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19 Ryegrasses[1]

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Two species in the genus *Lolium* are among the most important pasture/forage/turfgrasses in the world, *L. perenne* L., perennial ryegrass or English ryegrass; and *L. multiflorum* Lam., Italian ryegrass or annual ryegrass. Some cultivars of Italian ryegrass are annuals while others are perennials with stand persistence of four or more years. Westerwolds (Westerwolths) ryegrass is an annual, early maturing type of Italian ryegrass that is used in emergency situations where rapid growth and high yields are desired. There are diploid and autotetraploid cultivars of both species. Short rotation ryegrasses are hybrids of *L. perenne* and *L. multiflorum*.

SYSTEMATICS AND MORPHOLOGY

Taxonomy

In 1968, E.E. Terrell of USDA-ARS, published his taxonomic revision of the genus *Lolium*. He proposed that the genus be subdivided into eight species. Besides the two species that are important to agriculture, Terrell (1968) charac-

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

terized five species of *Lolium, L. subulatum* Vis, *L. canariense* Steud., *L. temulentum* L., *L. remotum* Schrank, and *L. persicum* Boiss. and Hohen, that are mostly annual weeds. *Lolium temulentum* L., is referred to as darnel in the literature and is thought to be the species mentioned in Scriptures as the one sown in an enemy's grain field to introduce ergot (Hitchcock, 1971). The eighth species, Wimmera ryegrass, *L. rigidum* Gaud., is another weedy species that intergrades with *L. perenne* and *L. multiflorum*.

Perennial and Italian ryegrass are self-incompatible and cross-pollinated, according to Terrell (1968), whereas *L. temulentum, L. remotum*, and possibly Wimmera ryegrass are self-compatible and self-pollinated. *Lolium* species are interfertile, and will cross with *Festuca* species as well, including meadow fescue and tall fescue. Restriction fragment length polymorphism (RFLP) studies indicate close homology between the perennial ryegrass genome and the meadow and tall fescue genomes (Xu et al., 1991, 1992). Natural hybrids of perennial ryegrass and meadow fescue frequently are found in Europe. Species of the *Lolium* genus, however, are not known to cross with any other genera (Borrill, 1976; Stebbins & Crampton, 1961; Terrell, 1966, 1968).

Distribution and Adaptation

Perennial ryegrass is thought to be indigenous to parts of Europe, Asia, and North Africa, but the first records of use with cultivation came from England about 1677 (Terrell, 1968). The evolution and spread of perennial ryegrass seems to have been closely associated with the evolution and development of ruminant livestock farming, with evolutionary adjustments in plant structure to grazing intensity (Breese & Tyler, 1986). According to Davies et al. (1973, p. 143–162), perennial ryegrass is rarely found naturally in ungrazed situations. Italian ryegrass is thought to be indigenous to Italy, where it was grown under irrigation as a cut forage crop in the thirteenth century (Beddows, 1953). Westerwolds ryegrass originated in the Westerwolde area of the Netherlands. Today these species are widely distributed throughout temperate zones on all continents and are extensively used in Europe, the British Isles, New Zealand, Australia, the Americas, and Japan. Perennial ryegrass has adapted well to variation in winter severity from the harsh continental climates of North America and Europe to the mild maritime climates of the British Isles and New Zealand.

Use in Agriculture

In temperate areas where ryegrass is well adapted, it is the primary grass used for pasture and silage in dairy and animal production. Many diploid and tetraploid cultivars of perennial and Italian ryegrasses, as well as short rotation ryegrasses, have been bred for use in pasture mixtures or for silage. In New Zealand, ryegrass species and cultivars are the predominant component in nearly all pasture mixtures, with perennial ryegrass and white clover forming the basis for permanent pastures for dairy production, sheep (*Ovis aries*) and cattle (*Bos taurus*). The only major exception is on dry soils where alfalfa and other drought-tolerant species such as orchardgrass and hardinggrass have proved superior. Limited use also is made of Italian and short rotation ryegrass either sown as monocultures in the fall or overdrilled into white clover-dominant or low-producing pasture to provide winter and spring feed for grazing. Italian ryegrass also may be included in permanent pasture seed mixtures to provide rapid early feed production.

In continental Europe, the United Kingdom, and Ireland, perennial and Italian ryegrass form the basis of most pastures for grazing and silage. While clovers and other grasses are sometimes included, normal practice is to sow monocultures and topdress with fertilizer N. The significance of ryegrasses to agriculture in these countries is reflected by the huge investments in research (Van Wijk & Reheul, 1991, for Europe; Hunt & Easton, 1989, for the last 50 yr in New Zealand).

In the USA Italian ryegrass is treated as a winter annual in the southern states, i.e., fall planted for winter grazing. Lack of stand persistence the following summer may be due to high summer temperatures, high humidity, drought, disease, and/or nematodes. Several cultivars of Italian ryegrass, such as 'Gulf' and 'Marshall', have been developed at universities in southern states for winter grazing. The seedings may be made in a prepared seedbed or broadcast seeded on a permanent sod. For turf purposes, diploid cultivars of perennial ryegrass have been bred at several locations in the USA and used in the Northeast, mid-Atlantic states, southern states, some north central states, and in Oregon and Washington. Turf cultivars of perennial ryegrass have been bred in New Zealand with emphasis on increasing winter growth, which is usually low in turf ryegrasses developed for continental temperate climates.

General Description

There are numerous characteristics that may be used to differentiate species within the *Lolium* genus. Select taxonomic characters that aid in differentiating between perennial and Italian ryegrass are presented in Table 19–1 and illustrated in Fig. 19–1 and 19–2; however, shoot development and leaf dimensions may be altered substantially by temperature, irradiance, water availability, and/or defoliation. This makes it difficult to use definitive criteria over a wide range of environments. An increase in temperature generally intensifies the effects of a

Table 19-1. Selected taxonomic characters of ryegrass that are different for perennial and Italian ryegrass.

	Species	
Taxonomic descriptors	Perennial ryegrass	Italian ryegrass
Spikelet flower numbers	Low	High
Awn	Typically absent	Typically present
Plant height	Short	Tall
Longevity	Perennial	Annual and perennial
Leaf blade width	Narrow	Wide
Leaf blade length	Short	Long
Leaf vernation	Folded	Rolled
Auricles	Present (short) or absent	Usually present (often long)
Ligules	Truncate or erose	Rounded, truncate, or erose
Root fluorescence	Typically nonfluorescent	Typically fluorescent

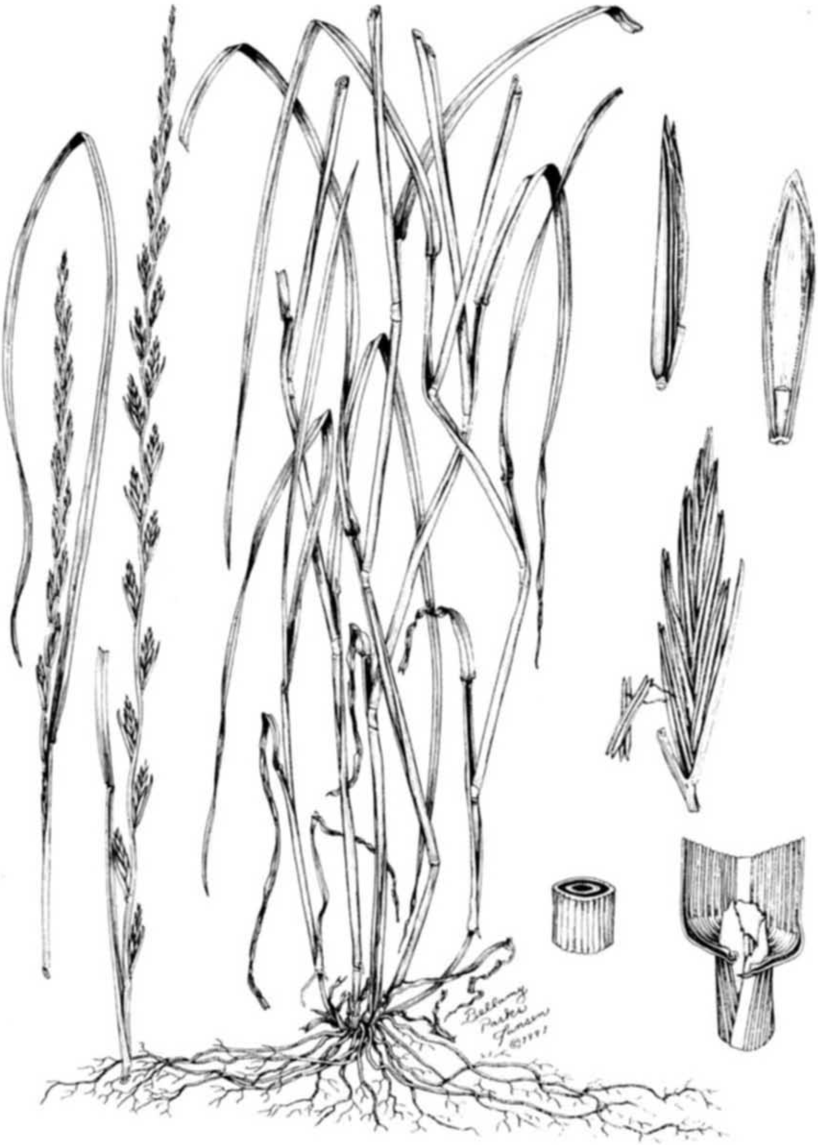


Fig. 19–1. Illustration of perennial ryegrass morphology.

reduction in irradiance on shoot development (Mitchell & Soper, 1958). The most reliable descriptors that may be used in differentiating between perennial and Italian ryegrass are presence or absence of awns, the folding or rolling of leaves in young shoots, and the number of florets per spikelet. Root fluorescence also has been used to differentiate the two species (Brougham et al., 1960), although the reliability of this character has been questioned (Pana, 1981).

Fig. 19–2. Illustration of Italian ryegrass morphology.

IMPORTANT AGRICULTURAL CHARACTERISTICS

The ryegrasses have several important performance characteristics which account for their widespread use and popularity. Among them are high herbage yield, a long growing season, tolerance to a wide range of environmental conditions and grazing practices, rapid seedling establishment, weed suppression, excellent persistence under close grazing, compatibility with white clover, and high forage quality and palatability.

Research trials in New Zealand, British Isles and Europe have shown that ryegrass yield in monocultures and mixtures is consistently high in grazed pastures or when used for silage. Yields exceeding 16 t ha^{-1} have been obtained in cutting and grazing trials under optimum environmental and soil fertility conditions. Ryegrass performs best under a high N status. Under maritime conditions, it has a relatively high winter and early spring production and has ability to recover from mild summer drought. Italian ryegrass provides excellent high-quality winter pasture in France, Germany, United Kingdom, Spain, Portugal and the southern states of the USA. For instance, Gates and Wyatt (1989) reported that individual animal performance was higher, and cost of weight gain was lower for beef cattle grazing Marshall annual ryegrass than they were for cattle grazing 'Forager' tall fescue over winter in Georgia. Its growth in the fall continues longer than reed canarygrass, smooth bromegrass, orchardgrass or timothy.

The seasonal growth of ryegrass-based pastures fits in well with sheep and cattle grazing system in New Zealand and Australia. Lambs are born in early spring and sold prior to onset of summer drought. Dairying and cattle raising also take advantage of high spring grass production by calving in early spring and obtaining peak production and growth during spring and early summer. During winter, animal feed requirements are met from residual pasture growth supplemented by hay or silage.

Tolerance to Environmental Conditions and Management Practices

While less tolerant than orchardgrass, timothy, or fescue species to freezing temperatures and summer drought, the ryegrasses show a high degree of tolerance to climatic variations in temperate climates. However, their ability to thrive under different management systems is their main advantage over other grass species. Perennial ryegrass in particular has the ability to withstand close continuous grazing and thus is ideally suited for intensive sheep and cattle grazing systems. Italian ryegrass, on the other hand, with its more upright and open growth habit is well suited to grazing systems involving lengthy intervals between grazings and for silage production. It retains its quality even when rest periods are relatively long. Ryegrass, especially the diploid perennial cultivars, will tolerate treading well (Edmond, 1966; Table 19–2).

Table 19–2. Relative herbage yields of a mixed pasture after treading by sheep (adapted from Edmond, 1966).

Sheep stocking rate	Whole pasture	Species composition				
		Perennial ryegrass	Orchardgrass	Timothy	Prairie grass	Yorkshire fog
ha^{-1}	% yield†					
0	100	100	100	100	100	100
20	89	104	55	71	68	13
40	79	95	35	59	61	12
80	73	91	25	41	71	1

† Percentage of yield obtained with zero grazing.

Seedling Establishment and Competitive Ability

The rapid germination and early seedling establishment gives ryegrass a competitive advantage over other companion species and can lead to major suppression and even death of these species. Italian and short-rotation ryegrass species are more aggressive than perennial ryegrass and may be included in seed mixtures to provide quick growth for early herbage production and to suppress weeds. Use of different seeding rates of the component species can be used to obtain a balance between rapid seedling growth, minimal suppression of companion grasses and clovers and weed suppression (Cullen, 1964; Cullen & Meeklah, 1959; Harris, 1968). In established pastures under intensive grazing management, weed infestation is minimized unless the sward is weakened by low mineral nutrition, poor management or insect damage.

Forage Quality

Among the cool-season grasses, ryegrass has few equals in regard to forage quality (Table 19–3). Ryegrasses accumulate high levels of total nonstructural carbohydrate (TNC) in their herbage in spring and fall (Jung, 1975; Jung et al., 1974, 1976; Waite, 1957; Waite & Boyd, 1953), and tetraploids generally accumulate more nonstructural carbohydrate than diploids. This readily available energy can be used for plant growth or as a source of readily available energy to herbivores. Levels of TNC are inversely related to temperature, and therefore summer levels of TNC in dry matter (DM) of ryegrass were low (approximately 60–120 g kg^{-1}) in the USA (Jung et al.,1974) and New Zealand (Thom et al., 1989), whereas summer levels were higher in Scotland (Waite & Boyd, 1953). On the other hand, cloudy weather causes low TNC levels (<100 g kg^{-1}) in Britain and Ireland in fall. This necessitates the use of supplemental carbohydrate or a chemical preservative to make good silage. In contrast, November concentration of TNC in 40 ryegrasses in Pennsylvania ranged from a high of 350 g kg^{-1} for Italian 'Tetra' to a low of 160 g kg^{-1} for 'Ariki' (Berg & Jung, unpublished data). Perennial ryegrass tetraploids, 'Barvestra' and 'Reveille,' also had high TNC concentrations, averaging 310 g kg^{-1} DM. Substituting ryegrass for other temperate grasses in the USA could increase available energy levels 20 to 50%, and thereby improve animal nutrition and production (Jung et al., 1976).

Palatability and DM intake of tetraploid ryegrasses by cattle generally are greater than those of diploids (Hageman et al., 1993; Vipond et al., 1993). Leaf strength was shown by Evans (1967) to be in the order perennial ryegrass > short

Table 19-3. Nutritive value of perennial ryegrass herbage at different plant growth stages (adapted from Waite et al., 1964).

Growth stage	Crude protein	Cell wall	DM dig.	Metabolizeable energy
	g kg^{-1}			MJ kg^{-1} DM
Young-leafy	185	400	860	12.0
Late-leafy	152	450	830	10.8
Head emergence	138	470	790	10.9
Seed setting	96	600	620	8.9

rotation ryegrass > Italian ryegrass, and was related to cellulose and sclerenchyma contents of the grass. Rumen microflora penetrate ryegrass leaf blade tissue more easily than that of other cool-season grasses (Grabber & Allinson, 1992). For instance, transverse sections of ryegrass and reed canarygrass leaves prior to and after 12 h digestion (Fig. 19–3) show the greater digestion of ryegrass leaf parenchyma than that of reed canarygrass. In studies with 300 finely ground leaf samples, mean in vitro dry matter digestibility (IVDMD) concentration was 774 g kg^{-1} for two tetraploid perennial ryegrasses grown in binary mixtures with alfalfa, whereas it was 694 g kg^{-1} for comparable samples of 'Pennlate' orchardgrass (Jung et al., 1982). Dry matter digestibility of ryegrass decreased with advance in maturity, but not as rapidly as orchardgrass.

Growth Patterns

Growth of perennial ryegrass in controlled environments has been extensively researched (Hunt & Halligan, 1981). The temperature optimum for growth of perennial ryegrass was reported to be 18 to 20°C (Mitchell, 1956), and growth responses to changes in irradiance occurred from 10 to 30°C (Mitchell, 1953). Hunt and Halligan (1981) reported that ryegrass plants showed saturation-type growth kinetics with irradiance, but the shape of the irradiance response curve was temperature dependent. Maximum growth at 20°C resulted from a greater partitioning of dry weight to leaf than at lower temperatures, as well as a higher net assimilation rate than at other temperatures (Hunt & Halligan,1981). Between 7 and 20°C, leaf area changes compensated for changes in net assimilation rate over a range in irradiance, and resulted in near maximum growth rates; however, at 30°C and above, changes in leaf area were not sufficient to maintain near maximum growth rates. Over the range 7 to 33°C, there did not seem to be an optimum temperature for leaf or root appearance or for tillering (Hunt & Thomas, 1985). Thus, the latter authors concluded that irradiance and temperature determined the rate of leaf appearance through effects on the rate of assimilate supply and utilization at the stem apex. Leaf appearance rates in turn determined potential rates for production of tillers or roots by determining the sites available.

Ryegrass swards are composed of populations of competing tillers (each with two growing leaves at any one time), whose initiation and death follow a seasonal rhythm (Hunt & Easton, 1989; Hunt & Field, 1978; Korte et al.,1984; L'Huillier, 1987). Ryegrass tiller densities increased in winter, when tiller death was low, and decreased after flowering, when tiller death was high. L'Huillier (1987) found that rate of perennial ryegrass tiller appearance was highest in summer (41.3 tillers m^{-2} d^{-1}) and lowest in spring (18.4 tillers m^{-2} d^{-1}) in a New Zealand dairy pasture. Likewise, rate of tiller death also was highest in summer (50.6 tillers m^{-2} d^{-1}) so that there was a net loss of tillers. Brougham (1970) reported that ryegrass persistence was improved when ryegrass/white clover pastures were grazed less intensely in summer. Grazing management had a large effect on tiller density in pastures. Set stocking or continuous grazing resulted in higher densities than rotational grazing, because fewer tillers were removed by eating when continuously grazed. Tiller death rate in spring and summer was greater at a stocking density of 2.77 cows ha^{-1} than at 4.28 cows ha^{-1}.

Brougham et al. (1960) showed that different plant types in ryegrass hybrid 'Manawa' were favored by intensive vs. light grazing. Under 2 yr of intensive grazing, the sward was composed mostly of perennial types of ryegrass, whereas under light grazing, the sward was composed mostly of Italian types of ryegrass. Root fluorescence and morphology of the inflorescences under these conditions maintained the same associations as in the parent species, suggesting that introgression within the hybrid population was limited. Similarly, Valentine and Charles (1975) reported that plasticity in 'S23' perennial ryegrass was great. Some genotypes had high mean yields and good responses to increased levels of N while other genotypes had high mean yields but were not as well adapted to high N levels.

Hunt and Easton (1989) reported that similar growth rates are often obtained from relatively low population densities of large ryegrass tillers and high population densities of small tillers. When grown as spaced plants, all ryegrass leaf buds develop into tillers and tiller number increases exponentially until intertiller competition becomes significant (Davies & Thomas, 1983; Hunt & Halligan, 1981). Tillering ceases when tiller bases are heavily shaded by high accumulation of herbage, and tillering resumes only after herbage removal (Hunt & Field,1978; L'Huillier, 1987; Mitchell & Coles, 1955). The adverse effects of shade on growth and tillering of ryegrass were found to be amplified by higher temperatures (Mitchell, 1953). Tiller production was affected less by shading in Italian ryegrass than in perennial ryegrass (Evans, 1964). Nitrogen fertilizer enhances turnover rate of ryegrass tillers (Hunt & Mortimer, 1982).

The shoot apex of ryegrass is positioned within the base of an enveloping leaf sheath (Cooper, 1950). At each node along the axis of the shoot apex, leaf and bud primordia are formed. When conditions are suitable, the leaf primordia elongates to form a leaf, and the bud may form a new vegetative tiller. The shoot apex of Italian ryegrass is longer than that of perennial ryegrass, but in general, size of the stem apex or primordium is not closely correlated with leaf dimensions at maturity (Mitchell & Soper, 1958). In spring, a transformation occurs during shoot development, that results in the formation of reproductive tillers and the emergence of an inflorescence. Perennial ryegrass was reported to have an obligate vernalization requirement of at least 2 wk at 4°C or lower before inflorescence development was initiated (Evans, 1960). This physiological process terminates the vegetative shoot (Evans & Grover, 1940). According to Cooper (1950), the time elapsed between initiation of inflorescence development and head emergence is approximately 4 to 5 wk.

Time of cessation and severity of autumn grazing in Ireland subsequently affected tissue turnover during winter, spring, and early summer as well as herbage availability in the following spring (Carton et al.,1988a, b). Early (September) cessation of autumn grazing was associated with produciton of leafier tillers and greater leaf growth in spring than that from swards grazed later in autumn. Additionally, autumn and winter grazing of ryegrass/white clover swards in Northern Ireland increased the number of clover growing points in April, provided that clover stolons were not buried during grazing (Laidlaw et al. 1992). Under warmer conditions in New Zealand, intermittent top removal in autumn increased tiller density and winter survival, provided stubble height was adequate to maintain energy reserves (Brougham, 1970; Hume & Lucas, 1987).

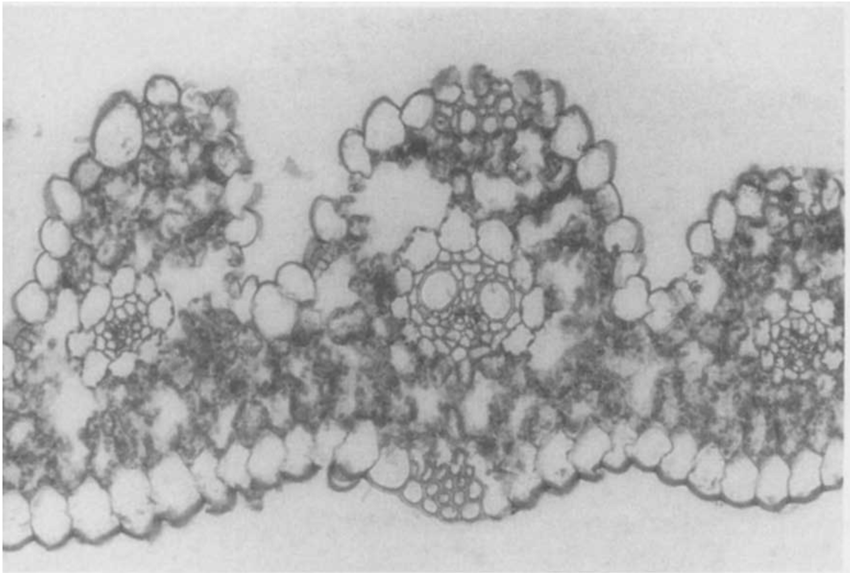


Fig. 19-3a & b

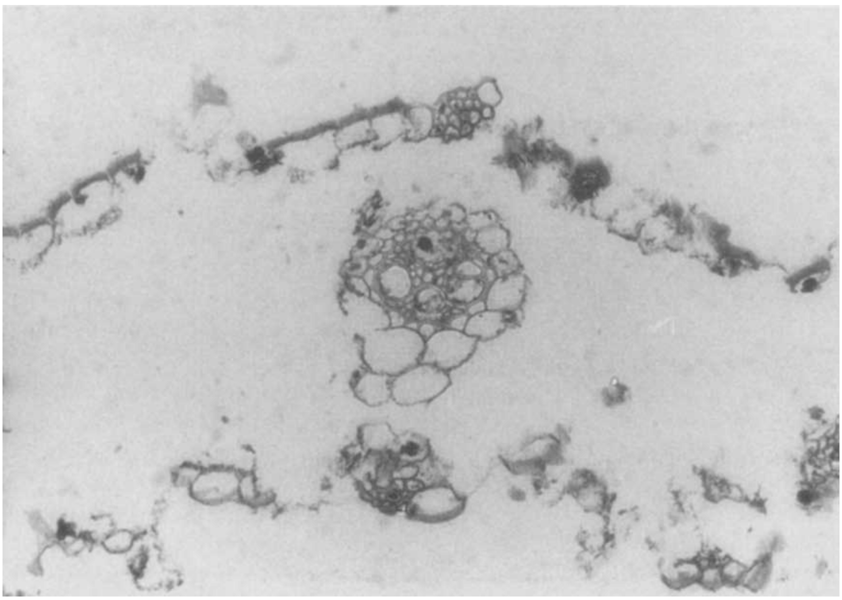


Fig. 19–3. Transverse sections (X250) of 'Bison' short rotation ryegrass (*A* & *B*) and 'Palaton' reed canarygrass (*C* & *D*) prior to (*A* & *C*) and after 12 h in vitro fermentation (*B* & *D*) (adapted from Grabber & Allison, 1992).

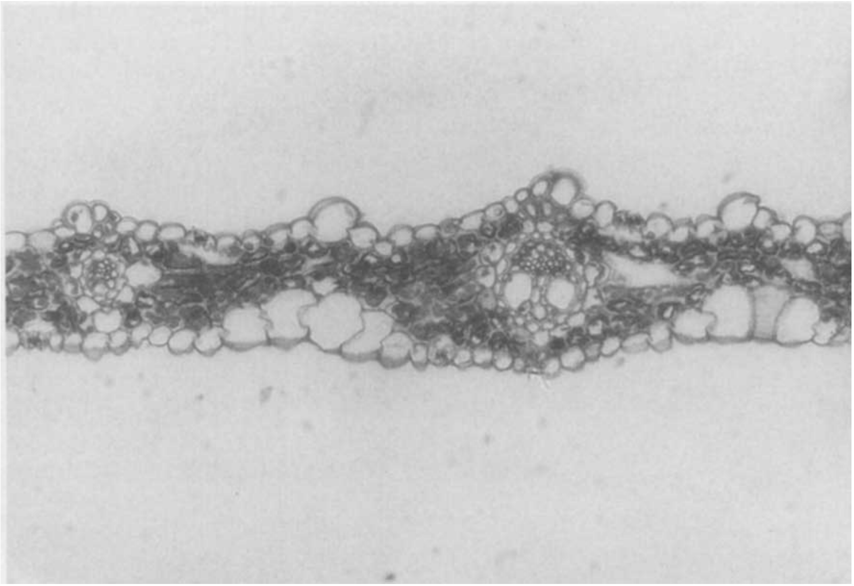
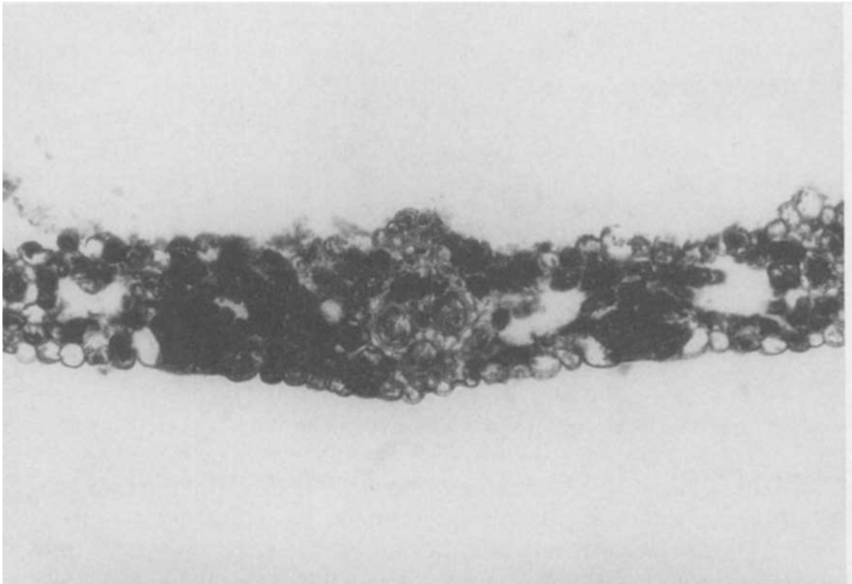


Fig. 19-3c & d



In a series of experiments, Cooper (1950, 1951, 1952, 1954, 1960a,b) found that the critical day length for heading of Irish accessions of Italian ryegrass varied, some were heading in a 9-h d, while others had not headed even when day length was extended to an 11-h d. Cooper suggested that the vernalization requirement and critical day length for heading of ryegrasses seemed to be closely related to the geographical origin of the species or cultivar. Mediterranean types of ryegrass tend to have no vernalization requirement and a lower critical day length, whereas ryegrasses adapted to northwest Europe have a stronger winter requirement and a higher critical day length. Cooper (1950, 1952) also reported that when ryegrass cultivars are moved to regions where latitude, altitude, and temperature are different, their dates of heading and rates of herbage maturation may change, but the order in which cultivars would head would not change. On the other hand, the relative ranking of 10 perennial ryegrass cultivars for productivity and seasonal growth in Wales was considerably different, depending on whether the cultivars were grown at a lowland (30-m) or an upland (305-m) site (Davies et al.,1984). Only 35% of the variation in productivity and seasonal growth at the two locations could be attributed to cultivar.

Perennial ryegrasses have a very wide range of heading dates that allows for management flexibility. Currently, Dutch cultivars are available that head as early as the beginning of May and as late as mid-June in Europe or Pennsylvania, USA. This allows farm managers to select ryegrass cultivars that have ontogenetical cycles that are similar to those of other species in mixtures or those that are best suited to a particular management. Additionally, the use of later-heading cultivars extends the period of time in which a high proportion of leaves is available to the grazing animal. Carton et al. (1989) discussed the importance of reducing the extent of reproductive growth in grazed swards and the difficulties in attaining this goal in rotationally grazed swards. Inflorescences of perennial ryegrass generally emerge only in the spring, whereas inflorescences of Italian and short rotation ryegrasses emerge from every crop. An exception to this pattern with perennial ryegrass can occur during dry weather when additional reproductive stems emerge in later cuts (Korte & Chu, 1983). High rates of N fertilizer were found to advance floral initiation and inflorescence emergence 1 wk in perennial ryegrass and up to 3 wk in Italian ryegrass (Wilson, 1959).

Tetraploid plants of perennial ryegrass generally have wider and darker leaves, more robust tillers, a lower tiller population, and a lower percentage DM than diploids (Van Wijk, 1988). Diploid plants generally have a high tiller population and sward density. The more open sward structure of tetraploids frequently has resulted in underestimates of stand persistence.

Legume Compatibility

While the aggressive ryegrass characteristics can cause suppression of legumes during establishment, this is seldom a major problem. The compatibility of ryegrass with legume depends on soil drainage, availability of nutrients (especially N), weather conditions, season, legume species, grass cultivar, intensity of grazing, length of the grazing rotation and insect damage. Soil N levels affect the balance of ryegrass and clover in mixtures during early pasture development.

Ryegrass has difficulty competing strongly when soil N levels are depleted, but becomes more aggressive as soil N levels are raised through N fixation by clover. Excellent ryegrass-white clover pasture swards persist in New Zealand indefinitely. Usually, however, the legume is reduced to less than 20% after a few years because of grass competition. The sward then becomes self-regulating; N fixation becomes inadequate once the clover content falls, resulting in less ryegrass growth. Ryegrasses generally rank intermediate in aggressiveness between timothy (least) and orchardgrass (most) in the northeastern USA, whereas the ryegrasses are more competitive in maritime climates (Cullen, 1964; Davies et al., 1960; Jung & Shaffer, 1993; Jung et al., 1991; Sears, 1950; Stapledon & Davies, 1928).

When perennial and Italian ryegrass were grown in binary mixtures with alfalfa in Pennsylvania, the yield of the companion grasses were similar in the first-cut, whereas yield of Italian ryegrass was 300 and 100% higher than that from perennial ryegrass in the second- and third-cuts, respectively (Fig. 19–4; Jung & Shaffer, 1993). Italian ryegrass penetrated the alfalfa canopy in summer while perennial ryegrass did not.

When alfalfa-ryegrass mixtures were grazed in Pennsylvania, a species relationship prevailed that was dynamic through the grazing season. Tetraploid ryegrass contributed approximately 30 to 35% of the total yield of the mixture each spring, 20% in summer, and 50% in fall (Jung et al., 1982). In comparison, the orchardgrass component in mixtures with alfalfa, continued to increase each year, and became the dominant species in the mixture. Orchardgrass leaves penetrated the alfalfa canopy throughout the growing season, whereas those of perennial ryegrass did not. Alfalfa stands persisted 6 yr with ryegrass and only 3 yr with orchardgrass; however, harvest frequency markedly influences botantical composition of the stand. When rest periods between grazings/cuttings exceed 35 d, alfalfa has the competitive advantage, whereas when rest periods are less than 30 d ryegrass has the advantage. Nitrogen fertilizer will increase species competition, and at high rates, alfalfa persistence in ryegrass mixtures may be reduced to 2 or 3 yr.

Evaluations of ground cover potential of ryegrass mixed with alfalfa in Wisconsin showed that southern Wisconsin provided the better environment for screening perennial ryegrass, while northern Wisconsin was better for screening Italian ryegrass (Casler & Walgenbach, 1990).

LIMITATIONS TO PRODUCTION

Environmental Stresses

Ryegrasses are not as tolerant of high temperatures or drought as smooth bromegrass, but more so than timothy (Mitchell, 1956). They tolerate day temperatures of at least 35°C, but level of tolerance for day temperatures undoubtedly depends on night temperature (Baker & Jung, 1968). Maritime climates are often characterized as having lower night temperatures in midsummer than continental climates such as those of the midwestern states in the USA. Ryegrass is

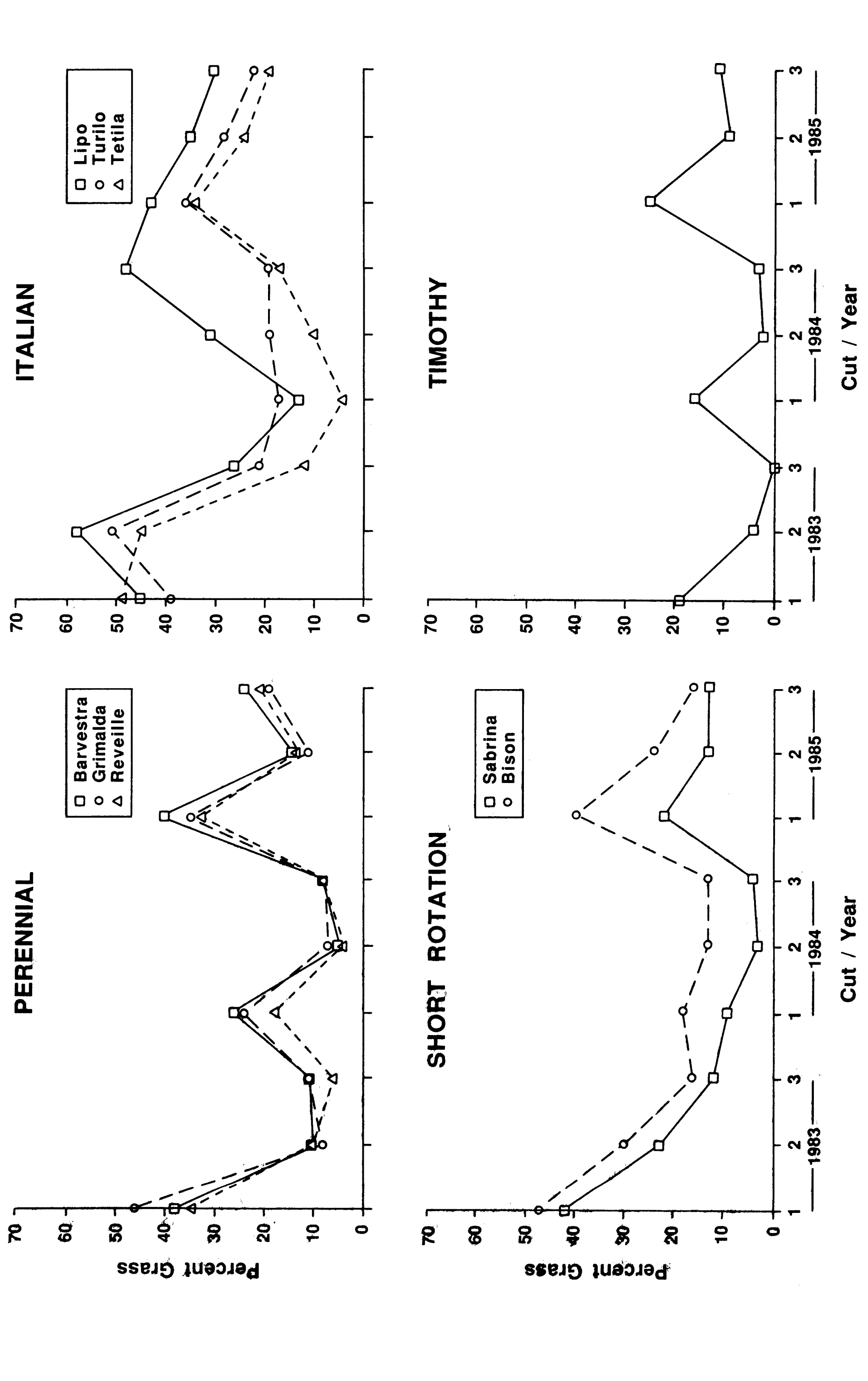


Fig. 19–4. Grass content (g kg^{-1}) of binary mixtures with alfalfa on two Pennsylvania dairy farms (adapted from Jung & Shaffer, 1993).

not considered to be a drought-tolerant species. It turns brown in the northeastern and central USA when dry weather prevails for an extended period of time. In New Zealand, ryegrasses have not been as drought tolerant as tall fescue, orchardgrass, or phalaris (hardinggrass). Some ryegrass cultivars are able to recover from drought more quickly than others. Van Wijk (1988) concluded from observations in Belgium and Great Britain that tetraploid ryegrasses were somewhat more drought tolerant than diploids.

Lack of winterhardiness was a serious problem with cultivars of both perennial and Italian ryegrass when these species were introduced to the USA. Much progress has been made in identifying cold-tolerant germplasm. Some improved cultivars of both species have persisted under grazing/hay/turf conditions for more than 4 yr in Pennsylvania. In one trial, winter injury of 40 ryegrass cultivars (Table 19–4) ranged from 4% for two perennial diploids, Pennfine (turf) and Barenza (forage) to 90% for two Italian ryegrasses (data not shown) in the third harvest year. Eight cultivars of perennial ryegrass had mean winter injury ratings of less than 9%. In Vermont, winter survival of perennial ryegrass with short subcrown internode lengths averaged 52%, whereas cultivars with long subcrown internode lengths averaged only 28% survival (Wood & Cohen, 1984).

Cold tolerance of landraces of perennial ryegrass was shown to be negatively correlated with relative leaf expansion rate at low temperatures, and with mean winter temperature at their places of origin (Table 19–5). Humphreys and Eagles (1989) and Tyler and Charlton (1979, p. 43–46) suggested that earlier-heading genotypes of perennial ryegrass are less tolerant of freezing than late-heading genotypes, although they were able to find good freezing tolerance in all heading categories. Breese and Tyler (1986) reported that three Swiss perennial ryegrass cultivars were most unusual because they were early growing in spring, winter hardy, very early flowering and yet persistent under grazing.

Lorenzetti et al. (1971) reported that cold tolerance in perennial ryegrass under controlled environment was not closely related to winterhardiness in the field. Periods of warm weather in winter often reduce plant cold tolerance in the field, especially with plants that do not develop a high level of dormancy.

Diploids are used extensively in turf mixtures in the northeastern and part of the north central USA. Recommended cultivars are considered well adapted to these conditions. Studies in Ohio showed that stand persistence of diploid perennial ryegrass was improved when it was grown in mixtures with Kentucky bluegrass, *Poa pratensis* L. (Niehaus,1973).

Sometimes snow molds incited by *Microdochium nivale* (Fr.) Samuels and I.C. Hallett, *Fusarium nivale* (Fr.) Sorauer, or *Typhula* spp. can cause problems with stand persistence. The diseases occur more frequently when autumn top growth is excessive and is not removed (Braverman et al., 1986). Diploids are more susceptible to snow mold than tetraploids (Van Wijk, 1988). In nordic countries, fungal diseases that occur during winter, often constitute a serious threat to productive stands of perennial ryegrass (Årsvoll, 1973; Ekstrand, 1955; Mäkelä, 1986). Jönsson and Nilsson (1992, p. 25–34) reported that snow mold resistance could be more easily improved in perennial ryegrass of south Scandinavian origin than in ryegrass of more northerly origin. Selection for snow mold resistance

Table 19-4. Percentage winter injury and disease ratings of perennial ryegrass cultivars based on visual estimated at Rock Springs, PA, June 17 (unpublished data, C.C. Berg & G.A. Jung).

Cultivar	Country of origin	Winter injury	Crown rust†	*Drechslera*†
		%		
		Diploid forage		
Barenza	Netherlands	4.5	5.0	5.5
Karin	Netherlands	6.2	4.9	6.5
Premo	Netherlands	6.7	4.9	5.0
Wendy	Netherlands	7.0	5.0	6.5
Angela	Netherlands	7.5	5.2	7.0
Barlenna	Netherlands	11.2	5.0	4.5
Carla	Netherlands	12.5	4.9	7.0
Lamora	Netherlands	13.2	4.8	5.0
Splendor	Netherlands	13.7	4.4	5.0
Pelo	Netherlands	14.5	5.2	5.0
Animo	Netherlands	16.2	5.2	4.5
Mombassa	Netherlands	16.5	5.1	5.0
Linn	USA (Oregon)	17.5	5.4	5.5
Delta	Sweden	18.0	5.7	5.0
Epic	USA (Minnesota)	21.2	5.2	5.0
Springfield	Netherlands	27.5	4.9	5.5
Bocage	France	41.2	5.2	5.5
Barbantia	Netherlands	67.2	5.0	5.0
Permanent pasture	New Zealand	70.7	4.9	5.5
Ariki	New Zealand	73.2	5.1	5.5
Melle	Belgium	78.7	5.1	6.5
S-321	UK (Wales)	83.7	5.4	4.0
		Diploid turf		
Pennfine	USA (PA)	3.7	6.0	5.0
NK-200	USA (MN)	6.2	6.4	5.0
Norlea	Canada	8.7	6.8	5.5
NK-100	USA (MN)	28.7	4.8	4.5
		Tetraploid forage		
Barvestra	Netherlands	12.0	3.4	4.5
Reveille	Netherlands	18.7	3.4	4.0
Terhoy	Netherlands	35.0	3.5	4.0
Petra	Netherlands	77.5	4.2	5.5

† Based on a visual rating of 0 to 9, where 0 = no disease, 1 = trace, 5 = moderate level, and 9 = severe infection.

shifted yield towards a larger first-cut, i.e., a distribution of yield similar to northern Scandinavian type.

Italian ryegrass cultivars also exhibit a wide range of winterhardiness. The mechanism(s) of cold tolerance needed for southern latitudes (USA) may be different than those needed for northern latitudes. Italian ryegrass does not become dormant in winter in the south, and therefore active tillers must tolerate rapid shifts in temperature over a short time span. Insufficient cold hardening can become a problem under these conditions and can result in loss of stand. Eagles (1984) showed that cold tolerance of Italian ryegrass cultivars increased as the hardening temperature was lowered from 10 to 2°C and the duration of harden-

Table 19-5. Growth responses of climatic races of perennial ryegrass at low temperatures (adapted from Cooper, 1963).

Climatic races and cultivars of perennial ryegrass	Relative leaf expansion at 5 °C	Relative leaf expansion In December	Survival at −5 °C	Mean temperature of winter month
	%	%	%	°C
Algiers	26.6	28.0	0	9.6
New Zealand	13.8	14.8	20	5.8
Oregon	12.4	13.9	13	4.8
Irish	12.2	12.8	47	5.6
Devon	11.1	13.2	36	6.1
Melle	9.5	13.7	57	1.3
Pejbjerg	7.6	11.0	73	−0.1
Russian	7.7	9.7	92	−3.6

Table 19-6. Influence of hardening temperature and duration on the LT_{50}† values of three Italian ryegrasses (adapted from Eagles, 1984).

Hardening temperature	RvP 7d	RvP 14d	Optima 7d	Optima 14d	Grasslands Paroa 7d	Grasslands Paroa 14d
	°C					
Unhardened	−7.3		−5.7		−6.2	
10	−8.8	−10.2	−8.7	−9.8	−7.7	−9.0
8	−9.3	−11.6	−9.7	−10.6	−8.2	−9.7
6	−9.7	−11.8	−10.4	−10.9	−8.1	−10.0
4	−10.3	−12.4	−10.3	−11.9	−8.3	−10.3
2	−11.0	−13.6	−10.7	−12.7	−9.0	−10.6

†LT_{50} = temperature at which 50% of the population is killed.

ing was extended from 7 to 14 d (Table 19–6); however, the rate and extent of the changes in cold tolerance differed among cultivars.

Tamura and Hoshino (1979a, b) found differences among and within both diploid and tetraploid Italian ryegrass cultivars for survival under snow. Cultivars with the highest concentration of TNC generally showed the best survival under snow. Late-heading diploid cultivars generally had a higher concentration of TNCs.

Hides (1979) showed significant improvement in cold tolerance in Italian ryegrass with two cycles of selection in a controlled environment. He also demonstrated the possibility of obtaining a high level of cold tolerance with good growth potential during winter and early spring. Marshall Italian ryegrass, a very cold-tolerant cultivar, was the result of 29 yr of natural selection under field conditions in north Mississippi where temperatures fluctuate frequently during the winter months (Arnold et al., 1981).

Pest Problems

Diseases

In the northeastern USA, crown rust caused by *Puccinia coronata* Corda, stem rust caused by *P. graminis* subsp. *graminicola* Z. Urban, bacterial wilt caused by *Xanthomonas campestris* pv. *graminis*, and *Drechslera* (*Helminthosporium*) spp. can be problems with perennial ryegrass, depending on weather conditions and cultivar susceptibility. Plant pathologists, R.T. Sherwood and K.E. Zeiders, rated 40 monocultures of ryegrass cultivars for crown rust and *Drechslera* susceptibility (Table 19–4). Heavy rust infections negatively impact forage palatability. Resistance to both rust and *Drechslera* was high in three tetraploids, Reveille, 'Terhoy,' and 'Barvestra'. It was evident that potential use of turf cultivars for pasture would be limited by susceptibility to rust. Disease loads are generally lower on pasture herbage than on hay crops and diseases are controlled by chemicals in some turf situations.

In the southeastern USA, crown rust and blast (foliar disease caused by *Pyricularia grisea* Cke.) can be major problems on Italian ryegrass. Crown rust is controlled by using resistant cultivars and blast is controlled by planting ryegrass late in the fall. Additional information on diseases of ryegrass may be obtained from Braverman et al. (1986). Crown and stem rusts are the most common diseases of ryegrass in New Zealand, but fungal saprophytes have been found to produce toxins that cause facial eczema (Brook, 1963). Also, Gallagher et al. (1981) isolated potent neurotoxins, lolitrem A and lolitrem B, from plants in staggers-producing pastures. Hunt and Easton (1989) recently reviewed ryegrass disease problems and progress toward control in New Zealand.

Insects

Grass grub (*Costyletra* spp.) is an important pest of ryegrass (and other cool-season grasses) in most places where grass is grown (Potter & Braman, 1991). Grub larvae eat ryegrass roots, rendering the plant more susceptible to drought. Apparently ryegrass is one of the preferred plant species of the insect (East et al., 1979; Radcliffe, 1970).

It has been well established that the endophytic fungus *Acremonium lolii* Latch, Christensen and Samuels imparts some insect resistance to perennial ryegrass. The endophytes in Italian ryegrass are probably a different species than *A. lolii* (Latch et al.,1987). The fungal endophyte grows in the intercellular spaces in the leaf sheath and stem of ryegrass (Fletcher et al., 1990). In the absence of the Acremonium endophyte, the Argentine stem weevil (*Listronotus bonariensis*) often interferes with stand establishment and vegetative reproduction, and reduces stand persistence of perennial ryegrass in New Zealand (Barker et al., 1989; Prestidge et al., 1985). Annual production losses to this insect in New Zealand were estimated to be $120 to 150 million (NZ). When the endophyte is present, peramine is produced which deters feeding and oviposition of adult Argentine stem weevils (Gaynor & Hunt, 1983; Gaynor & Rowan, 1985). The presence of the endophyte also has been reported to confer higher levels of resistance to the Russian wheat aphid, *Diuraphis noxia* (Clement et al., 1992) and greenbugs, *Schizaphis graminum* (Breen, 1992).

McGee et al. (1991) reported that *A. strictum* isolated from perennial ryegrass was inhibitory to five species of fungi commonly associated with grass. On the other hand, high endophyte levels in ryegrass can reduce herbage palatability and average daily liveweight gains of animals; and induce ryegrass staggers, a neuromuscular syndrome (Fletcher & Harvey, 1981). Ryegrass staggers occurs when plants are under environmental stress and when pastures are grazed severely. Ryegrass staggers is thought to be caused by the toxin, lolitrem B, but it is unclear whether lolitrem B is of fungal or plant origin(Fletcher et al.,1990). Efforts are being made in New Zealand to introduce types of *Acremonium lolii* (Latch, Christensen, and Samuels) into ryegrass that impart insect resistance with minimal adverse effects on animal performance. *Acremonium lolii* (Latch, Christensen, and Samuels) induces a different physiological disorder in animals than does *A. coenophialum* Morgan-Jones and Gams in tall fescue. Chapter 15 (Sleper & West, 1996) describes the situation in tall fescue. Hunt and Easton (1989) state that treatments in many New Zealand research trials probably were confounded with endophyte level, raising a question as to the validity of their conclusions. Fletcher et al. (1990) and Van Heeswijck and McDonald (1992) reviewed the impact of *Acremonium* endophytes in New Zealand and Australia. Other insects causing ryegrass damage in New Zealand include porina, *Wiseana cerumata* Walker, black beetle, *Heteronychus arator* (F) and black field cricket *Teleogryllus commodus* (Barratt et al., 1990). Slugs, *Deroceras reticulatum*, and *Arion intermedius* also can be a problem in pastures (Barker, 1991).

Latch et al. (1987) reported that seeds from 80% of collections of perennial ryegrass from center of origin or from old pastures in Europe were found to be infected with endophyte, whereas only 25% of commercial European cultivars had infected seed. Additionally, 66% of seed samples of Italian ryegrass growing in the wild in Italy contained endophyte but none of the eight commercial Italian ryegrass cultivars released by the Welsh Plant Breeding Station were infected.

Seed Production

Most ryegrass seed in the USA is produced in the Pacific Northwest, primarily in Oregon and Washington. The climate is ideally suited to cool-season grass seed production (Youngberg & Wheaton, 1979). Mild winter and spring temperatures coupled with a slow steady rainfall pattern are conducive to grass seed development while dry summers are favorable for harvesting of high-quality seed. This area can produce annual ryegrass seed yields in excess of 2200 kg ha^{-1} (Nelson et al., 1992; Prine et al.,1989). In 1989, over 81 000 ha of annual and perennial ryegrass were harvested for seed in Oregon alone (Miles, 1990).

Seed production problems include reduced isolation for production of certified seed due to the long history of grass seed production in this region. Blind seed disease, incited by *Gloeotinia temulenta* (Prill & Delacr.) M. Wilson, M. Noble & E. Gray, a serious problem of ryegrass seed production in the early 1940s, is favored by moderate temperatures and moist conditions at the time of seed harvest (Calvert & Muskett, 1945; Hardison, 1962). The disease results in the production of many seeds which will not germinate. The practice of open-field burning of stubble, introduced in the 1940s,, provides excellent control of blind seed disease. Field burning also stimulates reproductive tiller development and serves as an economical means of straw removal to provide clean fields for herbicide applications used to control weedy species and volunteer seedlings (Frakes, 1973). Concerns about air pollution are limiting the practice. Current legislation is set to phase out the field burning by 1998. Potential ramifications include increased potential for blind seed disease, seed yield reduction, increased difficulty in the production of certified seed, and increased costs.

The time between seed harvest in the Pacific Northwest and time of fall planting in the southern USA is relatively short, particularly for late-maturing ryegrass cultivars. Inclement weather or transportation problems can make it difficult to get seed to the producer in the southern USA in time for early fall seeding. The long distance between the area of seed production and the area of utilization also greatly increases transportation costs for ryegrass seed.

Stem rust epidemics also can drastically reduce seed yields (Meyer, 1982; Welty & Barker, 1992). Fungicide application reduces disease severity and improves seed yield. Few cultivars have been developed that are resistant to stem rust.

BREEDING HISTORY

Europe and New Zealand

Until 1930, most ryegrass used in Europe originated from seed harvested from good natural stands, where little or no direct selection had been made. Another way of seed supply was collecting seed from the floor of the hayloft after clearing the hay. Beddows (1953) reported the earliest record of perennial ryegrass used in pure, or relatively pure state, as far back as 1677.

The dominance of certain types of perennial ryegrass in these natural stands made the farmers aware of the differences between locations. By actually choosing the site with the most favorable characteristics for seed harvesting, the first selections were made. One of these early selections that became well-known was that made by William Pacey around 1790. Pacey was the first farmer to produce seed of a persistent leafy strain of perennial ryegrass (Beddows, 1953), and he can therefore be designated as one of the first grass selectionists. Seed lots harvested from natural stands were named after their places of origin (e.g., Devon Eaver, Kent Indigenous, Irish Commercial, Oldenburger, Lundbaek) and were traded all over Europe.

Italian ryegrass originated from irrigated farmlands in northern Italy. It was probably introduced into maritime Europe in the nineteenth century. Most commercial seed was imported from Italy where it was harvested from natural stands.

The first directed breeding efforts on ryegrass were undertaken in Germany at the beginning of the twentieth century by private breeding companies (Anonymous, 1987). These companies already were involved in the commercial seed production of natural populations.

A strong impetus to ryegrass breeding was the foundation of the Welsh Plant Breeding Station in Wales (United Kingdom) in 1919. The aim of the station was to breed crops that were adapted to relatively high rainfall areas. Its first director, Sir George Stapledon, had a special interest in grassland husbandry, resulting in the development of improved grass varieties. Worldwide and indigenous collections were made resulting in perennial ryegrasses such as S23 (late flowering), 'S24' early flowering and 'S101' (late flowering) during the 1930s. Until the 1970s, these cultivars played an important role in British agriculture.

Commercial seed firms in the Netherlands started to have interest in grass breeding around 1930, as is evident from the descriptive cultivar lists from that period. In Belgium, the Governmental Station for Plant Breeding was established near Gent in 1932, embarking on a grass breeding program, which is still in operation. In Denmark, ryegrass breeding was started around 1900 at a testing farm in Tystofte after a Mr. Nielsen, a teacher, had started competitive yield trials between species in Orslev, Sealand, in 1870 (Bogh, 1989).

In France, the breeding of ryegrasses was initiated in 1949 by the Institut National de la Recherche Agronomique (INRA) in Versailles near Paris. One of the first perennial ryegrasses developed was the cultivar 'Primevere'.

After World War II, grass breeding was intensified in all European countries. The introduction of Plant Breeder's Rights in the 1960s, rewarding the breeders for their efforts, further stimulated ryegrass breeding activities by commercial seed companies in Denmark, France, Germany, and the Netherlands.

During the 1950s, the development and breeding of tetraploid ryegrasses started, in the Netherlands especially, although the application of doubling the chromosome number in ryegrasses was reported earlier at the U.S. Regional Pasture Research Laboratory (Myers, 1939). The first tetraploid cultivars of perennial ryegrass did not reach the same levels of persistence, sward density and herbage yield as diploid cultivars, especially under intensive management systems; however, a new generation of Belgian and Dutch tetraploid cultivars came on the market in the 1980s that equaled the performance levels of the best diploid cultivars. In Italian ryegrasses, where persistence and sward density do not play such an important role as in perennial ryegrass, tetraploid cultivars gained popularity straight from their introduction, because of their high DM yield.

Van Wijk and Reheul (1991) concluded from results of government testing institutes of Belgium, the Netherlands, and the United Kingdom, that an average 0.5% increase per year in perennial ryegrass DM yield has been achieved over a 25-yr period. The increases in yield were associated with improved stand persistency. Winterhardiness, disease resistance, and digestibility showed varying responses to breeding. Seed yield has not been improved and apparently has not been a primary objective in breeding. From British and Dutch trials, it was concluded that increases in DM yield in Italian ryegrass were of the same magnitude as those of perennial ryegrass, while the Belgian results did not show a clear improvement. Advances in tetraploid ryegrass have been more significant, compared to those in diploids, especially in view of the relatively short period that there have been breeding programs for tetraploids.

Research at the Welsh Plant Breeding Station has shown that there is considerable variation in perennial ryegrass for physiological characters associated with resistance to water stress, cold tolerance, disease resistance, and nutritive quality (Breese & Tyler, 1986). Additionally, these authors pointed out that while selections can be made for these physiological characters, selection for any one character elicits correlated responses in others, indicating pleiotropic effects of the same genes or complex linkage relationships gene sets. Selection and breeding of ryegrass cultivars in New Zealand over the past 50 yr was recently reviewed by Hunt and Easton (1989).

United States of America

Ryegrass seems to have been introduced to the USA during colonial times, but the exact date is uncertain (Schoth & Weihing, 1962). The use of common ryegrasses derived from European landraces was in practice in the USA prior to the release of the first improved cultivar, Gulf, by the Texas Agricultural Experiment Station in 1958 (Weihing, 1963). Early spring is the most critical period for forage in the southern USA, and the distribution pattern of yield generally favors diploid Italian ryegrass. Consequently, breeding efforts in the USA have concentrated on diploids.

Perennial ryegrass breeding efforts in North America also began in the 1950s. 'Norlea' was released by the Canada Department of Agriculture in 1958 and 'Linn' was released by the Oregon Agricultural Experiment Station in 1961 (Hanson, 1972). Most of the perennial ryegrass breeding since this time has focused on the development of turf-type cultivars. 'Manhattan' was released in 1967 as an improved turf-type (Funk et al., 1969). 'Pennfine' was released in 1969 as a turf-type with improved disease resistance (Duich et al., 1972). Numerous turf-type cultivars have been developed since, as evidenced by the number of Crop Science registrations of perennial ryegrass cultivars. A list of ryegrass cultivars released by public agencies is presented in Table 19–7.

Ryegrass cultivars are synthetics or populations. The primary method of ryegrass breeding has been phenotypic recurrent selection; however, progeny testing has been utilized in some cases. Crosses are generally made using a mutual bagging technique. The amount of self-fertilization is so small under these conditions as to make emasculation unnecessary (Emara, 1970). Hayward (1985) reported that it may be advantageous to transfer self-fertility from *L. temulentum* to *L. perenne* or to *L. multiflorum* to overcome the genetic losses that occur during seed production, using current breeding methods.

Ecotype selections also have played a major role in recent cultivar development with such cultivars as Marshall (Arnold et al., 1981) and Florida 80 (Prine et al., 1986). Both of these cultivars were developed from germplasm that was collected from old naturally reseeding pastures of ryegrass in the southern USA. Marshall traces to an old stand of common ryegrass planted in 1949 while Florida 80 traces to germplasm from several cultivars.

Selection and Genetic Variation

Crown Rust Resistance

Resistance to crown rust has been a major objective for ryegrass breeders. Crown rust can significantly reduce forage yield and quality (Hides & Wilkins,

Table 19-7. Cultivars of forage-type ryegrasses released by public agencies in North America.

Cultivar	Year of release	Releasing agency	Maturity	Distinguishing characteristics	Reference
Italian ryegrass					
Gulf	1958	Texas AES†	Medium	Crown rust resistant	Weihling, 1963
Astor	1964	Oregon AES		Superior forage yield in coastal areas of Oregon and Washington	Hanson, 1972
Florida rust resistant	1965	Florida AES	Early	Crown rust resistant Good seed production	Chapman & Webb, 1965
Magnolia	1966	Mississippi AFES‡	Medium	Crown rust resistant 30% nonfluorescent seed	Bennett & Johnson, 1968
Marshall	1980	Mississippi AFES	Late	Good cold tolerance High forage and seed yield Good reseeding ability	Arnold et al., 1981
Florida 80	1982	Florida AES	Early	Crown rust resistant Good reseeding ability	Prine et al., 1986
Jackson	1989	Mississippi AFES	Medium	Crown rust resistant Good cold tolerance High forage and seed yield	Watson et al., 1990
Surrey	1989	Florida AES	Medium	Crown rust resistant Good cold tolerance High forage and seed yield	Prine et al., 1989
TAM-90	1990	Texas AES	Medium	Crown rust resistant Good cold tolerance High forage and seed yield	Nelson et al., 1992
Wimmera ryegrass					
Wimmera 62	1962	SCS & California AES	Early	Good drought tolerance Lower soil fertility requirement	Miller, 1963
Perrenial ryegrass					
Norlea	1958	Canada Dep. Agriculture	Late	Good cold tolerance High forage yield	Hanson, 1972
Linn	1962	Oregon AES	Late	High seed yield	Hanson, 1972

† AES = Agriculture Experiment Station.
‡ AFES = Agriculture & Forest Experiment Station.

1987; Lancashire & Latch, 1966; Latch & Potter, 1977; O'Rourke, 1975; Potter, 1987). Crown rust also makes for an undesirable appearance in turfgrasses. Hayward (1977) and McLean (1985) reported high heritabilities for crown rust resistance and recommended phenotypic recurrent selection for crown rust resistance. Wilkins (1975) reported that resistance in Italian ryegrass was quantitatively inherited with both major and minor genes for resistance; however, Hides and Wilkins (1978) reported that much of the resistance to crown rust was under the control of one or two major genes. Mansat and Betin (1979) stated that resistance was due to numerous additive factors. Selection response was similar in diploids and tetraploids. McVeigh (1975) reported that resistance in turf-type perennial ryegrass was either controlled by one dominant gene or was quantitatively inherited depending on the germplasm source.

Many of the early improved cultivars of Italian ryegrass were developed to incorporate crown rust resistance (Braverman, 1967). The cultivar, La Estanzuela 284, which was introduced from Uruguay as a source of crown rust resistance, was an extremely important germplasm source in the development of early USA cultivars of Italian ryegrass such as Gulf, Magnolia and Florida Rust Resistant (Bennett & Johnson, 1968; Chapman & Webb, 1965; Hanson, 1972). These cultivars were all resistant to crown rust and early to intermediate in maturity, similar to La Estanzuela 284. Magnolia seems to contain some perennial ryegrass genes as evidenced by the high percentage (25–50%) of nonfluorescent seedlings produced.

Stem Rust Resistance

Stem rust is a major problem in many of the ryegrass seed-producing areas of the world and can reduce seed yields by as much as 93% (Meyer, 1982). Stem rust is normally controlled by fungicide application; however, genetic variation for resistance is available in perennial ryegrass (Meyer, 1982; Welty & Barker, 1992) and Italian ryegrass (Nelson et al.,1992). Resistance is quantitatively inherited with minor and possibly major genes contributing (Rose-Fricker et al.,1986). Heritabilities of stem rust resistance were higher prior to anthesis. Rose-Fricker et al. (1986) observed that seedling reactions to rust differed from the responses of mature plants, and they recommended that selection at the mature plant stage would be more successful. Welty and Barker (1992) recommended a two-stage screening procedure in which genotypes are first evaluated as 14-wk old plants in a controlled environment followed by evaluation as mature plants in the field.

Leaf Spot Resistance

Leaf spot caused by *Drechslera* spp. can reduce the yield and quality of ryegrass forage. Lam (1985) observed that *D. siccans* reduced the DM digestibility and water-soluble carbohydrate content of Italian ryegrass. The total amino acid content also was reduced with the reduction of arginine, lysine, and phenylalanine being greater than that of the other amino acids. The severity of disease caused by *Drechslera* is increased by N fertilization (Lam & Lewis, 1982). Matthews (1971) reported that *Drechslera* spp. were widespread in certified ryegrass seed lots in New Zealand. Wilkins (1973) observed variation for resistance to *D. siccans* within and between species of ryegrass in the field, but not in the greenhouse. Tetraploids were more resistant than diploids, but it is not certain that ploidy level was the reason for the resistance. He also found genetic variation between and within cultivars of perennial ryegrass for resistance to *D. catenaria* in the greenhouse.

Spraying with fungicide to control *Dreschlera* increased seed yield of S24 perennial ryegrass by 15 to 43% due to an increase in the number of seeds per spikelet (Hampton & Hebblethwaite, 1984). The increased seed yield was attributed to increased leaf area duration, brought about by the delayed senescence rather than direct pathogenic effects.

Blast Resistance

Blast is a foliar disease caused by *Pyricularia grisea* (Cke.) Sacc. on ryegrass seedlings that can totally destroy a stand in 1 to 2 wk. High levels of resistance to blast have been reported in plant introductions of ryegrasses (Trevathan, 1982). Most of the resistant introductions were of European origin. Bain (1972) observed a small degree of tolerance in Italian ryegrass breeding lines. Moss and Trevathan (1987) found differences in levels of resistance among cultivars of Italian ryegrass; however, to date, no resistant cultivars have been released. The disease can be successfully controlled by avoiding early planting in the fall when conditions are highly conducive for the development of blast in the southern USA (Bain, 1972; Carver et al., 1972).

Virus Resistance

Wilkins and Hides (1976) found that ryegrass mosaic virus (RMV) reduced the yield of susceptible genotypes 27% and that of more tolerant genotypes 13 to 15%. However, there was no difference in percentage mortality between the susceptible and more tolerant genotypes. Italian and perennial ryegrass both show genetic variation for resistance to RMV (Doherty & Doodson, 1980; Gibson & Heard, 1976; Wilkins & Catherall, 1974). Wilkins (1987) was able to successfully transfer polygenic resistance to RMV from perennial ryegrass to Italian ryegrass by hybridization and repeated cycles of backcrossing. Dale (1977) demonstrated that RMV could be eliminated from Italian ryegrass by meristem tip culture. Ryegrass mosaic virus infection reduced the amount of crown rust in 'Lemtal' Italian and S24 perennial ryegrass by up to 75% compared to virus-free plants (Latch & Potter, 1977).

Catherall and Parry (1987) found that leaf symptoms (chlorotic streaks) of barley yellow dwarf virus (BYDV) were not a good indicator of the degree of yield loss in different cultivars. Some cultivars showed yield loss from BYDV while others showed an increase. All cultivars showed a yield reduction in the roots. They concluded that a better technique for screening for resistance is needed before much progress in breeding for resistance will be possible. Italian and perennial ryegrass show genotypic variation for reaction to BYDV (Wilkins & Catherall,1977). Tolerance as measured by yield was inherited in a totally additive manner, whereas, tolerance as measured by symptom expression exhibited both additive and nonadditive control.

Maturity

Anthesis date is one of the major factors controlling the distribution of forage yield and quality in ryegrass. Peak growth rates are attained just prior to anthesis (Wareing & Phillips, 1981). Forage quality declines sharply following head emergence (Ballard et al.,1990; Griffith, 1992). The decline in quality occurs at similar rates for medium- and late-heading cultivars, as temperature steadily rises. Breese (1961) observed that inheritance of anthesis date was quantitative in nature and controlled by many genes, but the type of gene action varied for annuals and perennials. Annuals exhibited a high degree of dominance and epistasis, while perennials were primarily additive. Hayward (1967) also reported that anthesis time was largely additive with some indication of maternal control. Hayward and Breese (1968) reported that date of ear emergence showed significant additive, dominant, and specific reciprocal differences in perennial ryegrass.

Cooper (1954, 1959a, b, c) practiced several cycles of divergent selection for date of ear emergence in two perennial ryegrass populations. Response was rapid and asymmetric in both populations with the response toward lateness being greater than the response toward earliness. Heritabilities for date of ear emergence were high. McLean and Watson (1992) practiced two cycles of divergent selection for anthesis date within four cultivars of Italian ryegrass that represented extremes in maturity. Response was asymmetric with the early maturing diploid cultivar showing a greater response to selection for earliness than for lateness. Realized heritabilities for date of anthesis were generally high.

Dry Matter Yield and Yield Components

There has been limited emphasis placed on direct selection for forage DM yield in the USA where breeders have relied on indirect yield increases resulting from improved disease resistance and cold tolerance, and altered maturity dates. Bugge (1984) reported a heritability for DM yield in Italian ryegrass of 0.48. Rashal and Kholms (1983) found heritabilities for total seasonal DM yield in Italian ryegrass ranging from 0.37 to 0.77. Heritability of DM yield was generally high for the first two cuttings, but was very erratic in the third cutting. Establishment cut, autumn, and total forage yields in perennial ryegrass were inherited in an additive manner with significant reciprocal effects (Hayward & Breese,1968). England (1975) found heritabilities for yield of 0.24 for spaced plants, 0.35 for swards, and 0.59 for rows. Yields of rows and spaced plants showed a high genetic correlation with yield of swards; however, rows were more efficient than spaced plants in selecting for yield (England, 1976). Rhodes (1971) found that heritability of yield in swards was higher under frequent cutting (0.86) than under infrequent cutting (0.64). Fujimoto and Suzuki (1975) practiced three generations of selection for increased yield in Italian ryegrass. Realized heritability was higher in 'Waseyutaka' than Magnolia. They observed significant heterosis and inbreeding depression for DM production. Dry matter yield showed high genetic correlations with plant height, tiller number, and fresh weight. Hayward (1983) found a slow positive response to selection for yield in perennial ryegrass. There was a significant genotype × environment interaction and narrow-sense heritability for yield was low. Watson et al. (1983) found that cultivars of Italian ryegrass vary in their yield stability. Diploid cultivars showed a much wider range in yield stability than tetraploids.

Emara and Edwards (1971) observed genetic variation for juvenile leaf dimensions and growth-rate traits. There seemed to be nonallelic interactions for many of these traits. Tillering and weight-related traits exhibited heterosis, but not leaf dimensions. Seedling leaf dimensions showed additive genetic variation and reciprocal differences (Edwards & Emara, 1970). Tiller number, dry weight per plant, and dry weight per tiller showed high heritabilities at the seedling stage, while heritabilities for leaf dimensions and appearance rate were more variable (Cooper & Edwards, 1961). Rhodes (1973) reported narrow-sense heritabilities in excess of 0.75 for tiller angle, tiller number, leaf length, and leaf rigidity. Tiller angle and leaf length were highly correlated with DM yield. Edwards and Cooper (1963) practiced three generations of divergent selection for leaf size and leaf appearance rate in Italian and perennial ryegrass cultivars. There was considerable additive genetic variation, and selection resulted in significant changes in both leaf size and leaf appearance rate. Due to a strong negative association of leaf size and leaf appearance rate there was no increase in yield due to selection. Cooper and Edwards (1961) also observed a negative genetic correlation between weight per tiller and number of tillers, which would make it more difficult to improve yield by selecting for yield components. Selection for leaf length resulted in a much greater increase in yield than did selection for tiller angle or leaf rigidity (Rhodes & Mee, 1980). Selection for leaf angle had little or no effect on yield.

Seed Yield

Elgersma et al. (1989) found high broad-sense heritabilities for number of spikelets/spike, number of florets/spikelet and 1000-seed weight, whereas heritabilities for seed yield and number of inflorescences in Italian ryegrass were generally low to intermediate. Genetic correlations of seed yield components with seed yield were low. Inflorescence number, inflorescence length, number of spikelets/spike, and spikelet length all show considerable additive genetic variation and high heritabilities (Cooper, 1960a; Edwards & Emara, 1970). Heritability for number of florets/spikelet is low (Cooper, 1960a). Cooper (1960a) found a high negative genetic correlation between the number of florets/spikelet and number spikelets/spike in perennial ryegrass, whereas McLean and Watson (1992) found no correlation in Italian ryegrass. Selection for lateness generally increases the number of spikelets/spike while selection for earliness decreases the number of spikelets/spike (Cooper, 1960a; McLean & Watson, 1992). Cooper (1960a) also observed that selection for earliness increased, and selection for lateness decreased the number of florets/spikelet in perennial ryegrass; however, McLean and Watson (1992) found no relationship between number of florets/spikelet and maturity date in Italian ryegrass.

Forage Quality

Genetic variation exists for many forage quality characteristics in ryegrass including: digestibility, nonstructural carbohydrate content, N content, lysine

Table 19-8. Performance of sheep fed fresh, high and low magnesium selections of Italian ryegrass (adapted from Moseley & Griffiths, 1984).

Variable measured	Cultivar	
	High Mg	Control
Mg in herbage (g kg^{-1})	2.8	1.9
DM intake (g day^{-1})	966	770
DM digestibility (g kg^{-1})	711	716
Mg intake (g d^{-1})	2.23	1.20
Apparent availability of Mg (g kg^{-1})	401	334
Rumen soluble Mg (g kg^{-1})	490	370

content, methionine content, crude fiber content, Mg content, and relative feed value (Breese & Tyler, 1986; Bugge, 1978; Casler, 1990; Tamura & Hoshino, 1979b; Tamura et al., 1981; Tyler & Hayward, 1982; Vose & Breese, 1964). Bugge (1984) reported heritabilities of 0.56 for fiber content and 0.86 for in vitro digestibility in Italian ryegrass. In Norway, tetraploid cultivars of Italian ryegrass were superior to diploid cultivars in digestibility of DM and in protein content (Skaland & Volden, 1973). Researchers in Wales (Moseley & Griffiths, 1984) reported that when sheep were fed Italian ryegrass selected for high Mg concentration, DM intake and intake and apparent availability of Mg were greater than for the control cultivar (Table 19–8). Since ryegrass herbage quality usually is higher than that of other cool-season grasses, emphasis in ryegrass breeding programs needs to be given to improving yield potential, seasonal distribution of yield, time of head emergence, disease resistance and stand persistence. See Chapter 14 (Casler et al., 1996) for a brief review of selection progress.

Aluminum Tolerance

Among forage species, ryegrasses are considered relatively tolerant of Al-toxicity (Edmeades et al., 1992; Pieres et al.,1992). Wheeler et al. (1992) reported that they screened perennial ryegrass seedlings for tolerance to Al and selected 13 lines for superior vigor and color in the presence of Al. Plants selected for Al tolerance in solution culture had significantly higher yields before drought and after recovery from drought, than three recommended cultivars and four experimental lines that had been selected for high yields in the presence and absence of N, and for drought and grass grub resistance.

In the southern states of the USA, Italian ryegrass is often grown on acidic soils that may have high concentrations of soluble Al. Rengel and Robinson (1989) observed that increasing the Al concentration, increased the K/(Ca + Mg) ratio of ryegrass shoots, thus increasing the potential for grass tetany. They observed genetic variation for Al tolerance as measured by root and shoot DM production, with Marshall and Gulf being more tolerant than 'Wilo' and 'Urbana'. Nelson et al. (1989) also reported cultivar differences for Al tolerance as measured by hematoxylin staining of roots; however, they reported that Gulf was susceptible to Al toxicity.

Potential for Future Improvement

Hybrid production remains a possibility in ryegrasses. Wit (1974) developed cytoplasmic male sterile (CMS) lines of Italian and perennial ryegrass from progenies of intergeneric hybrids of *Lolium* spp. and meadow fescue. A CMS system could be utilized to produce F_1 hybrid seed since a restorer line would not be necessary for a forage crop. Thorogood and Hayward (1992a,b) were able to transfer the gene for self-compatibility from darnel to Italian and perennial ryegrass. This single gene, S_c, which acts in a gametophytic manner would facilitate the development of inbred lines for use in hybrid combinations. The uniformity of an F_1 hybrid would be advantageous from a turf standpoint; however, the value of hybrids for forage-type cultivars is less clearcut.

Molecular biology offers many promising areas for the future development of ryegrasses. Intergeneric hybridization with *Festuca* and interspecific hybridization within the genus *Lolium* offers the potential for the improvement of both genera (Buckner et al., 1985; Eizenga et al., 1991). Takamizo et al. (1991) produced a flowering intergeneric somatic hybrid between tall fescue and annual ryegrass. The hybrids displayed inflorescence and leaf morphological characteristics which were intermediate to the parents. Murray et al. (1992) proposed the use of a strain of *A. lolii* as a vector for the transfer of foreign genes into ryegrass. Genome mapping and the elucidation of phylogenetic relationships in *Lolium* can be greatly facilitated by the use of RFLP analysis (Xu et al., 1991, 1992).

It is likely that U.S. breeding programs will continue to emphasize diploids while European, and Japanese programs will exploit tetraploids to a greater extent in the future.

SUMMARY

Ryegrasses are used extensively throughout the world because they provide high yields and quality forage/pasture and excellent turf in a wide range of environments. Few species can tolerate the range in environmental conditions and grazing managements under which the ryegrasses are grown. Grass breeders have shown continued improvement in the performance of new diploid and tetraploid ryegrass cultivars over a 40-yr period. Among the advantages that are noteworthy are in the improved winter-hardiness and disease resistance, and the wide range of time of head emergence of the newer cultivars. The research with the new type of endophytic fungus in New Zealand offers considerable promise if the researchers are successful. Use of turf diploids of perennial ryegrass for pasture may be limited by high endophytic fungus levels and rust susceptibility of some cultivars.

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