then having infrequent cutting treatments (Burger et al., 1958, 1962; Carter & Law, 1948). In a four-cut system in Canada, meadow bromegrass had lower initial yields than smooth bromegrass but had higher regrowth yields (Knowles et al., 1993).

Nitrogen fertilization at moderate rates does not result in increased IVDMD, but does result in an increase in herbage N concentration (Sanderson & Wedin, 1989b). Most of the increase in herbage N concentration is due to an increase in N concentration of cell solubles, only slight increases in N concentration in brome cell walls were noted by Sanderson and Wedin (1989b).

Stocking rate on smooth bromegrass should be sufficient to prevent the formation of flowering culms. Flowering culms are usually not grazed by livestock and because they probably exert apical dominance, they reduce tillering and new leaf formation.

There are no reports of antiquality factors of smooth bromegrass inhibiting animal performance. Fairbourn (1983) reported the presence of the alkaloid perloline in 'Manchar' smooth bromegrass and 'Regar' meadow bromegrass when grown at Cheyenne, WY, under irrigation. The samples in which perloline was detected had depressed IVDMD values. The presence of alkaloids in smooth bromegrass has not been verified by other research; however White (1987) reported a fungal endophyte in fresh collections of nodding bromegrass. Ergot sclerotia can cause problems to livestock if grazed or if smooth bromegrass is harvested for hay after sclerotia have developed (Allison, 1946). This is usually past the growth stage when smooth bromegrass is normally harvested for hay. Ergot consequently is a problem for livestock producers only if they have mismanaged their pastures or hayfields.

The potential for grass tetany problems exist with smooth bromegrass. In Wisconsin, smooth bromegrass had excessive K/(Ca + Mg) ratios at all stages of maturity and deficient levels of P, Ca, Mg, S, Zn, Fe, and Cu at all stages of maturity for moderately producing dairy cows (Casler et al.,1987a). There is considerable variation in mineral concentration due to year, locations, and whether the bromegrass is in a pure or mixed stand (Casler et al.,1987a). It is unlikely that the mineral levels of smooth bromegrass can be improved enough by breeding to meet the needs of dairy cattle.

Seed Production

Seed production practices for smooth bromegrass are similar to those for other cool-season grasses (Holzworth & Weisner, 1986; Atkins & Smith, 1967; Wheeler & Hill, 1957). Most of the agronomic practices used to produce smooth bromegrass seed were initially determined empirically, validated through commercial production, and refined with additional experimentation. Seed fields can be solid or seeded in rows. If seeded in rows, the rows are often allowed to close by the rhizomatous spread of the plants. Row widths of 60 to 90 cm produce similar results (Canode, 1968). Seeding rates to establish seed fields range from 80 to 100 seeds per linear meter of row. In Washington, the optimum N rate for seed production of smooth bromegrass seed was 67 kg ha^{-1} (Canode, 1968). Seed is usually harvested after the caryopses are in the hard dough stage and when culms have dried 6 to 10 cm below the panicle. Shattering is usually not a problem at this stage. In the USA smooth bromegrass seed is harvested by direct combining the seed field (Wheeler & Hill, 1957). The cutter head should be elevated so that most of the panicles are harvested with a minimum amount of leaf and stem material. In Canada, seed fields are often swatched and windrowed prior to combining (R.P. Knowles, 1993, personal communication).

Management practices for meadow bromegrass seed production are similar to those for smooth bromegrass. Meadow bromegrass will shatter easier than smooth bromegrass (Knowles et al.,1993) and more care is needed during the harvesting operations to prevent seed losses. Meadow bromegrass seed needs more processing than smooth bromegrass seed to remove awns and pubescence, which improves the flow of seed in planters (Knowles et al.,1993).

It is usually not economical to harvest smooth bromegrass seed fields with seed yields less than 100 kg ha^{-1}. A quck way to estimate seed yields is to count the number of heads per square meter and assume 1 kg ha^{-1} of seed for each panicle that is counted (Wheeler & Hill, 1957). Seed yields of 336 to 560 kg ha^{-1} are typical with adequate N fertilization in the central Great Plains and are usually in the 784 kg ha^{-1} range in the Pacific Northwest. Meadow bromegrass yields from seed fields of the new cultivars range for 350 to 600 kg ha^{-1} (Knowles et al., 1993).

Bromegrass seed can maintain excellent viability over 20 yr if stored at low temperatures (–7 to –18°C) (Acikgoz & Knowles, 1983). If low temperature storage is used, drying seed does not measurably improve viability. Bromegrass seed that is stored under room conditions for 4 or more years often has greatly reduced viability and vigor and may not be suitable for commercial plantings.

SUMMARY OF BREEDING HISTORY

Selection

The first recorded breeding work on smooth bromegrass was conducted in the early 1900s by two Kansas farmers (Achenbach Brothers, 1921). Around 1900 they bought bromegrass seed from Nebraska and seeded it with alfalfa on their farm in Washington County, Kansas. By the 3rd yr the planting was almost a pure stand of vigorous brome. They subsequently planted an unadapted brome which did poorly. The Achenbach Brothers then went back to their first planting and "selected the tallest, best filled, and lightest colored plants and the two of us personally hand stripped these heads, getting enough seed to start a seed field" (Achenbach Brothers, 1921). The seed field was the breeder seed field of 'Achenbach' bromegrass. The Achenbach Brothers had used one cycle of mass selection to develop the cultivar.

Initial breeding work by experiment stations on smooth bromegrass was initiated between 1910 and 1920 at several experiment stations. This work documented the existence of substantial phenotypic variation among bromegrass strains and clones (Keyser, 1913; Waldron, 1921). This initial work did not lead to the development of any cultivars, and except for sporadic efforts, formal breeding programs on bromegrass were not reinitiated until the drought of the 1930s stimulated breeding work at several locations. The breeding programs used available germplasm resources, primarily domestic germplasm sources such as old plantings that had been in existence for sufficient periods of time to have become naturalized.

The evaluation work documented the existence of "southern" and "northern" strains of smooth bromegrass (Newell & Keim, 1943; Knowles & White, 1949). The souther types, which were believed to trace from the Hungarian introductions, were the best adapted to the central Great Plains and the southern part of the Cornbelt while the northern strains were best adapted to the Northern Plains, the upper Midwest and northeastern states, and to the adjacent provinces of Canada (Thomas et al., 1958; Newell,1973; Walton, 1980).

The first series of cultivars, other than Achenbach, did not involve any formal breeding work other than selection among existing ecotypes or strains. For example, seed from several old plantings in Nebraska proved superior to other germplasm sources and were traced to a common origin. These fields were certified and were the source of the cultivar 'Lincoln' which is still widely used (Hanson, 1972; Newell, 1973). Other cultivars developed in a similar manner were Fischer and Homesteader (Hanson, 1972; Newell, 1973). This initial selection work among accessions and germplasm sources and the outstanding attributes of some of the selected strains such as Lincoln resulted in the largest single-sep improvements that have been made in smooth bromegrass to date.

The next phase of smooth bromegrass improvement was an era in which bromegrass breeders apparently were mimicking breeding work that was being done in maize. Breeders at several locations attempted to improve smooth bromegrass by inbreeding. The inbreeding work demonstrated that most smooth bromegrass plants will produce some selfed seed and it also demonstrated that inbreeding results in a decrease in vigor and decreased forage yields (Hayes & Schmid, 1943; Hawk & Wilsie, 1952; McDonald et al., 1952). Hybrid cultivars were not developed because of the problems of controlling pollination in the seed field. The breeding work on improving smooth bromegrass via self-pollinated breeding schemes was a failure, no cultivars were developed from this research.

The next phase in smooth bromegrass breeding work involved the testing of progeny produced by polycross nurseries or by open pollination. Parents that had the best combining ability were selected to the parents of synthetic cultivars. This breeding work was based on several studies that demonstrated the effectiveness of the procedure for improving several different traits (Lebsock & Kalton, 1954; Knowles, 1955). This breeding system went through several stages of development and many modifications, but is generally known as the half-sib progeny breeding system (Vogel & Pedersen, 1993). Cultivars that were developed using this breeding system include Blair and Baylor (Hanson, 1972).

The current era of smooth bromegrass breeding has emphasized the use of population genetic breeding methods including improved methods of progeny testing and mass selection including Recurrent Restricted Phenotypic Selection System (RRPS). The breeding systems differ in the manner in which plants are selected for crossing. Once plants are selected, virtually all intermating is conducted using polycross mating systems (Vogel & Pedersen, 1993). 'Badger' smooth bromegrass was developed using population improvement breeding methods (Casler & Drolsom, 1992).

Plants in polycross nurseries need to be isolated from other sources of pollen of the same species. Based on information on pollen dispersal, Jones and Newell (1946) recommended an isolation distance of at least 360 m for smooth bromegrass. Knowles (1980) used a pubescent seedling marker to evaluate genetic contamination. When nonpubescent and pubescent strains were in adjacent plots, 45% off-type seedlings were produced on the border rows, but less than 10% were produced at 10m from the border. Similar results were obtained with a yellow-leafed marker (Knowles & Ghosh, 1968). The current isolation requirements for the production of foundation and certified seed are based on these studies and vary depending on the width of non harvested border surrounding the harvested area and class of seed being produced. In Nebraska, the isolation distance for foundation and certified seed production without nonharvested border areas are 300 and 50 m, respectively (NCIA, 1987). The field isolation distance used by smooth bromegrass breeders will depend upon the degree of potential contamination a breeder is willing to accept.

The objective of polycross nurseries is to randomly intermate all the selected clones so gene frequencies are fixed (Vogel & Pedersen, 1993). Hittle (1954) demonstrated that nonrandom pollination can occur in smooth bromegrass polycross nurseries. Progeny derived from different polycross ramets differed significantly for each of seven traits indicating nonrandom pollination. Knowles (1969) also demonstrated nonrandom pollination in polycrosses by using a dominant, yellow leafed marker. The best procedure that a breeder can use to achieve random mating in a polycross nursery is by random placement of clones in each replication of a polycross.

Genetic studies of cross- and self-incompatibility in smooth bromegrass indicate that most plants are self-incompatible but some plants can produce some selfed seed (Adams, 1953; Ghosh & Knowles, 1964). Cross fertility with specific plants is quite variable indicating the existence of a genetic incompatibility system (Adams, 1953). Additive genetic effects are associated with general levels of fertility, while nonadditive effects are associated with specific cross-incompatibility effects (Adams, 1953). Nonrandom pollination occurs in smooth bromegrass polycross nurseries (Hittle, 1954) and most likely in seed production fields. The nonrandom pollination is probably due to differential cross-fertility among clones (Adams, 1953).

Because smooth bromegrass is a cross-pollinated species for which mechanisms of pollination control are not available for production of hybrids, synthetic varieties are currently the only available method of developing and releasing improved cultivars. Knowles (1973) demonstrated that synthetics can be based on as few as four clones without having inbreeding affecting forage yields in subsequent generations of increase. Seed yields, however, may be depressed when as few as five clones are used but this will vary with the specific clones (Knowles, 1973). Stability of synthetic cultivars during the seed increase process is essential. Rincker et al. (1984) demonstrated that the synthetic cultivar Saratoga, which is based on five clones, maintained very good population stability during two generations of seed increase under diverse environmental conditions.

No F1 hybrid bromegrass cultivars have been developed to date. Research by Craigmiles et al. (1965) indicates that an F1 hybrid could produce 15 to 20% more forage than the best adapted cultivars and synthetics containing the same clones as used to produce the hybrid. Knowles (1955) obtained similar results at Saskatoon, Canada. In the latter study, the hybrid seed was produced by allowing two self-incompatible clones to intermate. It should be feasible to develop F1 hybrid cultivars of bromegrass by using self-incompatible clones that flower at about the same time. Parental clones could be vegetatively propagated for planting in alternate rows in seed production fields. All the seed harvested from a seed field of two self-incompatible clones would be F1 seed.

The initial production of hybrid seed from specific clones could be obtained in the greenhouse. Only 10 g of seed can seed a 1- by 5-m plot and this quantity of seed can be produced from crosses in the greenhouse. In a greenhouse study, Dunn and Lea (1981) investigated spatial isolation requirements for bromegrass using a homozygous recessive virescent mutant plant. When distance from pollen parents and the mutant were 0, 1.5, 3.0, 4.5, and 7.5 m, the percentage of green or outcrossed seedlings were 81, 41, 13, 7, and 1% respectively. These results indicate spatial requirements in greenhouses need to be at least 7 m or more if separate sets of brome plants are being intermated without bagging inflorescences in the same house.

The initial breeding work on meadow bromegrass in North America was the initial selection work that resulted in the development of Regar (Foster et al., 1966). Fifteen clones were selected from the plant introduction, PI173290, and were intermated in a polycross to produce the synthetic cultivar. Most of the subsequent breeding work on meadow bromegrass has been conducted by the Agriculture Canada breeding program at Saskatoon, Saskatchewan. Emphasis has been on improving seed yields. Two cultivars, Fleet and Paddock, have been developed by the program and have seed yields that are over 65% larger than seed yields of Regar (Knowles, 1990a,b).

Traits Selected

The polyploid nature of bromegrass combined with its self-incompatibility plus the difficulty of emasculating bromegrass florets has limited studies on the inheritance of qualitative traits, i.e., those controlled by a small number of genes. The studies that have been completed have provided valuable marker genes for bromegrass. Knowles (1980) used repeated cycles of mass selection to develop pubescent and nonpubescent seedling strains of smooth bromegrass. Pure breeding nonpubescent types were the most difficult to achieve requiring seven to eight generations of mass selection. Controlled crosses showed partial dominance for pubescence. Dunn and Lea (1978) reported that a viresent seedling trait was inherited as a single, tetrasomic recessive and the gene symbol vr was assigned to the trait. Ghosh and Knowles (1964) report that a chlorophyll mutant in bromegrass that resulted in plants with bright golden yellow stems, leaves, and inflorescences was controlled by a dominant gene ($\underline{Y}_1$) that was inherited on a tetrasomic basis and usually occurred in the simplex form.

Numerous studies have been conducted on quantitative traits using either diallel experiments or experiments based on the analyses of S1 or half-sib families. These studies have documented the existence of genetic variation among bromegrass genotypes or within bromegrass populations for forage yield, forage quality traits, disease resistance, morphological traits including leaf, sheath, and panicle characters, seed yield, seedling vigor, as well as other traits (Jessen & Carlson, 1985; Berg et al., 1983; Casler et al.,1987b; Walton, 1980; Lessman & Kalton, 1965; Knowles et al., 1970; Tan & Dunn, 1976; Tan et al.,1979; Trupp & Carlson, 1971). These studies have been conducted using quantitative genetic theory that is based on diploid organisms such as maize and assumes normal diploid and solely Mendelian inheritance and also assumes that the genetic population is mated at random (Falconer, 1981). As indicated in previous sections, these criteria are not fully met in bromegrass, so the results of the quantitative genetic studies in bromegrass probably require reinterpretation.

In addition to problems due to meiotic irregularities, there also are mitotic irregularities in smooth bromegrass that may affect intraplant variation for morphological characteristics (Tan & Dunn, 1977). These irregularities include endomitosis, fragments, chromosomes excluded from the spindle, anaphase bridges, laggards, and micronuclei (Tan & Dunn, 1977). These miotic irregularities produce phenotypic diversity that is not usable or easily detectable by a breeder.

Considerable emphasis has been placed on improving forage quality of smooth bromegrass. Genetic variation has been reported for IVDMD of smooth bromegrass herbage, concentration of cell walls, cell wall composition, and rate of digestion of cell wall constituents (Ross et al., 1970; Casler, 1978; Casler et al., 1987b; Collins & Drolsom, 1982; Christie & Mowat, 1968; Vogel, 1983).

Divergent phenotypic selection for IVDMD, neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) concentrations resulted in populations that were signficantly different for these traits demonstrating that it is feasible to genetically modify the forage quality of smooth bromegrass by breeding (Carpenter & Casler, 1990). The first smooth bromegrass cultivar with improved forage digestibliity, Badger, was released in 1992 (Casler & Drolsom, 1992). It ranges from 10 to 30 g kg^{-1} higher in IVDMD than 'Rebound'. According to Casler and Drolsom (1992), Badger averaged over 11% higher average daily gain than Rebound when both were grazed by ewes and lambs (*Ovis aries*) in a replicated grazing trial at Arlington, WI.

Kamstra et al. (1973) conducted a sheep feeding trial to compare two synthetics and the cultivar Sac. Hay of the two synthetics had significantly higher (30 g kg^{-1}) IVDMD and in vivo digestibility than hay of Sac and produced average daily gains that were 2× those produced by lambs fed Sac. Hay of the two synthetics did not differ in IVDMD and produced similar gains when fed to lambs. This research clearly demonstrates that improvement in smooth bromegrass IVDMD can improve animal performance and that IVDMD provides similar relative measures of forage digestibility as in vivo digestibility.

Potential for Genetic Improvement

Although breeding work has been conducted on smooth bromegrass for over 50 yr, developing smooth bromegrass cultivars with significant improvement over the initial land varieties such as Lincoln has been difficult. Breeders have been using breeding systems such as progeny testing and RRPS that are designed to be used with species that have regular meiosis, diploid inheritance, and which can be random mated. Bromegrass does not behave as a diploid during meiosis, it has meiotic irregularities, and mating may not be random due to cross compatibility problems. Ratios from genetic studies (Ghosh & Knowles, 1964) indicate a tetrasomic type of inheritance. Consequently breeders have had some formidable obstacles in improving smooth bromegrass even though there is substantial genetic variation in bromegrass for virtually every trait that has been tested.

Most of the genetic improvement in smooth bromegrass has been achieved by selection of superior accessions or ecotypes and then by using population improvement or strain building procedures to improve the superior accessions. These procedures have resulted in productive, widely adapted cultivars, but have utilized only additive genetic variation. Although heretosis has been documented in smooth bromegrass, no system of producing bromegrass hybrid cultivars on a commercial scale has been developed. Because the forage yields of smooth bromegrass have been increased only about 5 to 10% in over 50 yr of breeding synthetic cultivars, developing and evaluating F1 hybrid cultivars should be a priority of smooth bromegrass breeders. Selfing would not be necessary in the development of F1 hybrids (Knowles, 1955). Superior clones could be identified and maintained indefinitely. Tissue culture techniques can accelerate the vegetative increase of specific clones. Mechanical transplanting equipment can reduce the labor and cost of vegetatively establishing seed production fields.

Table 17-2. Smooth and meadow bromegrass cultivars, year and location of release, and principal attributes.†

Cultivar	Originator	Year released	Type	Principal attributes
Achenbach	Achenbach Bros. & Kansas AES‡	1944	Southern	First cultivar developed
Lincoln	USDA & Nebraska AES	1942	Southern	Broad adaptation, high forage and seed yields
Saratoga	New York AES	1955	Southern	Yield & regrowth yield
Manchar	USDA, Washington & Idaho AES	1943	Intermediate	Reduced rhizomes & seed yields
Carlton	Agriculture Canada, Saskatoon	1961	Northern	Improved seed yields
Baylor	Rudy-Patrick Co.	1964	Southern	Yield, disease resistance
Blair	Rudy-Patrick Co.	1964	Southern	Disease resistance, leafiness quality
Sac	Wisconsin AES & USDA	1962	Southern	Seed quality, disease resistance
Fox	Minnesota AES	1968	Southern	Seedling vigor, disease resistance
Magna	Agriculture Canada, Saskatoon	1968	Intermediate	Seed yields & quality
Rebound	South Dakota AES	1978	Southern	Regrowth yields
Polar	Alaska AES & USDA	1965	Polar and smooth brome hybrid	Winter hardiness
Signal	Agriculture Canada, Saskatoon	1983	Intermediate	Seed yield & quality
Radisson	Agriculture Canada, Saskatoon	1990	Southern	Forage yield
Badger	Wisconsin AES	1990	Southern	Forage digestibility
Regar	USDA	1966	Meadow	First cultivar of species
Paddock	Agriculture Canada, Saskatoon	1987	Meadow	Seed yield
Fleet	Agriculture Canada, Saskatoon	1987	Meadow	Seed yield

† Information extracted from Casler and Drolsom (1992); Hodgson et al. (1971); Knowles (1990a, b); Hanson (1972); Surprenant and Knowles (1990).
‡ AES = Agriculture Experiment Station.

In addition, molecular genetic approaches to improve smooth bromegrass have not been evaluated. Methods of propagating smooth bromegrass via tissue culture have been developed (Chen & Marowitch, 1985) and it is possible to regenerate smooth bromegrass plants from cells in suspension cultures. Because of the meiotic irregularities that exist in smooth bromegrass, the only way that genetically transformed smooth bromegrass plants could be used as cultivars would be as parents of F1 hybrid cultivars.

CULTIVARS

Smooth bromegrass cultivars used in the USA are predominately "southern" types while in Canada both "southern" and "northern" germplasm sources have been utilized (Table 17–2). In the north central region of the USA, the southern types have higher forage yields than the northern strains (Thomas et al., 1958). The first mountain bromegrass released was the cultivar Regar (Hanson, 1972; Foster et al., 1966). The first mountain bromegrass that was released was Bromar (Law & Schwendiman, 1946). Polar bromegrass is the most winter hardy brome species cultivar (Hodgson et al.,1971). It is based on 11 interspecific clones from smooth bromegrass and pumpelly bromegrass. The most widely planted bromegrass in the USA is probably Lincoln.

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